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HUMAN COLONIZATION OF ASIA IN THE LATE PLEISTOCENE

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Wenner-Gren Symposium Supplement 17

Danilyn Rutherford

What do you do when new evidence overturns preconceptions within your discipline? From March 18 to 24, 2016, an internationally diverse group of 18 hominin paleontologists, archaeologists, geneticists, and geochronologists, along with the Wenner-Gren Foundation's outgoing president, Leslie Aiello, and symposium coordinator, Laurie Obbink, gathered at Tivoli Palácio de Seteais in Sintra, Portugal, to confront this dilemma (fig. 1).

On almost a daily basis, there are news reports on recent findings that are changing our understanding of how modern humans came to inhabit almost every corner of the world. Beginning in the 1980s, the old story of our origins as a unilineal progression along a long chain of ancestors from the australopiths to *Homo erectus* to Neanderthals to modern *Homo sapiens* began to change. At that time increased knowledge of the African fossil record together with genetic studies of contemporary humans lent support to the theory that modern humans originated in Africa and that the European Neanderthals were our cousins rather than direct ancestors. Various chronologies and routes were proposed for modern human migration out of Africa, but the general consensus favored a single wave with little, or no, interbreeding with populations that might have been encountered along the way.

More recently new dating techniques, advances in genetics, and startling fossil finds are throwing even this tale into disarray. There is evidence for extensive interbreeding of modern humans with Neanderthals and with other extinct hominin lineages. There is also evidence for more than one modern human migration out of Africa. Our story is no longer just our own.

Some of the most exciting recent discoveries have been in Asia, where the scholars who participated in this symposium work. The discussions in Sintra circled around a series of thorny questions. How many waves of modern humans left Africa? Did they arrive in fits and starts, and what routes did they take? What was the nature of their assimilation with hominins who colonized the region in earlier times? Did novel forms of human behavior begin in single regions and then spread, or were there multiple sites where modern human populations developed new means of thriving in diverse environments? The participants drew on the latest research—which in many cases was their own—to weigh possible answers.

Scientists now know more about how temperature, altitude, latitude, and water level might have shaped dispersal patterns as fluctuations in the environment closed off, then reopened, possible pathways of migration. The latest excavation data suggest that modern humans crossed South Asia into southern China well before they arrived in Europe, reaching Southeast Asia before a second wave of migration north (see Bae, Douka, and Petraglia 2017; see also Buzhilova, Derevianko, and Shunkov 2017; Graf and Buvit 2017). In the diverse settings, ecological constraints changed the ways human populations used existing tools at the same time they were developing new skills (see Bae 2017). Rock art in one Sulawesi site dates to 40,000 years ago (see Aubert, Brumm, and Taçon 2017). There is evidence of open sea fishing dating to roughly the same time. Instead of simply spreading, novel behaviors developed in different places to adapt to different ends.

The participants also considered the fossil record, which is full of surprises. For example, are some of the fossils once classified as *H. erectus* in fact Denisovans known from ancient DNA to have been widespread throughout eastern Asia? Data from modern populations, combined with the evidence from ancient DNA, speak of "failed dispersals and large-scale population replacements and admixture, as well as repeated colonization of geographic regions" (Sikora 2017; see also Reyes-Centeno et al. 2017). One interesting question is whether the disappearance of the enigmatic species *Homo floresiensis* (the Hobbit) from the island of Flores related to the arrival of modern humans in island Southeast Asia.

The participants may not have come to a consensus, but they did begin the hard work of determining which models the data support and which they do not. What do you do when new evidence rocks your academic world? Stay alert, stay nimble, stay in conversation, and hang on for the ride.

This symposium follows in a long tradition of Wenner-Gren Symposia on human evolution that began with one of the first symposia held at Burg Wartenstein castle in 1959, "Social Life of Early Man" (Washburn 1961). More recently meetings have been held on the origins of the genus *Homo* (Antón and Aiello

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Figure 1. Participants in the symposium "Human Colonization of Asia in the Late Pleistocene." *Front row, from left*: Adam Powell, Chris Bae, Martin Sikora, Michael Petraglia, Patrick Roberts, Katerina Harvati, Fabrice Demeter. *Middle row*: Sue O'Connor, Kelly Graf, María Martinón-Torres, Knut Bretzke, Yuichi Nakazawa, Leslie Aiello. *Back row*: Robin Dennell, Max Aubert, Alexandra Buzhilova, Tom Higham, Jimbob Blinkhorn, Youping Wang. A color version of this figure is available online.

2012), the Middle Stone Age and the Middle Paleolithic (Kuhn and Hovers 2013), and the evolution of fire (Sandgathe and Berna 2017). Although these and other meetings have touched on some of the issues raised here, such as the evolution of human behavior, human adaptation, and human-environment interactions, this is the first meeting to address the dispersal of humans into eastern Asia. Our knowledge of the evidence for human evolution in this area of the world has increased exponentially in recent years, making the issues addressed here some of the most important and timely in the field of human evolution.

Wenner-Gren symposia provide a unique opportunity for invited scholars to meet for intensive discussion of important issues in anthropology. Symposia are partnerships between the Foundation and the academic organizers, and we are always looking for new and important ideas from all branches of anthropology for future symposia and eventual publication in *Current Anthropology*. We are eager to hear from anyone who has in mind a topic that could spur the kind of field-furthering conversations that made this symposium so productive. Information about the Wenner-Gren Foundation, the symposium program, and what makes for a good symposium topic can be found on our website at http://wennergren.org/programs /international-symposia.

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Human Colonization of Asia in the Late Pleistocene

An Introduction to Supplement 17

by Christopher J. Bae, Katerina Douka, and Michael D. Petraglia

The origin and evolution of modern humans continues to be of great interest to the scientific and public communities alike; the field has long been dominated by findings from Europe and Africa. With new discoveries of hominin fossils and archaeological sites, in addition to the application of recent genomic and paleoclimate modeling studies, findings from Asia are serving to revolutionize the field of modern human origins. The identification of Neanderthals and Denisovans in Siberia, for example, along with growing fossil and archaeological evidence for the presence of early modern humans in East and Southeast Asia, much earlier than originally thought, places the spotlight on the evolutionary history of our species in Asia over the last 125,000 years. Exciting and unanticipated new discoveries call for a need to critically reexamine the Asian record. Taking a multidisciplinary perspective, a group of active researchers participated in a week-long Wenner-Gren symposium titled "Human Colonization of Asia in the Late Pleistocene" (#153) in March 2016. Here we review the major themes and findings emerging from the symposium and discuss avenues to move the field forward.

Background

Significant paleoanthropological findings routinely are reported from Europe and Africa owing to prolonged and large-scale research campaigns on the part of multidisciplinary teams. However, compared to these two relatively well-known regions, the Late Pleistocene record of Asia is poorly known, with fewer long-term and systematic research efforts. This is unfortunate given major paleoanthropological discoveries in Asia since the late nineteenth century by scholars such as Eugene DuBois, as well as the results of subsequent explorations in the first several decades of the twentieth century, led by scientists such as Davidson Black, Pierre Teilhard de Chardin, Wenchung Pei, Ralph von Koenigswald, Franz Weidenreich, and Hallam L. Movius (see Dennell 2001; Norton and Braun 2010). Indeed, Asia has always had major paleoanthropological potential simply due to the fact that the landmass is much larger than either Europe or Africa, and its extensive latitudinal, longitudinal, and

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altitudinal breadth covers a great range of environments, including tropical forests, deserts, steppes, permafrost zones, and even open seas and oceans. Major riverways (e.g., Indus, Irrawaddy, Yangtze) connect different biomes and would have thus facilitated movement of modern humans—as recently was suggested for the European Upper Paleolithic (Hussain and Floss 2015). On the other hand, geographic barriers such as mountains and plateaus (e.g., the Himalayas, Qinling Mountain, Qinghai-Tibetan Plateau), deserts (e.g., Thar Desert, Gobi Desert), and large river systems may have served as impediments, at times, for the geographic spread of hominins, animals, and vegetative communities. During major stadials when sea levels dropped, corridors would have been created, connecting various islands to form larger landmasses in Southeast Asia; Sakhalin and Hokkaido would have been connected to mainland Siberia, and the boundary of eastern China would have extended several hundred kilometers farther east, as far as the Korean peninsula. Thus, the topography, geography, and environments of Asia were dynamic across the Late Pleistocene, acting as a canvas for the expansion, contraction, and extinction of human populations. This dynamism and diversity is reflected in Asia today, as this continent contains some 48 countries, more than 2,200 languages, and some of the highest population densities in the world.

Over the past decade or so, a plethora of new research findings in Asia and reanalyses of previously identified sites and materials have caused us to question popular models put forward to explain the origin of our species and our species' relationship to closely related ancestors (a point made in many articles in this special issue). As a consequence, the traditional

multiregional model, where *Homo erectus* begat mid-Pleistocene *Homo*, who in turn begat modern Chinese and Aboriginal Australians (Wolpoff, Wu, and Thorne 1984; Wu and Poirier 1995), simply does not work. We now know that Neanderthals ranged much farther eastward than was previously realized (Krause et al. 2007) and that at least two other hominin populations were inhabiting eastern Asia contemporaneously, that is, the Denisovans (Reich et al. 2010) and *Homo floresiensis* (Brown et al. 2004; Sutikna et al. 2016). This is in addition to the growing evidence from genetics that demonstrates that modern humans can trace their origins to Africa (Cann, Stoneking, and Wilson 1987; Ingman et al. 2000; Jorde et al. 2000). Thus, any suggestion that the Chinese and Indonesian *H. erectus* populations lived largely in isolation and were directly ancestral to the modern Chinese and Aboriginal Australians has fallen by the wayside; instead, with so many different biological groups present in the region, it would appear the picture is a great deal more complex. Interestingly, an increasing number of studies suggest that *H. erectus* was the ancestral population of *H. floresiensis* and that that particular micropopulation likely lived largely in isolation for extended periods of time (Kaifu et al. 2011; but see Aiello 2010; Baab 2016; Martinón-Torres et al. 2017; and van den Bergh et al. 2016 for further discussion and alternative hypotheses). The same case cannot yet be made for the Denisovans, although Prüfer and colleagues (2014) found evidence of gene flow from an unknown hominin into the Denisovans, hypothesizing that this archaic hominin might be *H. erectus*.

The traditional Out of Africa 2 or Replacement model to explain the origin of modern humans also has not been faring very well in recent years. There is increasing evidence that the hypothesis that proposes modern humans dispersed from Africa after 60 ka and replaced the indigenous hominin populations of Eurasia with no interbreeding (Stringer and Andrews 1988) is no longer accurate. Though early genetic studies supported the single-origin claims (e.g., Krings et al. 1997; but see Templeton 2002), whole genome studies and the retrieval of ancient DNA have now complicated this situation. A review of the plethora of genetic studies published in the past decade (e.g., Fu et al. 2015; Green et al. 2010; Prüfer et al. 2014; Skoglund and Jakobsson 2011; Stoneking and Krause 2011) indicates that interbreeding between modern humans, Neanderthals, and Denisovans occurred on at least a semiregular basis. This is not a new hypothesis, as assimilation/hybridization advocates have long made this argument based on the hominin fossil record (Smith et al. 1989, 2017; Trinkaus 2005). Furthermore, there is increasing evidence from archaeology, hominin paleontology, and geochronology that modern humans were in different areas of Asia before 60 ka, which is the date traditionally adhered to by Replacement hypothesis advocates (Bae et al. 2014; Liu et al. 2010*b*, 2015; Mijares et al. 2010; Norton and Jin 2009; Petraglia et al. 2007). This latter argument is consistent with the fossil finds of early modern humans in the Levant between 120–70 ka at sites like Skhul and Qafzeh (e.g., Grün and Stringer 1991; Grün et al. 2005). Indeed, the traditional Out of Africa model, which contended that modern humans rapidly

dispersed along the Indian Ocean rim using a coastal route at 60 ka (Macaulay et al. 2005; Mellars 2006*b*; Oppenheimer 2009) is difficult to sustain as the sole scenario explaining the peopling of Asia by our species (Groucutt et al. 2015). For example, it is possible there were multiple dispersals out of Africa where some groups initially followed the southern route while other groups of foragers took a northern route, seemingly supported by archaeology and genetic data (e.g., Di and Sanchez-Mazas 2011; Kaifu, Izuho, and Goebel 2015; Karafet et al. 2001; Norton and Jin 2009). Further, we know from aDNA evidence that several early modern human lineages did not contribute much to the genetic makeup of later modern human populations in Eurasia, as shown by the genetic analyses of the Ust'-Ishim femur (Siberia) and the Pestera çu Oase mandible (Romania; Fu et al. 2014, 2015).

Given the uncertainties of all of the present models, and in light of a great deal of new information, revised models for the origin and dispersal of *Homo sapiens* are clearly needed, with an appreciation for a more complicated demographic history and a better understanding of the timing and route(s) of dispersal across Asia. In figure 1, we illustrate the currently known spatial ranges of Neanderthals, *H. sapiens* prior to their exit from Africa, and Asian populations (Denisovans and mid-Pleistocene *Homo* as well as late-surviving(?) *H. erectus*). The Denisovan range covers only the area around the Altai where the fossils have been discovered. Modern human DNA suggests a high percentage of Denisovan ancestry in the native populations of Near Oceania and Melanesia (Reich et al. 2011); however, it is not clear whether this represents the extremities of the Denisovan geographic range or is the effect of human migrations and/or long-term isolation of these populations. The Denisovan range will likely need to be adjusted with further understanding of Denisovan population structure and distribution. Possible pathways of major *H. sapiens* dispersals from ~120–100 ka onward are shown with lines and arrows, while presumed areas of interbreeding are noted with circles and stars. For example, evidence for Neanderthal–modern human admixture events (at least two) are present in DNA obtained from the Ust'-Ishim femur as well as in the Pestera çu Oase mandible, directly dated at ~45 and ~42–37 ka, respectively (Fu et al. 2014, 2015; Trinkaus et al. 2003). This is a simplistic view of processes that took place over tens of millennia and therefore should be perceived only as a rough guideline rather than a precise model. This view will evolve as our understanding of the Quaternary Asian human evolutionary record improves. Indeed, a series of recent genetics papers (e.g., Malaspinas et al. 2016; Mallick et al. 2016; Pagani et al. 2016) suggests that the figure will soon need to be revised.

Topic and Rationale

One point that is becoming increasingly clear from the analysis and reanalysis of fossil finds and excavation of archaeological sites across Asia is that a great deal of important new information is yet to be recovered, understood, and integrated into
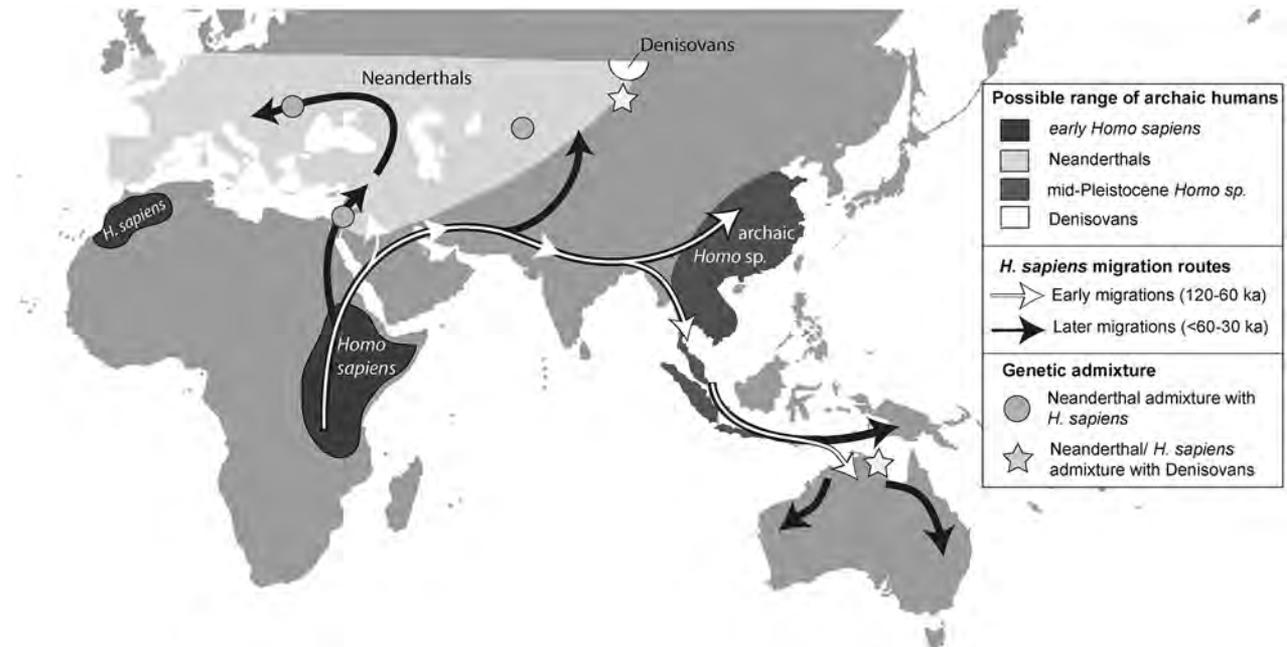
Figure 1. The various dispersal models for modern humans from Africa and into Asia. These models include proposed timings and directions of these dispersals. In addition, possible areas of geographic overlap with indigenous hominin groups (e.g., mid-Pleistocene *Homo*, *Homo neanderthalensis*) are presented with zones of likely genetic admixture between the different populations. A color version of this figure is available online.

evolutionary models. Fossil and archaeological studies, combined with newly obtained paleoenvironmental and genetic data, are contributing to a rethinking of our views about the biological and behavioral evolution of hominins in the Late Pleistocene; these revised discoveries and theories should influence the discipline for the coming decades. For these reasons, we thought that it was the right time to bring together a group of multidisciplinary experts (hominin paleontology, archaeology, geochronology, genetics) who were actively working in Asia on similar issues and questions.

In recognition of the increasing importance of the Asian record for understanding the evolutionary history of modern humans, the Wenner-Gren Foundation invited us to organize a symposium titled "Human Colonization of Asia in the Late Pleistocene." The symposium was subsequently convened and held in March 2016 in Sintra, Portugal. The Wenner-Gren Foundation has, of course, a long and established history of organizing small, invitation-only symposia focused on topics currently being intensively debated in anthropology and related subjects. As pointed out by Leslie Aiello, then president of the foundation, human evolution was a primary focus of the organization since its inception, and many classic edited volumes focused on paleoanthropology have been published (e.g., Lee and DeVore 1968; Washburn 1961). Following on the tracks of recent paleoanthropology-focused Wenner-Gren symposia, particularly "Human Biology and the Origins of *Homo*" (Antón and Aiello 2012), our symposium continued down this path.

The three coeditors of this volume invited scholars to the symposium based on several criteria. First and foremost, participants were chosen because of their active scientific research programs in Asia across various disciplines, including hominin paleontology, archaeology, geochronology, and genetics. Second, we were also aware of the need to invite scholars from countries within Asia itself; thus participants included persons from Australia, China, Japan, and Russia. Third, we took account of gender balance, well aware of conferences that are exclusively, or almost completely, male dominated. And finally, we also thought it important to give a voice to junior and mid-level scholars, rather than hearing only from our older, venerated colleagues. Thus, the symposium held in Sintra was composed of a rather nice mix of senior- and junior-level researchers as well as male and female participants. All major regions of Asia (western and eastern, southern and northern) were covered, including both major biogeographic zones (Palearctic, Oriental). Further, we sought to cover as much longitudinal, latitudinal, and even altitudinal variability as possible. Moreover, we were able to compare mainland and island settings for contrasting views of evolutionary processes. During the week-long meeting, each participant was able to contribute a great deal of new information and be involved in discussions about the need for new models and interpretations of the Asian record. We were also delighted to see the warm and friendly interactions at the symposium, with new friendships and future collaborations formed.

The "Human Colonization of Asia in the Late Pleistocene" symposium was organized with the idea that we would be able to turn our attention to a series of questions relevant to modern human origins research from a multidisciplinary perspective. For instance, we wished to address whether modern humans initially dispersed from Africa and into Asia only once and at ca. 60 ka. Alternatively, we were interested in investigating whether there were multiple dispersals potentially predating the 60 ka event. If so, we sought to evaluate the nature of the paleoanthropological and paleoenvironmental evidence. We were also interested in exploring views about the route(s) of modern human expansions across Asia and how humans expanded to the outer extremes of the world, across Australasia, western Europe, and eventually, the New World. Another significant topic explored concerned what hominin groups were present in different areas of Asia, and what was the nature of their interactions with modern humans moving in for the first time (e.g., extinction, assimilation, nonrecognition/avoidance)? Indeed, we thought it would be interesting to examine what role, if any, did a so-called modern behavioral toolkit play in facilitating the advance of modern humans throughout Asia. Ultimately, the main goal of the symposium was to evaluate the Late Pleistocene human evolutionary record of Asia based on what we thought we knew, thereby synthesizing multidisciplinary studies during discussions, while at the same time allowing us to think about how to move the discipline forward. We review each of these themes briefly here.

In Brief: What Do We Think We Know?

The field of human evolution is currently largely focused on various models that explain the emergence, exodus, and interbreeding of our species out of Africa and into Asia, particularly various iterations of the Out of Africa 2 and Assimilation models. Based on data from several different fields, and at the time of the Sintra symposium in March 2016, most practitioners support the following points for both of these models. Modern humans first appear in East Africa sometime between 195–160 ka (McDougall et al. 2005; White et al. 2003), based on fossil and geochronological evidence and supported by early analyses of global human mtDNA sequence variation (Vigilant et al. 1991) and subsequent studies on genetic diversity and population substructure in Africa (for an overview, see Tishkoff et al. 2009). Since the time of the symposium, fossil discoveries have been published to suggest that early modern *Homo sapiens* was present across Africa by 315 ka (Hublin et al. 2017; Richter et al. 2017), suggesting an even greater complexity and possible population structure within the African continent itself. As conventional thinking goes, at around 120–100 ka, modern humans expanded into the Levant where they survived until ca. 70 ka (Grün and Stringer 1991; but see Millard 2008 for slightly younger end estimates). Most Out of Africa 2 proponents have argued that this earlier appearance of modern humans outside of Africa represents an initial failed dispersal event. It was not until well after the Toba super-eruption (~74 ka)

that a single dispersal wave out of Africa occurred, usually estimated to be around 60–50 ka (Kaifu, Izuho, and Goebel 2015; Stoneking and Krause 2011). Some proponents of the single and late wave hypothesis argue that the dispersal event was rapid and moved along the coast of southern Asia and Southeast Asia, eventually reaching Australasia (Macaulay et al. 2005; Mellars 2006a; Oppenheimer 2009).

Proponents of the Assimilation model suggest that admixture occurred in multiple places during multiple events (Dennell and Petraglia 2012; Smith et al. 1989, 2017; Trinkaus 2005). Although not necessarily one of the core criteria of the Assimilation model, it may be implied that multiple dispersals out of Africa occurred, starting during the early part of the Late Pleistocene. One of the primary fossils to support the argument for an earlier dispersal/hybridization event is the partial mandible from Zhirendong, southern China, that dates to ~113–100 ka (Liu et al. 2010a) or more recently to ~110–106 ka (Cai et al. 2017). Further reports of early modern humans from China (Lunadong, Huanglongdong, and perhaps Fuyandong) also support this scenario. The Assimilation model does not necessarily promote a particular direction for human dispersals and admixture events. Genetic studies published since 2010 have clearly indicated some level of admixture between the various hominin populations that were present in Asia during the Late Pleistocene (Currat and Excoffier 2011; Kuhlwilm et al. 2016).

In addition to human biology, the spread of so-called modern human behaviors during the Late Pleistocene appears to have occurred initially over northern Asia and then southward. An absence of what may be considered one of the core pieces of evidence of modern human behavior, blade and microblade technology in Southeast Asia, including southern China, suggests that these behaviors may have stopped someplace in central China (Norton and Jin 2009). However, given the direct evidence for early rock art in Sulawesi around 40 ka (Aubert et al. 2014) and indirect evidence of boating/rafting technology to arrive at Callao in the Philippines at approximately 67 ka (Mijares et al. 2010) and Australia between 60 and 50 ka at Madjedbebe (Clarkson et al. 2015), several lines of evidence suggest that modern humans were in the region at a relatively early date.

Topics Discussed in Sintra

The symposium was convened with many active Asia specialists in attendance, and thus we hoped to gain new insights about the occupation history of the continent. Each presentation was followed by detailed discussion about the specific paper and related topics generally. A great advantage of the symposium composition was that, for the most part, the participants brought their own primary data to the table for discussion. Although there was little clear-cut, unanimous support for any of the primary questions proposed at the outset of the symposium, as evidenced from the discussions and follow-up papers found in this volume, many authors altered their views on various subjects in light of new data and hearing opinions from other

participants. Below we discuss themes emerging from the papers, outlining information about archaeology, hominin paleontology, geochronology, and genetics.

Laying the Foundation: Contributions from Archaeology

The archaeological record serves as a fundamental backdrop on which all models project. As Bretzke and Conard (2017) justifiably note, the relative paucity of hominin fossils and consequently ancient DNA from across large expanses of the Asian continent make it difficult to generate robust models for hominin dispersal patterns and interactions. Data for such modeling can be collected, however, from large-scale archaeological survey and excavation projects. A number of archaeology-oriented papers in this volume provide the critical necessary footing to contribute to such models currently being debated: Bretzke and Conard (2017) cover Southwest Asia; Buzhilova, Derevianko, and Shunkov (2017) discuss Central Asia; Graf and Buvit (2017) review Siberia; Blinkhorn and Petraglia (2017) cover the Indian subcontinent; Wang (2017) reviews China; and Nakazawa (2017) discusses Japan. In addition, more general reviews of the East Asian record are provided by Bae (2017) and O'Connor and colleagues (2017) for island Southeast Asia. All of the authors examine the nature of regional records, while at the same time discussing their data with respect to broader topics such as the timing and route of modern human dispersals.

Dennell (2017) lays the foundation for understanding paleoenvironmental variation across Asia during the Late Pleistocene. Knowledge of the paleoenvironment is, in fact, one of the underlying themes in many of the archaeology papers because of the importance of hominin behavioral adaptations in the face of environmental variations (e.g., temperature, altitude, latitude, bathymetry). Climate change and sea level fluctuations also have consequences, as barriers may have risen up and subsequently disappeared (see also, especially, O'Connor et al. 2017, and to some extent Bae 2017; Bretzke and Conard 2017. Obviously, paleoenvironmental factors would have impacted behaviors such as subsistence strategies, tool production, and landscape movements.

Although one must be wary of drawing arrows when illustrating the direction and mode of human movement across Asia, such demonstrations do at least allow us to generate a general idea of dispersal patterns. The variations on the Out of Africa 2 and Assimilation models both agree that modern humans dispersed out of Africa and initially arrived in Southwest Asia. Based on the regional archaeology survey papers presented here, it would seem there is support for an initial movement of humans through South Asia, possibly arriving in southern China by marine isotope stage (MIS) 5 and/or 4. This is supported by hominin fossil sites such as Zhirendong, Lunadong, Huanglongdong, and Fuyandong (Bae et al. 2014; Liu et al. *a*, 2010*b*, 2015; but see Michel et al. 2016) and indirectly by archaeological sites from India like Jwalapuram with Middle Stone Age–like stone tool industries (Petraglia et al. 2007).

Based on current data, no sites associated with modern humans have been found in northern Asia and/or Siberia that date to MIS 5 or 4 (Buzhilova, Derevianko and Shunkov 2017; Graf and Buvit 2017). No sites in Europe currently exist that are clearly assigned to modern humans that date to these marine isotope stages either (Higham et al. 2014). This is despite the finding from a recent paleoclimate modeling study (Timmermann and Friedrich 2016) that a climate corridor may have been present between 90 and 80 ka that could have allowed modern humans to move from Southwest Asia into Europe. Accordingly, it might be argued that modern humans initially moved through South Asia and arrived in Southeast Asia before the advent of MIS 3 (Boivin et al. 2013; Petraglia et al. 2010). A second later dispersal then occurred northward, eventually reaching Siberia, that originated either in Southwest Asia or, less likely, as some earlier genetics studies suggested (e.g., Jin and Su 2000), from southern China.

A third underlying theme among the archaeology-centered papers is the role of so-called modern human behaviors in successful and unsuccessful dispersals by modern *Homo sapiens* across Asia. In particular, it is fairly clear that a set of novel behaviors accompanied, and perhaps facilitated, colonizations of regions like the Japanese archipelago and island Southeast Asia (Bae 2017; Nakazawa 2017; O'Connor et al. 2017). Some of these behaviors may have included different functional uses of ground stone tools like axes and the independent development of equipment for fishing. Further, as Bae (2017) notes in this volume, it may be possible that different ecological constraints caused the disappearance of blade/microblade technology when modern humans were moving into Southeast Asia from either South and/or North Asia (see also Bar-Yosef et al. 2012). If so, what does this say about humans' ability to adapt to new environments? Surely if they were able to produce rock art in Sulawesi by 40 ka (Aubert, Brumm, and Taçon 2017; Aubert et al. 2014) and were capable of pelagic deep sea hunting around the same time (O'Connor et al. 2011), humans in the region were clearly remarkably adaptive. The ability for modern humans to adapt well in southern Asia is clearly evident from the detailed studies of Sri Lanka's early rainforest habitation (Roberts et al. 2015) and the occupation of Niah Cave in Borneo (Barker et al. 2007). Although local extinction events may have occurred, the presence of modern humans in Southeast Asia appears fairly continuous for the past 40 ka at least.

What Do the Fossils Say?

Understanding the nature of the variation in the hominin fossil record is critical to developing ancestor-descendant or sister-sister relationship models between different hominin populations. A range of species appear to be present in Late Pleistocene Asia, namely modern *Homo sapiens*, *Homo neanderthalensis*, *Homo floresiensis*, Denisovans, and perhaps late-appearing *Homo erectus* and/or mid-Pleistocene *Homo*. Here, Kaifu (2017) and Martinón-Torres et al. (2017) provide useful reviews of the Asian hominin fossil records, the former covering the earlier

periods until the late Middle Pleistocene, while the latter paper details the Late Pleistocene hominin fossil record from China. Buzhilova, Derevianko, and Shunkov (2017) and Demeter et al. (2017) contribute detailed discussions of the important fossils from Central Asia (Teshik Tash, Uzbekistan), Siberia (Denisova and other caves, Russia), and Tam Pa Ling (Laos), particularly in their broader settings.

Kaifu (2017) discusses the relationships between the different *H. erectus* populations from China and Indonesia and determines that a great deal of variation exists. Interestingly, Kaifu (2017) finds that *H. erectus* populations geographically juxtaposed between Zhoukoudian and Indonesia (e.g., Yunxian, Hexian, Yiyuan, Tangshan) do not simply display gradational variation between the two regions and may in fact represent a previously unidentified third *H. erectus* population. Kaifu (2017) also reviews the "late archaic *Homo*" record from eastern Asia. It should be noted that some authors refer to these fossils as "mid-Pleistocene *Homo*" given the nomenclatural baggage with assigning the word "archaic" to a taxonomic group (for various discussions, see Bae 2010; Tattersall 1986; Tattersall and Schwartz 2008; Xiao et al. 2014).

A question that was raised during the symposium included whether mid-Pleistocene *Homo* from China are the fossilized remains of the Denisovans. This idea was broached when it was fairly evident that the Denisovan and Xujiayao hominin molars are both extraordinarily large. Here, Martinón-Torres et al. (2017) also suggest that Denisovans may already be present skeletally in China in the form of the Xujiayao and/or Maba fossils or perhaps a yet to be identified hominin population (e.g., Penghu 1 from Taiwan). Since the conference, Smith et al. (2017) raised the same question, and a nonmetric analysis of the Denisova and Xujiayao teeth found several similarities (Zubova, Chikisheva, and Shunkov 2017). Further, Kaifu (2017) suggested late *H. erectus* from Indonesia may be the ancestral population of the Denisovans given their apparent presence in modern populations of island Southeast Asia. This would imply that a subpopulation of Denisovans later dispersed north to Siberia or that Denisova simply represents the northern edge of the distribution of this group. Interestingly, Zubova and colleagues (2017) found nonmetric similarities between the Denisovan and Sangiran *H. erectus* fossils from Indonesia as well. However, Buzhilova, Derevianko, and Shunkov (2017) found metric and morphological similarities between the Denisovan, Teshik-Tash, and Oase 2 dentition, suggesting gene flow between Europe and Siberia. The Teshik-Tash hominin fossils are generally assigned to *H. neanderthalensis* (Gremyatskii 1949; Krause et al. 2007), while Oase 2 is considered an early modern human (Trinkaus et al. 2003). We are intrigued by the possibility that Denisovans may already be present in the skeletal record in the form of *H. erectus*, Chinese mid-Pleistocene *Homo*, Teshik-Tash Neanderthals, early modern humans, or a yet to be determined ghost lineage. We hope future research is directed to test this hypothesis.

Another interesting point raised by Martinón-Torres et al. (2017) is the possibility that some of the morphological anom-alies from *H. floresiensis* (e.g., rotated P4s, unique p3) may actually be the result of introgression between different hominin populations. The appearance of such anomalous traits could also be the result of inbreeding, but examples from Rebecca Ackermann's research on hybrids in nonhuman primates (e.g., Ackermann 2010; Ackermann, Rogers, and Cheverud 2006) does suggest this could be an alternative hypothesis that needs to be tested. If it turns out that Martinón-Torres et al. (2017) are correct, then *H. floresiensis* may not have lived in total isolation for more than a half-million years, as many studies suggest.

In addition to previous studies that argue for a pre–60 ka presence of modern *H. sapiens* in eastern Asia (e.g., Bae et al. 2014; Liu et al. 2010*a*, 2010*b*; Mijares et al. 2010; Norton and Jin 2009; Shen et al. 2002), Liu et al. (2015), Martinón-Torres et al. (2017), and Demeter et al. (2012, 2017) strongly promote Fuyan Cave (China) and Tam Pa Ling (Laos) as additional evidence for an early appearance of modern humans in the region. With the increasing hominin fossil record from the region, perhaps this should not come as that much of a surprise, as almost 1 decade ago Norton and Jin (2009:258) noted that "growing evidence suggests that modern humans may have been present in East Asia before ~50 kya." Although questions still need to be resolved about the dating schematic for Fuyan Cave (see Michel et al. 2016), the Tam Pa Ling evidence seems to be fairly robust as an early example of modern humans in the region by at least ~70 ka. If any, or all, of these sites (Luna, Huanglong, Fuyan, Tam Pa Ling, Callao Cave) can stand up to further scientific scrutiny, then any continued argument that dispersal by modern humans out of Africa did not occur until after 60 ka can be shelved. Needless to say, it is clear that geochronology plays a critical role in determining the importance (or nonimportance) of many of these proposed early sites.

The Importance of Geochronology

Besides the discovery of hominin fossils and archaeological sites, one of the most important questions that needs to be answered is how old the site and the materials are. In the past decade, extensive work in other parts of the world, namely Europe and Africa, have revealed significant discrepancies between previous chronologies and renewed dating attempts. For example, at over 100 Paleolithic sites (re)examined by the Oxford radiocarbon lab since 2006, as much as 70% of the previous dates were erroneous (Higham 2011). This has led to renewed discussion on the date and nature of Neanderthal extinction and the timing, tempo, and pathways of modern human expansion as well as the possible overlap of the two human species within Europe and the Near East (see, e.g., Mellars 2005, 2006*a*; Zilhão 2006; Zilhão and d'Errico 1999). The new radiocarbon chronologies, augmented with better statistical (Bayesian) methods, have already clarified aspects of many of these debates in Europe (e.g., see Higham et al. 2014 for the timing of the extinction of Neanderthals in Europe). Similarly in Africa, new dating programs mainly using luminescence dating and in particular, single-grain OSL (optically stimulated lumines-

cence), have elucidated long-debated issues such as the age and final manifestations of the Aterian and other Middle Stone Age facies both in the north, east, and south of the continent (e.g., Douka et al. 2014; Gliganic et al. 2012; Jacobs et al. 2008a, 2008b, 2012). In Asia a reliable chronological framework for the vast majority of its subregions is still lacking, although systematic application of such methodologies on a number of Asian sites is currently underway.

The two geochronology contributions to the symposium focus on major innovations and improvements to ¹⁴C and uranium-series dating methodologies and how these methodological advances can contribute to a better understanding of the Late Pleistocene Asian paleoanthropological record (Aubert, Brumm, and Taçon 2017; Douka and Higham 2017). Aubert and colleagues (2017) describe the U-series dating of a new series of sites from Sulawesi in Southeast Asia, while Douka and Higham (2017) discuss the results of redating of important sites from Georgia and Russia (Bondi Cave and Kostenki 14). Douka and Higham (2017) note that improved methods and the capability to incorporate various chronometric and paleoclimatic data into single-site regional and multiregional Bayesian models offer unique glimpses into human evolutionary pathways. Importantly, both papers (Aubert, Brumm, and Taçon 2017; Douka and Higham 2017) emphasize strongly the importance of using a combination of dating techniques and multiple dates from the same layers to narrow the age bracket of various sites. A good example that appears in this volume is Demeter et al. (2017), which presents a new human fossil from the lowest stratigraphic layer at Tam Pa Ling, almost 6 m below the surface, that was dated by a combination of methods to possibly as old as ~70 ka.

And the Genetics Say?

One area of research that is playing an increasingly important role in the Out of Africa debate is paleogenetics. Many genetic studies focus on analyzing ancient DNA from human fossils, while a good number of studies evaluate modern genetic data (e.g., mtDNA, Y-chromosome) to work backward in time. In both types of studies, data are used to reconstruct the timing of population extinctions and divergences and the degree of introgression between different populations. For instance, many genetic research teams are currently trying to determine the extent of the Denisovan distribution throughout Asia, particularly Southeast Asia, as reconstructed from various population genetic models. The Sikora (2017) contribution here is a review of the major genetic studies that focus on the Asian Late Pleistocene record. Interestingly, Sikora (2017) draws the conclusion "that failed dispersals and large-scale population replacements and admixture, as well as repeated colonization of geographic regions, were likely the norm rather than the exception throughout much of human history." Although not focused on genetic modeling, Reyes-Centeno et al. (2017) use dental nonmetric data to test various modern human dispersal models (single vs. multiple), many of which have

their foundation within genetic research. Sikora (2017) and Reyes-Centeno et al. (2017) both emphasize taking a careful approach to these genetic studies and that different methodologies may not properly map population histories correctly. For instance, relying solely on modern genetic data does not allow confident estimates of when two populations initially diverged, especially given the uncertainties surrounding variation in mutation rates (Scally and Durbin 2012; Sikora 2017).

Where Do We Go from Here?

At the conclusion of the symposium, we were unable to draw any unanimous conclusions to many of the questions that were posed. In some respects, we see this as a success and as an opportunity. The intent of the symposium was to bring in scientists from different disciplinary backgrounds to evaluate key questions and determine if there was a consensus after scientific scrutiny, particularly when viewed from multidisciplinary perspectives. Although none of the topics were entirely agreed upon, some did fare better than others. For example, one important conclusion drawn from the symposium and this resulting volume is that the dispersal out of Africa and into Asia should not be seen as a single unidirectional event but, rather, as a series of multiple dispersals in a multitude of geographic directions; such movements, and their tempo and relative success, were at least in part influenced by environmental factors (deserts, mountain ranges, reliable water sources, fluctuating bathymetry, etc.). However, since the symposium, a set of genetics papers was published in *Nature* (Malaspinas et al. 2016; Mallick et al. 2016; Pagani et al. 2016). They conclude that the primary human expansion out of Africa and across Asia occurred around 60 ka. Even among these recent papers, though, the Pagani et al. (2016) study differs in that Pagani and colleagues suggest that traces of earlier human dispersals in the modern gene pool, possibly as early as 100 ka, are present in modern-day Papuan populations. What is not yet clear from these studies is whether the origin of *Homo sapiens* is much older in Africa (Hublin et al. 2017) than estimated by most genetic clocks and whether we can thus suggest an earlier movement of modern humans out of Africa.

There are new testable hypotheses that were raised in Sintra and in the set of articles included in this special issue that will likely influence the future direction of human evolutionary studies in Late Pleistocene Asia. For instance, the question arises as to whether the Denisovans are already known and present in eastern Asia in the form of Chinese mid-Pleistocene *Homo*. The data appear to be already available to test this hypothesis, but this would need to be evaluated further. We can also ask the question as to whether available data support or refute single or multiple dispersal models and whether there was a pre- or post-Toba eruption appearance in the region. The detailed archaeology reviews of each of these different regions should allow us to be better able to connect the dots, so to speak, regarding the frequency, direction, and timing of dispersal patterns of modern humans and other populations.

More rigorous geochronological evaluations are only helping us to develop more robust models. Genetic studies will continue to force paleoanthropologists to rethink their data and models when certain "ghost" lineages appear.

All participants in the symposium agreed that more data are critical to addressing evolutionary and biogeographic questions, particularly from regions that have been subjected to less intensive multidisciplinary paleoanthropological research (e.g., Central and Southeast Asia). In line with this, we need to delve more deeply into the better-known records from places like China and the Indian subcontinent because, even there, there are vast pockets of largely unexplored areas from a fieldwork perspective. The diversity of interesting and important findings coming out of Asia on an annual, monthly, or even weekly basis argues strongly for the importance of the continued development of large-scale interdisciplinary research approaches to just about all regions of Asia.

The origin of modern humans will continue to be of enormous interest to both the public and the scientific community. As attested to by the various papers in this volume, there are a great deal of significant data coming out of Asia that are not only of public interest but are helping to turn the field on its head. Moving forward, we hope that this special issue serves to lay the foundation for an increase in multidisciplinary research in Asia focused on this topic. We are confident that this will lead not only to many additional important findings but also to the improvement and development of more robust models to explain the nature and timing of modern human dispersals across Asia and beyond. We hope that this special issue of *Current Anthropology* serves to encourage future generations of students interested in the origin and evolution of our species to pick up this baton.

Acknowledgments

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Human Colonization of Asia in the Late Pleistocene

The History of an Invasive Species

by Robin Dennell

Narratives of "Out of Africa 2"—the expansion of *Homo sapiens* across Asia—emphasize the pattern of human dispersal but not the underlying processes. In recent years, the main debates have been over the timing and frequency of dispersal. Here, I treat these issues as subordinate to biogeographic ones that affected the behavior of humans in Asia as an invasive species that colonized new environments and had negative impacts on indigenous hominins. I suggest that attention should focus on three issues: (i) geographic factors that molded human dispersal across Asia, (ii) behavioral changes that enabled humans to overcome previously insurmountable barriers, and (iii) demographic considerations of human dispersal and colonization of Asia, including interactions with indigenous competitors. Although a strong case can be made that humans dispersed across southern Asia before 60 ka, this should not detract from attention on the underlying processes of dispersal and colonization.

In recent years, discussion of the appearance of *Homo sapiens* in Asia (usually viewed as "Out of Africa 2" rather than as a process of indigenous evolution) has been dominated by three issues: (i) whether *H. sapiens* first appeared in various regions of Asia before 60 ka (e.g., Boivin et al. 2013; Dennell and Petraglia 2012) or after (e.g., Mellars 2006; Mellars et al. 2013); (ii) whether there were several dispersal events or only one (usually hypothesized as occurring ca. 50–60 ka); and (iii) when and how we can first identify "modern" human behavior in Asia. Most narratives rely upon three lines of evidence: archaeological, in which dated lithic assemblages (particularly those with blades) are treated as proxies of *H. sapiens*; a small, often ambiguous and poorly dated amount of human skeletal evidence; and genetic inferences from ancient DNA (aDNA) and modern populations (e.g., Klein 2009). Emphasis in most narratives has been on the pattern but not the process of dispersal. That is to say, most accounts are exercises in "joining up the dots," of indicating when *H. sapiens* likely first appeared in various parts of Asia and by which routes. Here, I attempt to place the evidence for the dispersal of *H. sapiens* across Asia in a biogeographical perspective that draws upon literature on the invasion biology of plants and animals and also on ideas from colleagues researching the colonization of the Americas and Australia. Although there is much ignorance, doubt, and

controversy over the Asian evidence, I suggest that we should attempt to write narratives that go beyond basic outlines of when "modern" tool kits and skeletal remains are first evidenced across a continent as large and diverse as Asia. Such "first appearance data" are provisional and relatively uninteresting as explanatory devices. In any case, the first appearance of humans in a landscape might indicate a short-term and unsuccessful presence in an area and not the type of sustained, repeated settlement associated with colonization that is the main concern of this paper.

Most researchers (myself included) assume that our species originated in Africa and that its subsequent appearance in Asia (and Europe) resulted from one or more dispersal events. Nevertheless, the East Asian Upper Pleistocene skeletal record is complex, and a simple replacement model is probably inappropriate (Martinón-Torres et al. 2016), especially in light of recent genetic evidence for interbreeding between *H. sapiens* and indigenous species of hominins (Fu et al. 2014, 2015; Reich et al. 2010, 2011).

Geographic Considerations

Regarding human dispersal across Asia, simple maps showing known sites and dates mask the most important topographic and climatic factors that most likely affected the rate and direction of dispersal.

Topographic Factors

In idealized circumstances, there are no impediments to a colonizing species dispersing into a new environment and

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occupying the entire space at a uniform rate. In reality, all environments offer "friction" that impedes, directs, and modifies the process of colonization. With the colonization of Asia by our species, the humans that dispersed across Asia and ultimately to North America and Australia had to traverse and inhabit an immense variety of landscapes. Some were occupied more or less continuously after colonization, others less so, and some were occupied rarely if at all. Following Veth's (2005) discussion of the colonization of Australia, we can begin by recognizing three types of terrain relevant to a dispersing species: refugia, barriers, and corridors.

Refugia, barriers, and corridors. The key point about these categories is that they are not immutable but are dependent upon two factors. The first is the prevailing climate, because under some climatic circumstances, barriers could become corridors (or vice versa). The second and more important is that, through changes in behavior, *H. sapiens* was able to find refugia in climatic downturns in areas that earlier hominins would have found uninhabitable and colonize or use as corridors parts of the Asian landscape that had previously been barriers.

Refugia. Refugia are areas that could still be occupied at times of increased aridity and/or decreased winter temperatures. Without refugia, a species would become regionally extinct because it had nowhere to live during the severest parts of a glacial/interglacial cycle. Refugia are also important as genetic bottlenecks; as stated by Bennett and Provan (2008:2453), "populations go through bottlenecks but come from refugia." (Strictly speaking, we should distinguish between glacial and interglacial refugia, but here the term "refugia" denotes only glacial ones.) Glacial refugia are areas where the climate was sufficiently mild and where there were sufficient resources for humans to survive climatic downturns, such as Heinrich events and marine isotope stage (MIS) 2. The main glacial refugia in Asia (as in Europe) for hominins (including *H. sapiens*) would have been along the southern edge of the maximum human range. Although current data do not permit the identification of Asian glacial refugia, some of the most likely are the Levant, the Caspian foreshore, the Ganges floodplain, and Deccan peninsula in India; the Yangtze Valley and parts of South China; and the Sunda Shelf of island Southeast Asia (Dennell 2009; Louys and Turner 2012; Rabett 2012 for Southeast Asia). All these areas probably served as refugia for earlier hominins, and their settlement records should indicate (when better known) occupation during MIS 2, when conditions were the most severe. Two others that may have been used as refugia after 40 ka are a conjoined Hokkaido-Sakhalin Peninsula in northeast Asia (Izuho 2014) and perhaps also "Greater Beringia" between 30 and 16 ka (Mulligen and Kitchen 2014).

Our species widened its range of glacial refugia in two ways. One was by adapting to tropical rainforest, which *H. sapiens* was the first hominin species to colonize (Roberts and Petraglia 2015). At present, the earliest examples are from Sri Lanka (see below), where rainforests were continuously occupied after 36 ka and were thus a glacial refugium. The second was at the northern limits of the hominin range, where *H. sapiens* (and perhaps Neanderthals) were able to survive climatic downturns by, for example, devising effective insulation in clothing and shelters or overcoming winter scarcity through food storage. As a consequence, *H. sapiens* may have been able to create refugia in northern areas that would have been previously uninhabitable. Beeton and colleagues (2013), for example, suggest that parts of Central Asia may have been a refugium throughout the last glaciation despite its harsh winter conditions. This possibility raises serious issues when considering the dispersal of *H. sapiens* across the northern part of the human range in Asia because of uncertainties over whether the presence of a site or group of sites in a cold period (such as a Heinrich event) indicates a successful adaptation in a refugium or a short-term failure by a population that foundered. At present, our information "is not sufficiently detailed to determine what sites can serve as evidence for survival through major natural calamities and what sites are those of people who perished" (Bar-Yosef 2017:66).

One measure of the effectiveness of a refugium is the ease with which species can disperse from it when conditions improve. Dispersal from the Levant either northward or eastward is easy, for example, relative to the Indian subcontinent, where dispersal outward is largely blocked by the Himalayas and Karakorum Mountains and the mountains of northern Myanmar, in much the same way as dispersal from an Italian refugium was blocked by the Alps (Hewitt 1999).

Barriers and corridors. The most obvious permanent barriers to human settlement in Asia before the terminal Pleistocene were areas above 3,000 m asl and deserts. The principal areas of high ground in Asia are shown in figure 1. The Anatolian Plateau, with its harsh winters, would also have been a barrier for much of MIS4 through to MIS 2 (Kuhn 2010). The height and extent of the Tibetan Plateau and adjoining Hindu Kush-Karakorum-Himalayan ranges made it inevitable that human expansion across continental Asia would split around them into a northern and southern route. This split might have occurred farther west because of the deserts of the Iranian Plateau and Central Asia. To the north, it may have been easier for humans to disperse north of the Pamirs into southern Siberia, as suggested by Goebel (2014), than southward across the corridor of the Taklamakan desert between the Tien Shan Mountains and the northern edge of the Tibetan Plateau. The principal Asian deserts (fig. 2) cover over 6 million square kilometers. Landforms vary from extensive dune fields (e.g., the Thar and Badan Jarain) to salt flats and playas (e.g., the Dasht-i-Lut) or stony pavements (e.g., the Gobi in China). Asian deserts are also either hot or cold, the latter being those in Central Asia, North China, and Mongolia, where winter temperatures are subfreezing for more than 2 months each year (Dennell 2013). As seen below, the deserts of Central Asia and North China and semiarid to arid Mongolia presented additional hazards to colonizers. The combination of mountain, desert,
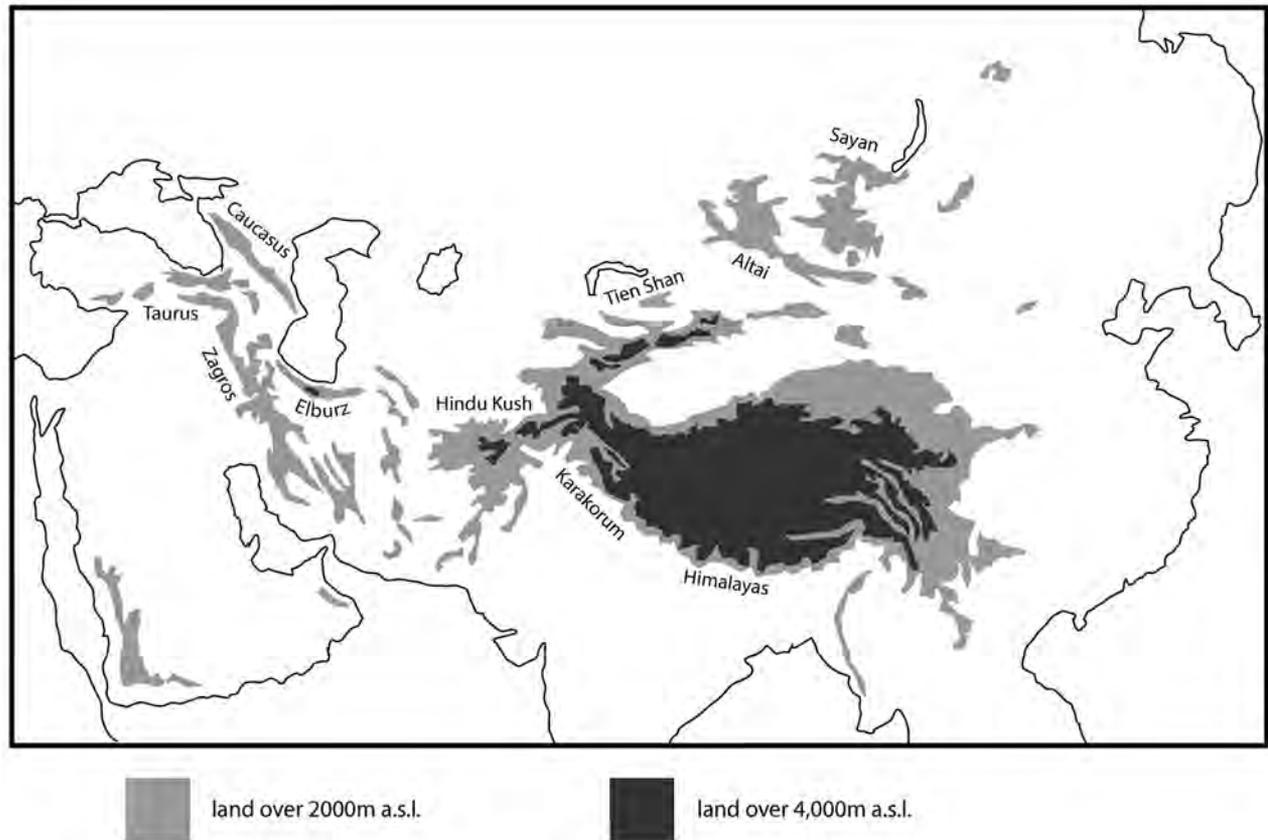
Figure 1. The principal mountain areas of Asia redrawn from *Philips New Reference Atlas* (1980).

and harsh climate across southwest and central Asia would inevitably have made a northern dispersal a much harder proposition than one along its southern flanks.

In continental Asia, barriers and corridors were sometimes interchangeable as part of the landscape dynamics of MIS 3. For example, mountain ranges, such as the northern Zagros and the Elburz in Iran, would have been barriers when snowlines were sufficiently depressed to prevent passage but corridors when the climate ameliorated. Similarly, deserts such as the Arabian and the Thar were likely barriers during arid periods but potentially corridors in moister episodes, such as MIS 5 and parts of MIS 4 and MIS 3, when there were active lakes and rivers (see Groucutt et al. [2015] and Rosenberg et al. [2011] for Arabia and Blinkhorn et al. [2013] for the Thar); the same is likely true of other Asian deserts, such as those of Central Asia and north and northwest China. Dispersal across continental Asia would have been harder when the climate became colder and drier because of the depression of snow lines and the expansion of deserts. As seen below, these conditions created additional hazards for colonizers that were not encountered across southern Asia.

Permanent corridors were probably low mountain passes and the lower parts of major river systems and their tributaries. The most useful for a species dispersing longitudinally were those trending west-east, such as the extinct ones in Arabia (see Breeze et al. 2015) and also the Ganges and Narmada in India and the Yellow and Yangtze rivers in China.

An important point about corridors is that they are not simply parts of the landscape through which people pass but may also be major areas of settlement. For example, the western Zagros Mountains are corridors between present-day Iraq and the Iranian Plateau and north-south between northwest Iran and the Arabian/Persian Gulf, but they have also been (and are) important areas of settlement in their own right. The same is likely true of Beringia (Goebel, Waters, and O'Rourke 2008) and the major river valleys of Siberia (Goebel 1999) and East and Southeast Asia.

Navigability (wayfinding) and ease of movement. The humans that dispersed across Asia had to traverse an immense variety of landscapes. From a colonizer's viewpoint, two important factors are navigability and ease of movement (Meltzer 2009:221–224). Areas offering easy movement and abundant landmarks (such as along major rivers or broad intermontane valleys) are easier to colonize than those with few landmarks and those that are difficult to traverse, such as mountain ranges, dense rain forest, or sand deserts. In addition, there was the need for potable water; Por (2004), for example, high-
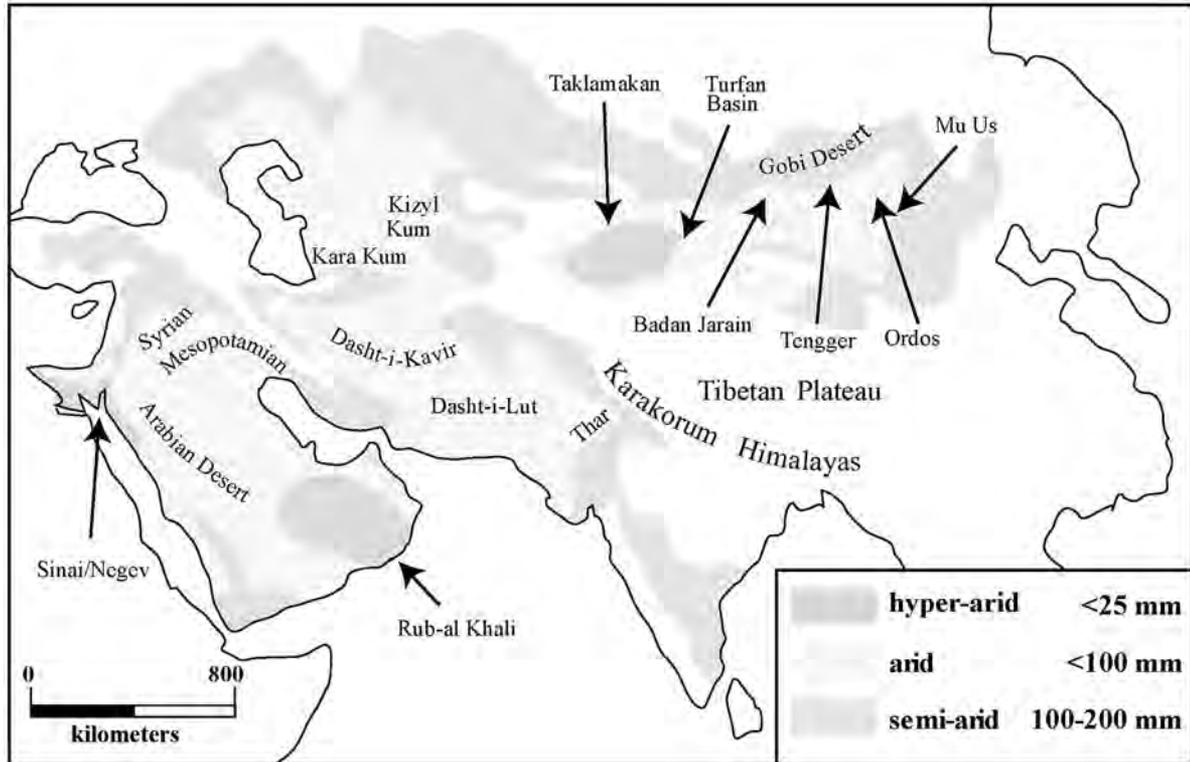
Figure 2. The principal desert areas of Asia. A color version of this figure is available online.

lighted the importance of springs along the southern edge of the Taurus Mountains to groups dispersing eastward from the Levant. Similarly, in deserts such as the Arabian (Breeze et al. 2015) and the Tengger (North China; Pachur, Wünnemann, and Zhang 1995; Zhang et al. 2002), the non- or moderately saline paleolakes that developed in the Upper Pleistocene would have been essential for human dispersal and survival.

Climatic Factors

The dispersal of *H. sapiens* across most of Asia occurred during MIS 3 and MIS 4, both of which were periods of climatic instability. At times, climatic change was short but severe, most notably in Heinrich events 4, 5, and 6 (ca. 38 ka, 45 ka, and ~60 ka; Blunier and Brook 2001) and are detectable in the East Mediterranean (Bartov et al. 2003), the Arabian Sea (Schulz, Rad, and Erlenkeuser 1998), and southern (Wang et al. 2001) and central (Porter and An 1995) China as well as in Greenland (Hemming 2004). Their effects would have been most strongly felt at the northern limits of the human range, north of 40°N (roughly from Beijing to Dmanisi, Georgia), and in desert/semiarid environments. In North China, for example, the decrease in rainfall of up to 50%–75% (Liu et al. 1995) resulted in the southward advance of desert at the expense of semiarid grassland; in Arabia and

the Thar Desert, decreased rainfall led to fewer lakes and permanent streams and increased dune mobility. In Central Asia, strengthened northern wind systems and weakened, rain-bearing westerlies reduced biological productivity and increased dust storms (see below) and loess deposition. Rainfall decreases would also have affected ecosystems in the southern parts of the human range in Asia (such as Central and South India and Southeast Asia) by causing some loss and fragmentation of habitats, and these too would have necessitated responses by humans. In Asia, climatic change had major consequences on coast lines, accessibility to upland areas, and the extent of deserts and steppe.

Coastal changes. Climatic changes affected coastal topographies by exposing or inundating areas of land and changing the length of rivers. In western Asia, the two main affected areas were the Arabian/Persian Gulf and the Red Sea. Regarding the Arabian/Persian Gulf, a sea level fall of 100 m would have exposed almost all of it as a sandy plain covering approximately 96,000 square miles (250,000 km², or approximately the same size as mainland Britain; Lambeck 1996) and allowing dispersal across its southern end from Oman into southern Iran. With the Red Sea, the Bab el Mandab crossing would have narrowed to <4 km during the last glacial maximum (LGM; Lambeck et al. 2011) and would thus have been less of an obstacle in cool periods.

Sea level changes were most pronounced in East and Southeast Asia. In East Asia, a fall in sea level of 120 m added 2 million square kilometers of coastal plain (Liu and Ding 1998:140) and briefly conjoined Hokkaido with Sakhalin Island but left Paleo-Honshu (Honshu, Kyushu, Shikoku) isolated across the Tsuguru Strait (Kudo and Kumon 2012; Yokoyama et al. 2007). In Southeast Asia, a comparable fall created Sunda, which conjoined mainland Southeast Asia with Sumatra, Java, and Borneo (Voris 2000). Conversely, rises in sea level fragmented this landmass into an archipelago and drowned the Molengraaf River, which flowed between Sumatra and Borneo. The repeated fissioning and fusing of islands in Southeast Asia may help explain the precocious development of seafaring (see, e.g., O'Connor, Ono, Clarkson et al. 2011), because there were ample opportunities and incentives for experimenting with different types of water craft as well as navigational skills and sailing techniques.

Altitudinal changes. In climatic downturns, lowered snow lines would have made some mountain passes unusable as corridors or usable for a shorter period each year. This was probably important in Southwest Asia, where summer snow lines were depressed by 1,200–1,800 m in the northern Zagros (Wright 1962), by 1,600 m in the Southeast Zagros (Kuhle 2007), and by 1,000–1,500 m in the Taurus and eastern Turkey (Sarıkaya, Çiner, and Zreda 2011), with the consequence of some habitat loss and fragmentation and greater restrictions on movement.

Deserts and semiarid landscapes in Central Asia and North China. Three major hazards would have impeded dispersal across the semiarid and arid regions of Central Asia and North China. These were drought, dust storms, and dzuds.

Drought. A dominant feature of arid and semiarid landscapes is their short-term variability in rainfall. "Average" totals mean little when the equivalent of 10 years' "average" rainfall might fall in a day, followed by 10 years of almost no rainfall. Long-term climatic trends toward greater aridity simply mean that extreme events, such as droughts, become more frequent and severe. Reductions in rainfall across Asia between MIS 4 and MIS 2 would have led to an expansion of deserts and, during periods of maximum aridity (as in the LGM), would have created a largely continuous desert belt ("aridistan") from Arabia through Iran and Central Asia into North China (Dennell 2009:256, 2013). Xiao et al. (1995) observed that, in North China, the winter monsoon (denoting increased aridity) peaked at 50 ka, 42 ka, and 30 ka. In southern Arabia, the movement offshore of the Indian summer monsoon would have made Arabia even drier than it is today (see Fleitmann and Matter 2009; Fleitmann et al. 2011; Glennie and Singhvi 2002). In the desert belt from Central Asia to North China, reduced rainfall would also have had two other undesirable consequences.

Dust storms. Mahowald et al. (1999:15895) note that, in the LGM, dust deposition in higher latitudes was up to 20 times

higher than at present due to stronger winds, an enlarged dust area attributable to reduced vegetation and soil moisture, and drier conditions that allowed dust to stay longer in the atmosphere. For example, the Tajik loess records show an increase in depositional rates from 12.1 cm/millennium at 250 ka but 20 cm/millennium thereafter (Yang and Ding 2006:336). Much of that loess would have been transported and deposited through dust storms. Typically, these mostly occur in spring, but they can happen year round. Central Asia is especially prone to dust storms. Orlovsky, Orlovsky, and Durdyev (2005) observe that these occur approximately 67 days/year in the Central Karakum desert of Turkmenistan and up to 146 days/year in western Turkmenistan. For comparison, the maximum frequency is 110 days/year in Mongolia, 102 days/year in southwest Kazakhstan, but only 20–30 days/year in Inner Mongolia (Wang 2004). The frequency, duration, and severity of dust storms would have increased under the drier-than-today conditions of MIS 4 and 3. Xiao et al. (1995:22) note that the Chinese Loess Plateau record of the last 130 ka shows "high-frequency, high amplitude variations . . . that imply rapid and significant changes in atmospheric conditions that affect dust transport and deposition."

Dust storms can be extremely hazardous, especially if they are long lasting. In 1910, one lasted 3 days in Turkmenistan and destroyed or buried much of the vegetation: an estimated 29,000 out of 30,000 cattle died during the storm, and many of those that initially survived the dust storm starved afterward (Orlovsky, Orlovsky, and Durdyev 2005:95). It can be assumed that the frequency and severity of dust storms would have increased during MIS 3 and especially MIS 2 and would have made human dispersal and survival in Central Asia and Mongolia especially hazardous, particularly if and when there was no suitable shelter.

Dzuds. Dzuds occur when a summer drought is followed by a harsh winter, usually with deep snow and abnormally low temperatures, causing animals to die from starvation and cold. They are a hazard particular to Mongolia but also occur in parts of Central Asia and North China. Five types are recognized (Begzsuren et al. 2004; Tachiiri et al. 2008). The severest occur when a summer drought is followed by deep snow (a white dzud); even worse is an iron dzud, when snow melts but then refreezes, thus forming an iron-hard ice crust over the surface that prevents animals from grazing. Livestock losses from dzuds in recent times have often been catastrophic for pastoral communities; for communities reliant on hunting, a severe dzud would provide a short-term bonus of frozen carcasses, but the hunting grounds would be depleted of prey the following summer and thus would have to be temporarily abandoned.

Colonizing Areas That Were Previously Barriers

As noted above, definitions of a barrier are dependent upon the colonizing abilities of an invasive species. Regarding *H. sapiens* in Asia, the Upper Pleistocene provides three examples of how

improved human abilities as a colonizer enabled them to convert a barrier into a corridor and resource zone.

Rainforests. The first were the rainforests of Sri Lanka and mainland and island Southeast Asia, which do not appear to have been occupied prior to the arrival of *H. sapiens* (see, e.g., Dennell 2014*a*, 2014*b*). Life in rainforests requires thorough knowledge of an extensive array of plant resources; the ability to hunt mammals, birds, and reptiles that live in dense vegetation or high in the tree canopy; and great skill at wayfinding. Sri Lanka currently has the earliest indisputable evidence of human settlement in rainforests at ca. 36 ka (Perara et al. 2011; Roberts et al. 2015). If Storm and colleagues (2005) are correct, humans were part of the Punung Fauna in Java ca. 100–125 ka during MIS 5 along with sun bear, orangutan, tapir, and other rainforest animals. Even if the identification of the Punung molar as *H. sapiens* is ambiguous (Polanski, Marsh, and Maddux 2016), the point still remains that "the presence of *H. sapiens* in a rain forest environment is more likely than occupation of this habitat by *H. erectus*" (Sémah and Sémah 2012:124). Evidence from Niah Cave (Barker et al. 2007) also indicates the use of rainforest resources, although perhaps not as exclusively as in Sri Lanka. The occupants of Niah inhabited a mosaic landscape that included rainforest, and thus they hunted monkey as well as pig and other animals. A Hoabinhian assemblage at Xiaodong, Yunnan Province, in Southwest China dated at 43.5 ka may provide another example of an early adaptation to rain forest. Pollen data indicate that the site was in rainforest, and the faunal remains are consistent with that interpretation (Ji et al. 2016). Isotopic analysis is needed to see whether these early Hoabinhians were living in rainforest.

The sea. The second barrier that was overcome was the sea. Previously, the only records of hominins crossing open sea before MIS5 are from Flores, which was reached at 1.0 Ma and 0.86 Ma, and Sulawesi, where hominins (type unknown) were present between 100 ka and 200 ka (van den Bergh et al. 2016). As most researchers rule out navigable boats at this time, the arrival of hominins on these islands may have been inadvertent via rafts of vegetation after tsunamis or cyclones (Dennell et al. 2013; Smith 2001). In the Upper Pleistocene, East and Southeast Asia show remarkably early evidence for the use of boats and/or rafts that could be steered. The earliest evidence is from Callao Cave, in the Philippines, where hominin remains (type unknown but possibly *H. sapiens*) date from 67 ka (Mijares et al. 2010); Japan, colonized ca. 38 ka (and a major colonization event that deserves greater attention by Western researchers; Izuho and Kaifu 2015); Okinawa, from ca. 36 ka (Kaifu et al. 2015); Timor, from 42 ka (O'Connor, Ono, and Clarkson 2011); and, of course, Sahel, with evidence from highland New Guinea by ca. 49 ka (Summerhayes et al. 2010) and mainland Australia by ca. 50–60 ka (Hiscock 2008; Roberts et al. 1994; Smith 2013). Timor

also shows evidence of pelagic fishing at 42 ka (O'Connor, Ono, and Clarkson 2011); what had previously been a barrier became not only a corridor but also a resource zone.

It has been proposed that humans dispersed across southern Asia to Australia via a coastal route (Mellars 2006; Mellars et al. 2013; Stringer 2000) and thus used a previously vacant (or rarely used) niche as a major corridor. Because this hypothetical dispersal occurred when sea levels were ~50 m lower than today (Mellars et al. 2013:10703), it is impossible to confirm or refute this hypothesis. As seen below, it is at least as likely that humans dispersed overland, particularly along river valleys or between lake systems.

Subarctic and Arctic northern Eurasia. The recent discovery that humans (possibly *H. sapiens*) were likely hunting mammoth by the Arctic Ocean at 72°N as early as 45 ka (Pitulko et al. 2016) shows that they had learned how to survive the extreme conditions of the Arctic, although it is too early to say whether this discovery denotes a failed dispersal or a short but successful foray. At the Yana site (71°N), repeated visits involving hunting, butchering, and occupation over a 3,000-year period starting at ca. 32 ka indicate unequivocally that humans (presumably *H. sapiens*) were able to operate in extremely cold environments (see fig. 3; Hoffecker et al. 2016; Nikolskiy and Pitulko 2013; Pitulko et al. 2004, 2014) and this leads us to consider the survival technologies that must have underpinned the colonization of arctic northern Asia.

Survival technologies. These primarily involved ways of being mobile over snow and ice and keeping warm, especially in winter. The invention of skis, snowshoes, and/or sledges would have enabled groups to move in winter across ice or compacted snow as easily (and perhaps more so) as across land in summer. Sewn, insulated clothing and footwear made from degreased and softened skins and furs would also have provided greater protection against the cold. The small toes of the 40-kyr-old individual from Tianyuandong, North China, provide a hint of what is currently the earliest indirect evidence of the habitual use of footwear (Trinkaus and Shang 2008). Additional requirements for survival in northern Eurasia would have been goggles against the glare from snow and ice; effective fire-lighting and food-storage techniques; effective cordage for sewing, lashing, tying, and so on; reliable lamps for coping with long winter nights; and well-constructed winter residences. Shipman (2015) has also highlighted the importance of dog domestication, perhaps as early as 32 ka in Siberia (Ovodov et al. 2011), in providing a hunting aid and potential pack animal. If humans were able to be mobile in winter by using improved methods of transport, they must also have developed their cognitive skills in navigation by starlight, given the short length of winter daylight at high latitudes. These and other innovations may have made it possible for humans to establish refugia in northern areas previously considered uninhabitable. (Nevertheless, Siberia was probably depopulated during the LGM; Graf 2014.)
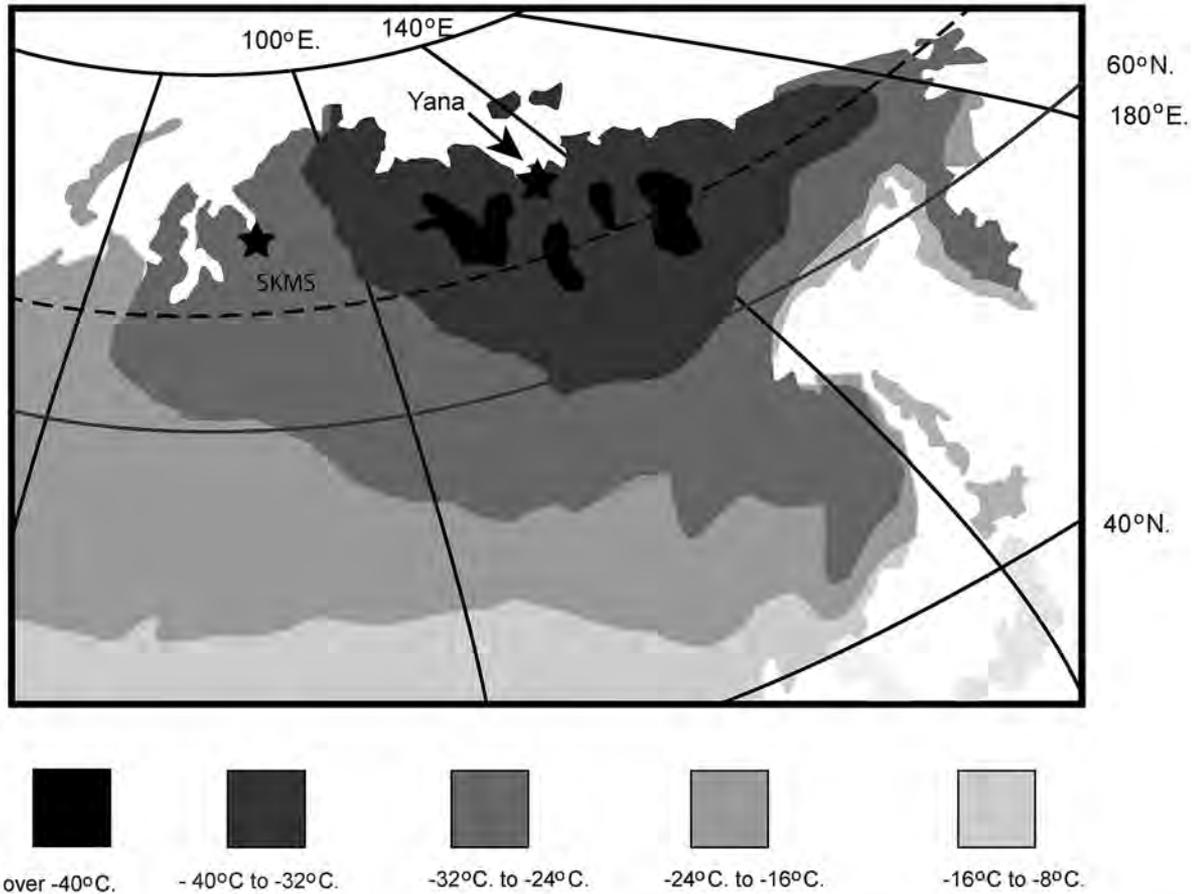
Figure 3. January average temperatures in northern Siberia and location of Yana and the Sopochnaya Karga mammoth site (SKMS). Redrawn from the *Encyclopedia of World Geography* (1974).

Hunting technologies. Shea and Sisk (2010) have drawn attention to the invention of stone-tipped projectiles in northeast Africa during the African Middle Stone Age and their subsequent use in the Levant. These, they argue, were a game-changer, as a heavier projectile point would have greater penetrating power and a more even flight, thus improving the hunter's aim and success rate. These, however, are little evidenced outside the Levant, so they may have had only a regional impact. Other innovations may have occurred in hunting technologies. For example, if the inhabitants at Niah Cave were able to remove toxins from plants before eating them (Barker et al. 2007), they may also have realized the value of adding toxins to projectiles to impair their prey. For hunting animals like monkeys in the tree canopy of Sri Lanka ca. 36 ka (Roberts et al. 2015), hunters may have relied upon bows and arrows or blow pipes and darts. Pit traps were another innovation that currently appears unique to Japan and dates from 38–35 cal ka (Sato 2015). In northern latitudes, traps, snares, and nets for trapping small, fur-bearing animals would have been another innovation that provided furs for clothing and other means of keeping warm in subfreezing temperatures (see Hoffecker 2005).

Biological Considerations: Dispersal and Invasion

Biological dispersal is a neutral term that refers to the expansion of the range of a species into a new habitat. A biological invasion denotes "any process of colonization and establishment beyond a former range" (Davis 2009:3) but is often used to refer to a dispersal that has negative consequences on either indigenous species or humans. Because invasive species of pathogens, insects, and plants often have major ecological or economic costs, many invasion biologists concentrate on those species deemed harmful to humans either directly (e.g., pathogens) or indirectly (e.g., crop pests). Here, humans are seen as an invasive species, in that this species rapidly (relative to the rest of the Pleistocene) spread across Eurasia and had negative impacts on contemporary hominin species, all of which were extinct by the end of the Pleistocene.

The history of "Out of Africa 2" can therefore be discussed as a narrative about ourselves as an invasive species (see, e.g., Shipman 2015) or as a weed species that was able to flourish in unstable environments (see, e.g., Cachel and Harris 1998). Literature on the ecology of invasive species (e.g., Clobert

et al. 2013; MacDonald 2003; Shigesada and Kawasaki 1997) often focuses on plants, insects, and small mammals, sometimes under laboratory or experimental conditions, and inevitably has a very short time-depth. This literature is thus not directly applicable to the type of coarse data relating to a large mammal such as *H. sapiens*, with a complex set of behaviors and operating over timescales rarely shorter than millennia. These studies are useful, however, as a source of ideas on (i) the importance of the metapopulation as a demographic unit; (ii) differential responses to differences in resource availability; (iii) the effects of habitat loss and fragmentation, especially at the edge of the inhabited range; and (iv) competition with indigenous residents.

Populations and Metapopulations

A biological population is "all individuals of a given species in a prescribed area" (MacDonald 2003:15). Depending upon the choice of scale, this can be an individual settlement, a region, a country, or a continent. In a colonizing situation, a newly arrived population can expand radially outward by forming new colonies: a classic example is the radial dispersal of the muskrat from its point of introduction in Austria in 1905 (Elton 1958). Species capable of long-distance dispersal tend to behave differently in the way they colonize and subsequently use landscapes by forming a metapopulation, or "a group of spatially separated populations occupying a nexus of favourable patches" (Smith 2013:75). Those that interact infrequently are "loose metapopulations": an example is subpopulations of arctic foxes inhabiting different islands. Others interact frequently and form "tight metapopulations," such as birds nesting and living in different but nearby woodlands (MacDonald 2003:15). Under circumstances where the human skeletal record is sufficiently detailed, it may be possible to model tight metapopulations as paleodemes (Howell 1999), thereby providing a way of integrating human skeletal and archaeological data.

Humans are a prime example of a species that is extremely good at forming tight metapopulations (or alliances or networks; see Spikins 2015) that maintain cohesion through kinship, ideology, or other forms of corporate identity. Hunters and foragers, for example, typically live in groups within an area that maintain contact in order to share information, exchange and obtain scarce resources (such as furs, obsidian, or ochre), and find mating partners (Wobst 1976). As is evident from the distance over which items such as obsidian were exchanged in the late Paleolithic of East Asia (Ikeya 2015; Kuzmin 2006), these metapopulations could maintain contacts across the sea and over distances of up to 1,000 km; other examples are anthraxolite and amber at the Yana rhinoceros horn site that came from 600 km away (Pitulko et al. 2014).

The behavior of metapopulations is crucial when considering colonization. First, "at any given latitude or effective temperature the structure of the subsistence resource base can vary widely in terms of predictability, patchiness and density in space and time" (Ambrose and Lorenz 1990:9). Consequently,

dispersal into a diverse environment is more effective if these differences are dealt with by a metapopulation formed of several integrated groups rather than a single, nucleated population. Second, dispersal takes place at the edge of the inhabited range and thus in the least familiarized part of the landscape. A metapopulation can move into new territory on a trial and error basis, with "a group of spatially separated populations occupying a nexus of favourable patches. During the dispersal phase, demographic and environmental stochasticity eliminate small populations in some patches, but these are recolonized by immigrants from other nodes" (Smith 2013:75). One major advantage of this pattern of dispersal is that a large area can be occupied in a short space of time provided that groups maintain sufficient connectivity with each other to ensure that each (or most) survives. Smith (2013:75), for example, estimates that the arid interior of Australia could have been occupied by only 25,000 people in 150 years, starting with a donor population of ∼500 that doubled every 25 years. Collectively, a species organized into metapopulations can also acquire far more knowledge of their environment as an information network than any group could obtain singly.

Sinks and Sources

The dynamics of metapopulations can also be modeled as "sources and sinks" along the lines proposed by Eller, Hawks, and Relethford (2004), Hawks (2009), and Pulliam (1988) and developed in an early Paleolithic context by Dennell, Martinón-Torres, and Bermudez de Castro (2011) and Martinón-Torres et al. (2016). To quote Hawks (2009), "a population sink is a region where the average rate of reproduction is below replacement levels. This region can remain populated only if individuals migrate in from other places. The places that reproduce above replacement are called population sources."

At a continental scale, the main source populations are in refugia. At a regional scale, source populations will tend to be south of the northern limit of expansion and/or in areas where resources are more abundant and predictable; new subunits of a metapopulation would be created from members of a source population. Population sinks would be at the limits of the current range and/or in areas where resources are less abundant and predictable. These groups within a metapopulation would require the import of members from other groups, and probably the import of mating partners, to remain viable (see fig. 4). Demographic expansion thus depends greatly upon (i) extinction rates in sink populations at the edge of the inhabited range and (ii) the ability of the main source populations to support sink populations, especially those at the edge of the range. This becomes difficult when population densities are low and intergroup distances are high.

Resource Variability

As Ambrose and Lorenz (1990) pointed out, the resources in a landscape can vary enormously in terms of availability,
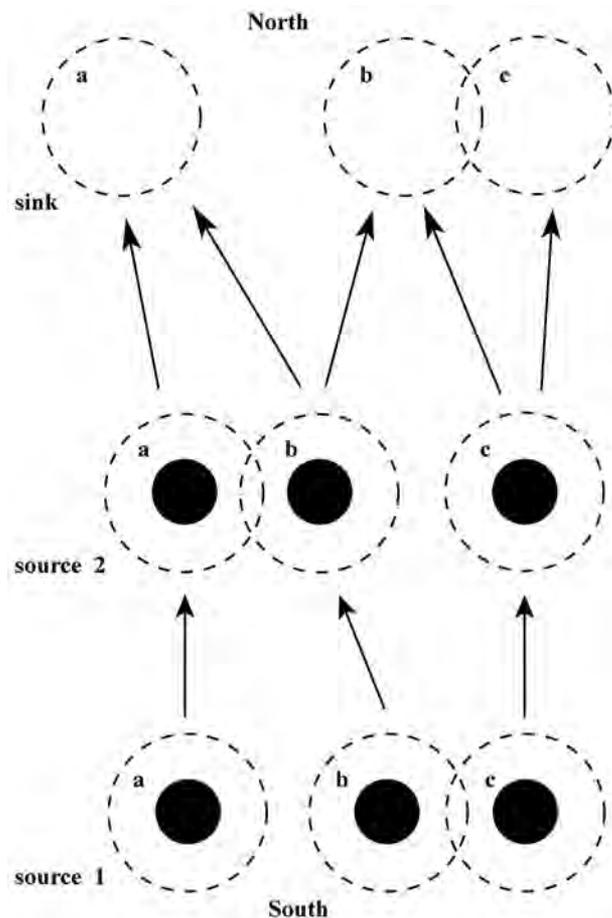
Figure 4. The dynamics of source and sink populations. The solid circles denote source metapopulations during cold periods when populations contract into refugia; the dashed circles indicate interglacial or interstadial conditions when expansion from them is possible. Here, the bottom row indicates three metapopulations in refugia; each is separated in glacial conditions, but in interglacial conditions, metapopulations *b* and *c* overlap. The middle row indicates how each expands in interglacial times and becomes a source population: here, demes 2*a* and 2*b* overlap, but 2*c* (derived originally from demes *b* and *c*) remains isolated. The top row indicates sink populations at the maximum expansion during an interglacial; here, metapopulation 3*a* (derived from 2*a* and 2*b*) is isolated, but 3*b* and 3*c* overlap, although each has a different ancestry. These sink groups are highly vulnerable to short-term climatic and mortality changes and would probably need recruitment from source populations farther south. Adapted from Dennell, Martinón-Torres, and Castro (2011), figure 6.

predictability, and patchiness, and they require different responses from a colonizing metapopulation. With humans, two broad strategies can be identified. Meltzer (2009:234–238) has usefully developed Beaton's (1991) categories of transient explorers and estate settlers to suggest how North America was colonized. He renames these as the cautious and the bold. "Cautious" groups are ones that remain anchored to patches of high year-round productivity. Over time, some may seek

similar locations nearby and develop those in turn, but generally, dispersal rates are slow; such groups "moved only slowly across the latitudes and longitudes, each daughter colony being spawned by the overflow of a saturated estate" (Beaton 1991:220–221). An example in Asia of such a process might be the Levant, with its rich coastal plain and inland lakes. Rather than envisaging human settlement there after 100–125 ka as a "failed dispersal" (Shea 2008), it might instead be an example of how cautious colonizers made the most of a rich environment, beyond which resources in the deserts and semiarid plains to the east were more scattered, harder to obtain, and a disincentive to dispersal.

"Bold" colonists are ones that move when productivity declines. These colonists inhabit areas that will not support long-term residence of the kind favored by cautious colonists, so they have a high incentive to move, and especially to "jump" across areas that are low in productivity (such as steppe or deserts; see fig. 5*a*). During sudden environmental downturns, for example, water resources might diminish and game become less plentiful; onward movement to new areas thus becomes risky, but it is nevertheless less risky than clinging to a declining resource base. Bold colonists tend to use mobility to explore and become familiar with large areas (Veth 2005); as an example, judging from where different types of stone were obtained, the occupants of Puritjarra at 35 ka in western Australia were probably familiar with ~10,000 km² of territory. Bold colonists also have a characteristic method of expansion "in which migrants generate new satellite colonies rather than simply expanding the occupied area from its periphery" (Smith 2013:75). They thus form a metapopulation of spatially separate groups, some of which may fail, but which can be replaced by colonists. An Asian example might be the colonization of the North China Plain, where resources were scarce, winters harsh, and few areas allowed intensive long-term occupation. Bold colonists are also ones that seek out naive prey that is unfamiliar with humans and thus easier to hunt; when the animals become more wary and vigilant, bold colonists will move to new areas where the prey is naive (Dennell, forthcoming).[1]

It is here that the contrast between short-term visitors and long-term residents (Dennell 2003) becomes important. In areas where resources are subject to fluctuations in availability, settlement is likely to have been intermittent and confined to moister and warmer intervals, punctuated by periods of settlement contraction or even abandonment during climatic downturns. In semiarid and arid areas where rainfall is highly variable, settlement records are likely discontinuous, as is also the case in high-latitude regions where winter temper-

1. Spikins (2015) points out that jump dispersals by bold colonists may be forced rather than voluntary. In metapopulations with strict norms of behavior, transgressors may be forcibly expelled. Although difficult to demonstrate from Paleolithic evidence, her suggestion is worth noting when considering instances of short-term human presence in areas such as off-shore islands or the Arctic that were far from the main areas of settlement.
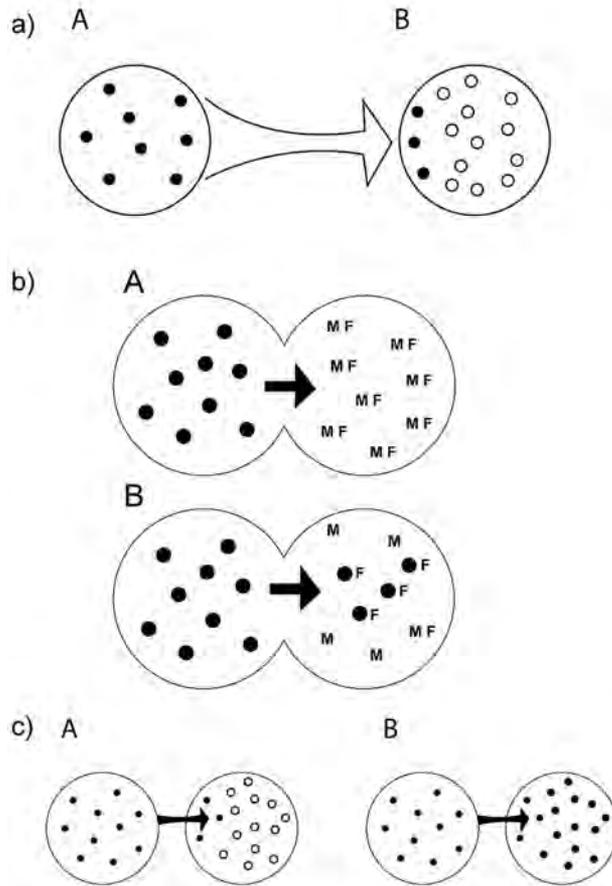
Figure 5. Three scenarios of colonizing metapopulations. *a*, Bold colonization by jump dispersal. Here, some groups (black circles) at the edge of a metapopulation take the risk of jumping across an area of low productivity (e.g., a desert or open sea) to find a better area than their present location. Although the risk of failure is high, success means that a new region can be colonized by descendant groups (white circles). *b*, Colonization and assimilation. In this scenario, part of a metapopulation (*A*; black circles) begins to invade an area occupied by a different type of hominin, shown as MF, with M = males and F = females. The invasive metapopulation then proceeds to assimilate the females of reproductive age (*B*), thus degrading the previous viability of the indigenous population. This type of scenario is indicated by evidence of gene flow from Neanderthals and Denisovans into *Homo sapiens* outside Africa and may also help explain the evidence for hybridization in the East Asian skeletal evidence for *H. sapiens* between marine isotope stage (MIS) 5 and MIS 3. *c*, Colonization and population replacement. Here, a metapopulation (black circles) begins to invade an area already occupied by other groups (open circles). In *B*, the indigenous occupants are replaced. This process may have been violent but may also have occurred because the incoming population outcompeted the local population for key resources and locations and destroyed their connectivity between groups. This scenario is one explanation for the replacement of Neanderthals by *H. sapiens* in western Eurasia.

atures are the key variable. Two related points are that the first appearance of humans in these types of unstable environments should not be mistaken for the onset of colonization: these might indicate, in Shea's (2008) words, a "failed dispersal" (or a

forced expulsion; Spikins 2015); and second, these areas are demographic "sinks" that could only be sustained by being replenished from an external source population in a refugium (Dennell, Martinón-Torres, and Bermudez de Castro 2011).

Habitat loss and fragmentation. The dispersal of *H. sapiens* into and across Asia began in MIS 5 and was completed mostly in MIS 4 and 3, both of which experienced a considerable degree of climatic and hence environmental change. The climatic instability of MIS 3 has been identified as a major reason why Neanderthals became extinct (see, e.g., d'Errico and Sánchez Goñi 2003); by implication, *H. sapiens* was able to better cope with such changes. The key factor here is how humans responded to habitat disruption or, specifically, loss and fragmentation.

Ecologists have paid considerable attention to the consequences of climatic and environmental change on plant and animal populations. Given current concerns over global warming, most of these studies consider the effects of increased temperatures: Pleistocene researchers, of course, have to consider also the consequences of climatic downturns involving lower temperatures. Climatic changes involve habitat fragmentation and loss that is most keenly felt at the edges of the inhabited range. Regarding habitat fragmentation, Baguette et al. (2013:381) point out that "habitat fragmentation is an inherent consequence of habitat loss: the progressive disappearance of a given habitat entails changes in both the area of remnant fragments and their spatial configuration, with consequences on the structural connectivity among remnants." They emphasize that, when suitable habitat has fallen to <40% of its original extent, the distances between fragments suddenly increase, with significant consequences: "By increasing the distance among such patches, landscape fragmentation is expected to increase dispersal costs, including loss of time and energy and the risk of getting lost" (Baguette et al. 2013:385). Dytham and Travis (2013:400) stress that "it is not the loss of habitat per se that is the most important element of fragmentation . . . it is loss of 'connectivity' that can be crucial for the survival of a species. This effect will be non-linear as there will be a threshold of habitat loss that will break the connectivity of a region." There are clear implications here for the importance, for widely dispersed groups in a metapopulation, of maintaining connectedness when habitats become fragmented.

Because *H. sapiens* as a colonizing species invaded areas containing indigenous resident populations, the crucial factors are how each was able to respond most effectively to habitat loss and fragmentation during climatic downturns, the opportunities offered by periods of climatic amelioration, and the extent to which *H. sapiens* disrupted the connectivity of the indigenous population. These points bring us to the subject of competition with resident populations.

Competition with Resident Populations

Unlike *H. sapiens* in Australia and the Americas, *H. sapiens* in Eurasia colonized a continent that was already occupied.

At the time of potential contact with *H. sapiens* (i.e., after MIS 5), Neanderthals were resident in Southwest and Central Asia, southern Siberia as far east as Okladinov Cave in the Siberian Altai (Krause et al. 2007), and perhaps even farther east. *Homo erectus* sensu stricto was present in China and perhaps also Southeast Asia (although it may already have become locally extinct by the time of contact), and *Homo floresiensis* was present on Flores, Indonesia, until 50 ka (Sutikna et al. 2016) and perhaps was present on other islands in the region. Two unknowns are an unknown resident population in South Asia that does not appear to have been *H. erectus* sensu stricto or *Homo heidelbergensis* (Athreya 2007) and the "Denisovans," known only from the gene sequence extracted from a finger phalanx and two teeth from Denisova Cave, in Siberia (Krause et al. 2010; Reich et al. 2010; Sawyer et al. 2015), that is also present in modern populations in Melanesia (Reich et al. 2011) and Tibet (Huerta-Sánchez and Casey 2015).

Little is known about how incoming metapopulations interacted with indigenous metapopulations across Asia at and after contact. Some geneticists argue that there was interbreeding between *H. sapiens*, Neanderthals, and Denisovans. As an example, Kuhlwilm and colleagues (2016:429) propose that there was "admixture among archaic and modern human populations, including gene flow from Neanderthals into modern humans outside Africa, Denisovan gene flow into the ancestors of present-day humans in Oceania and mainland Asia, gene flow into the Denisovans from Neanderthals, and, possibly, gene flow into the Denisovans from an unknown archaic group that diverged from the other lineages more than one million years ago." We may never know the nature of these encounters between *H. sapiens* and Neanderthals. However, when looking at colonial and imperial history, sexual relations between colonizer and colonized were overwhelmingly between European males and native females (see, e.g., Hyam 1991; Walter 2010). As a speculation, interbreeding between *H. sapiens* and Neanderthals and Denisovans may also have been largely between invasive male *H. sapiens* and indigenous female Neanderthals and Denisovans (see fig. 5*b*).

The long-term consequences of these encounters may have been negative (such as male hybrid infertility; Sankararaman et al. 2014) or positive if leading to "hybrid vigor," enhanced immunity (see Stewart and Stringer 2012), and the acquisition of beneficial genes such as those that facilitated life at high altitudes (Huerta-Sánchez and Casey 2015) or in cold environments.

At least four other scenarios of human-indigenous interaction can be envisaged: (1) taking over the indigenous species' habitat by, for example, more effective hunting of prime animals, preemptive use of key locations, and aggressive behavior toward the inhabitants (see fig. 5*c*); (2) coexisting but with little interaction; (3) occupying parts of the landscape (such as coastal regions) that were seldom used by indigenous groups (see Shigesada and Kawasawki 1997:104); and (4) introducing new diseases into Asia that were lethal to indigenous residents (Bar-Yosef and Belfer-Cohen 2001), just as, in recent times, smallpox decimated the indigenous Americans after Spanish contact.

Discussion

As argued above, the colonization of continental and island Asia by *H. sapiens* was likely a lengthy and complex process. One key aspect that underpins this process—particularly the colonization of the rainforest and the islands of South and Southeast Asia and Japan as well as colonization of the Arctic, Siberia, Central Asia, and North China, with their long subfreezing winters—is the importance of tight metapopulations or networks. In other words, groups within a defined human metapopulation were able to establish and maintain social links with each other and with other groups for sharing information, exchanging valued items (e.g., obsidian, ivory, and furs), obtaining mating partners, and maintaining genetic viability through recruitment or assimilation. By 40 ka, it is probable that such groups were defined and sustained by language, kinship, and perhaps ideology. Tight metapopulations were highly effective ways of colonizing new environments, particularly those as challenging as Siberia, the Arctic, and rainforests. "Modern" behavior is evidenced less by the type of artefact or the evidence of symbolism as by the ability to operate as part of a network with strong links between groups. "Trait lists" (or "shopping lists") of items of material culture deemed to indicate "modern human behavior" are clearly inoperable in Arabia, India, Southeast and Central Asia, China, and Australia, although they have some utility in the Levant and parts of Siberia. The underlying problem is that no single item or group of items is both unique to *H. sapiens* and universal across its range. A different perspective is acquired if one thinks of mental technologies expressed in ways of maintaining connectivity within networks over long distances, especially in challenging environments. Colonization of new habitats (e.g., the rainforest and the Arctic) is probably one of the clearest indicators of this type of mental technology, exhibited in solving problems and being adaptable. *Homo sapiens* may have been simply better at maintaining tight metapopulations as an invasive colonizing species than its predecessors.

As stated in the introduction of this paper, the intention here is to focus on the process of human dispersal from Africa, rather than on the outcome as a series of (often speculative) arrows that show little more than some of the routes that may have been taken and when these had been undertaken. The constraints of landscape and climate, the behavioral thresholds that were overcome in dispersal across Asia, or the likely behavior and impact of an invasive species have not been given the attention they deserve. In a similar vein, insufficient attention has been paid by Old World prehistorians to how colonization has been treated by those researching the Americas or Australia. For example, the contrasts between cautious and bold colonists or the importance of naive faunas are important themes that could be imported from Americanists, and Australian notions of corridors, barriers, and refugia are similarly capable of useful employment in discussions of the Asian evidence. The literature on the biology of dispersal and invasion also has great potential for investigating how *H. sapiens* extended its range across the largest continent.

The quality and quantity of archaeological and fossil skeletal data on the Asian story of "Out of Africa 2" is now far outstripped by the quality and quantity of climatic and environmental evidence on Asia during the last glacial cycle. This presents obvious incentives to archaeologists to improve the dating and calibration of their evidence, to venture beyond a cultural approach based almost entirely on lithic evidence, and to integrate their evidence with other disciplines. It is hoped that this volume will mark an important step in this process.

Acknowledgments

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A Genomic View of the Pleistocene Population History of Asia

by Martin Sikora

The advent of next-generation DNA sequencing technologies over the past decade has had a transformative effect on the study of human population history. Advances in the retrieval and analysis of ancient DNA from human remains for the first time offer a direct window into our genetic past. These data sets have revealed an increasingly complex picture of human demographic history in Asia, suggesting multiple waves of migration across the continent and repeated episodes of admixture with archaic humans such as Neanderthals and Denisovans. I review seminal earlier studies and discuss some of the more exciting recent results emerging from these data sets, ranging from the early dispersal into Australia and Oceania to the peopling of Far Northeastern Asia. I also highlight important limitations of genetic data and discuss open questions and future research directions.

The advent of next-generation DNA sequencing technologies over the past decade has resulted in an explosion in the amount of human population genetic data available. Large-scale sequencing projects of world-wide populations such as the 1000 Genomes Project (1000 Genomes Project Consortium 2012, 2015) have enabled population geneticists to move from the classical single-locus studies on mitochondrial and Y-chromosome DNA to much more powerful genome-wide studies, essentially transforming the field into a data-driven discipline (Pool et al. 2010). More recently, the advances in retrieval and sequencing of DNA from ancient remains (reviewed in Orlando, Gilbert, and Willerslev 2015) have had a truly revolutionary effect on the study of human history. These advances now make it possible to analyze genetic diversity in ancient individuals and populations, thereby providing a direct window into our past. What has emerged from these studies is a much more complex picture of human evolutionary history than previously thought, including large-scale population movements and replacements, as well as complex waves of gene flow between different groups (Allentoft et al. 2015; Fu et al. 2016; Green et al. 2010; Haak et al. 2015; Lazaridis et al. 2014; Raghavan et al. 2014; Reich et al. 2010; Seguin-Orlando et al. 2014; Skoglund et al. 2012; Slatkin and Racimo 2016).

While a great share of ancient DNA (aDNA) studies have been on European and West Eurasian prehistory, the focus is increasingly shifting toward other regions that are still understudied. Asia in particular has seen a comparable scarcity of ancient DNA studies despite its size and rich fossil history;

most studies have been restricted to Central Asia and the Eurasian Steppe (Slatkin and Racimo 2016). Despite the small number of studies, some of the most exciting findings of recent times stem from aDNA collected from some Asian fossils, such as the genome of the mysterious Denisovans (Meyer et al. 2012; Reich et al. 2010). In this paper I discuss what we have learned about the demographic history of Asia during the Pleistocene from these exciting new data. The focus of the paper is on genome-wide studies, as these have substantially more power for the inference of demographic processes than single-locus data sets used in earlier studies. The first section of the paper discusses the early dispersal of anatomically modern humans (AMH) out of Africa into Asia and onward to Australia and Oceania, examining the evidence for single-wave versus multiwave models as well as patterns of admixture with archaic hominins. In the second section I focus on subsequent dispersals through Asia, including the divergence of East Asians from western Eurasians as well as the arrival in the far northeast and onward into the Americas. The final part of the paper highlights some of the major open questions that remain or have emerged from the aforementioned studies and suggests some future directions.

Early Dispersal Out of Africa

Insights into the Timing of the Dispersal Inferred from Genome-Wide Studies on Modern Populations

The availability of genome-wide data from modern populations from both within and outside of Africa has facilitated detailed demographic modeling of their relationship. In simplistic terms, these approaches use patterns of genetic variation observed in the individuals of interest to fit different demographic scenarios, under the assumption of a statistical model

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relating genetic diversity to the underlying evolutionary processes. A useful framework for this is the so-called coalescent, a stochastic process that forms the basis of many widely used methods (Rosenberg and Nordborg 2002; Wakeley 2008). An important feature of these models is that the parameter estimates of the timing of demographic events are usually inferred as functions of the underlying mutation rate. An accurate estimate of the mutation rate is therefore necessary to convert the values back into real time. While the human mutation rate is currently an active topic of research (reviewed in Scally (2016)), the emerging consensus of the most recent studies suggests a rate of 0.5×10^{-9} mutations per base pair per year, which is roughly half of that previously used in most studies discussed below (Fu et al. 2014; Lipson et al. 2015; Rahbari et al. 2016; Wong et al. 2016). In light of this, all timings discussed below are based on the more recent slower rate.

One of the first studies to use genome-wide data to infer parameters of a demographic model for the out-of-Africa (OOA) dispersal was Gravel et al. (2011). The method compares the observed joint site frequency spectrum (SFS) between at most three populations to one expected under a particular demographic model, using an approach introduced by Gutenkunst et al. (2009). Using data generated from the 1000 Genomes Project (1000 Genomes Project Consortium 2012), their estimate for the divergence time between Africans (represented by Yorubans from West Africa) and the ancestors of OOA populations (represented by individuals of Northern European ancestry from Utah, Han Chinese from Beijing, as well as Japanese from Tokyo) was between 90 and 138 ka. A different approach based on Bayesian modeling of individual genome sequences was used by Gronau et al. (2011) to model the demographic history of six diverse human populations, including three individuals of African ancestry (San from South Africa, Bantu from South Africa, Yoruba from Nigeria). They obtained a similar estimate of the African–OOA divergence time, ranging between 88 and 110 ka. Harris and Nielsen (2013) showed that the length distribution of genomic segments that are identical by state between pairs of individuals can be used to accurately model the demographic history of their respective populations. In contrast to the previous studies, only individuals of European descent were used for estimating the OOA divergence time, resulting in a point estimate of 110 ka. The recent multiple sequentially Markovian coalescent (MSMC) method (Schiffels and Durbin 2014) uses relative cross-coalescence rates between pairs of haplotypes to study their divergence. An advantage of this method is that it allows the study of population separation as a function of time, thereby distinguishing scenarios of sudden versus gradual separations. They inferred a gradual separation of West African Yoruba and OOA populations possibly starting before 150 ka and lasting until 50 ka. Another noteworthy feature of this analysis is somewhat more recent divergence times (within the last 100,000 years) when using the East African Maasai as the representative African population, indicating possible ancestral population structure within Africa. Finally, three recent landmark studies reporting large-scale panels

of high-quality genome sequences from diverse worldwide human populations (Malaspinas et al. 2016; Mallick et al. 2016; Pagani et al. 2016) also support early divergence times of OOA ancestors from contemporary Africans. Malaspinas et al. (2016) used an SFS-based approach to model the divergence of Africans (Yoruba) from a hypothetical OOA population ancestral to a set of Eurasian and newly reported Oceanian populations. They obtain a point estimate for the divergence time of 127 ka (95% CI 83–170 ka), followed by a shared bottleneck for all OOA populations at 72 ka (95% CI 60–104 ka). Both Mallick et al. (2016) and Pagani et al. (2016) used the MSMC framework, with largely comparable results to Schiffels and Durbin (2014), indicating a gradual separation from Africans starting before 150 ka and substitutional divergence by 63–75 ka.

Taken at face value, these revised slightly earlier divergence time estimates are conflicting with the previously estimated 60–80 ka upper bound on the OOA dispersal obtained from mitochondrial DNA studies (Soares et al. 2012). However, there are a number of caveats to note. First, the estimated times are only informative about population divergence of extant human populations, which could substantially predate the actual dispersal times under scenarios of ancestral population structure within Africa prior to the OOA dispersal. Second, the more sophisticated recent methods like MSMC point toward more gradual models of divergence as opposed to the simplified instantaneous divergences assumed previously. A scenario of an early exit followed by continuous gene flow between an early OOA population and its African source group would be entirely compatible with the observed estimates (Schiffels and Durbin 2014). A final crucial point is that timings obtained from modern populations are naturally only informative about events in the history of those individuals that successfully contributed to the present-day human gene pool. Recent results from ancient DNA studies (discussed below) suggest that large-scale population turnovers and "failed" dispersals were likely common throughout human history, with modern inhabitants of a geographic region often being genetically very different from earlier peoples preceding them. In the absence of ancient DNA data from early OOA fossils, these times are therefore best interpreted as upper bounds for the actual dispersal times.

Single- or Multiwave Dispersal Out of Africa and Into Asia?

Scenarios of single- or multiwave dispersals can in principle be investigated by contrasting genetic divergence for diverse sets of populations within and outside of Africa. For example, a single OOA event would predict similar divergence between all modern non-African and African populations, whereas divergence should be older for populations deriving from an earlier wave. These analyses are, however, complicated by large-scale changes in human genetic structure after their initial dispersal, changes that have become apparent from ancient DNA studies in recent years and include admixture with archaic hu-

mans (discussed in subsequent sections; Pickrell and Reich 2014). Nevertheless, it can be argued that most recent studies are converging on broadly similar scenarios, with some remaining uncertainty regarding the contribution of a separate earlier OOA pulse to some populations and the number of independent major early dispersals across Asia after leaving Africa (Malaspinas et al. 2016; Mallick et al. 2016; Pagani et al. 2016; see fig. 1).

Evidence for a single OOA pulse has accumulated from many whole-genome studies. The MSMC analysis of Schiffels and Durbin (Schiffels and Durbin 2014) showed similar split times when using either European or East Asian genomes as OOA reference, consistent with a single divergence of those from the African ancestors. However, a limitation of this study is that only Han Chinese from Beijing were used to represent Asian populations in this analysis. Rasmussen et al. (2011) presented the first whole genome of an Aboriginal Australian, sequenced from an ~100-year-old hair. The estimated divergence time between this genome and an African genome was also found to be comparable to those with European or East Asian genomes (81–94 ka). A recent study of 35 full genomes from Melanesian populations showed that population size trajectories of those individuals are similar to other OOA populations. While not directly estimating population divergence, this analysis does suggest a shared bottleneck for all OOA populations. A similar pattern was observed in an analysis of whole genomes of 56 indigenous Arabian individuals (Rodriguez-Flores et al. 2016). Based on patterns of pairwise allele sharing, the authors argue that Bedouins occupy a basal position when compared to other non-African populations, suggesting that they are direct descendants from an early OOA group prior to their worldwide dispersal. Among the three recent large-scale genomic studies described in the previous section, Malaspinas et al. (2016) confirmed the result of Rasmussen et al. (2011) in a panel of 83 high-quality genomes from Australia, finding no evidence for different divergence times of Australians and other Eurasians from an ancestral OOA population. Mallick et al. (2016) used a phylogenetic framework incorporating population mixture events (a so-called admixture graph) to infer that genomes from Oceania can be adequately modeled without additional ancestry from a more deeply diverging modern lineage, again consistent with a single OOA. Nevertheless, contrary to those results, Pagani et al. (2016) do find evidence for the presence of low levels (>2%) of ancestry from an early OOA pulse in contemporary Papuans. The divergence time for this early expansion was inferred to be 120 ka, in line with archaeological evidence of the presence of AMH outside of Africa before 100 ka (Groucutt et al. 2015).

Whether the genetic diversity observed in present-day human populations is the result of one or two major waves of dispersals after the OOA dispersal remains more contentious. Rasmussen et al. (2011) reported an earlier divergence time estimate of the split of Aboriginal Australian from the ancestral Eurasian populations (62–75 ka) than those of East Asians from Europeans (25–38 ka), consistent with an early wave of dispersal into Oceania. This scenario is also supported by the demo-

graphic modeling in Malaspinas et al. (2016), who estimate that this early wave into Oceania diverged from other Eurasians at about 58 ka (95% CI 51–72 ka). However, Mallick et al. (2016) argue that such an early wave could have contributed at most a few percent of ancestry to present-day Oceanians based on admixture graph fitting. Unlike the SFS-based demographic modeling in Malaspinas et al. (2016), this approach assumes pulse-like mixture events without allowing for continuous gene flow between populations, which could be a contributing factor to this discrepancy.

Taken together, evidence from current whole-genome studies therefore strongly favor a single initial dispersal for all extant modern non-African populations, possibly including a small contribution of an earlier OOA dispersal into the ancestors of contemporary Oceanians. This was then likely followed later by multiple waves of dispersal across Asia, a model that is also consistent with results obtained from the analysis of ancient DNA from archaic hominins, discussed in the following section (fig. 1).

Admixture with Archaic Hominins

The publication of the draft genome of the Neanderthal in 2010 was one of the seminal moments in the history of next-generation ancient DNA studies (Green et al. 2010). The key finding of the study was that Neanderthals shared more genetic variations with modern humans from Eurasia than with Africans, suggesting a history of gene flow between Neanderthals and some groups of modern humans. Subsequent studies have confirmed and further elucidated the genetic legacy of admixture between AMH and archaic hominins, with current evidence pointing to at least three but possibly more distinct events.

All non-African modern human genomes investigated to date share a common signal of admixture with Neanderthals, harboring on average between 1% and 2% of Neanderthal-derived DNA (Prüfer et al. 2014; Sankararaman et al. 2016). Furthermore, Neanderthal DNA was already present in all early Eurasian AMH sequenced to date, including a 45,000-year-old Upper Paleolithic (UP) individual from Siberia (Ust'Ishim; Fu et al. 2014) as well as a 36,000-year-old UP individual from Russia (Kostenki 14; Seguin-Orlando et al. 2014; see fig. 2). The distribution of the length of segments of Neanderthal DNA in these genomes of UP individuals was used to infer the timing of admixture, which was estimated at between 50 and 60 ka (Fu et al. 2014; Seguin-Orlando et al. 2014). The combined evidence of the timing and shared pattern for all non-Africans suggests that the admixture likely happened in the ancestral population of all non-Africans and gives further support to the hypothesis of a single OOA dispersal of the ancestors of all extant non-African humans. Additional support also comes from the genome of an infant Neanderthal from Mezmaiskaya Cave in the Caucasus, which appears to be more closely related than European Neanderthals to the introgressed DNA found in non-African AMH (Prüfer et al. 2014). Despite this evidence for a shared early admixture event in non-Africans, population differences
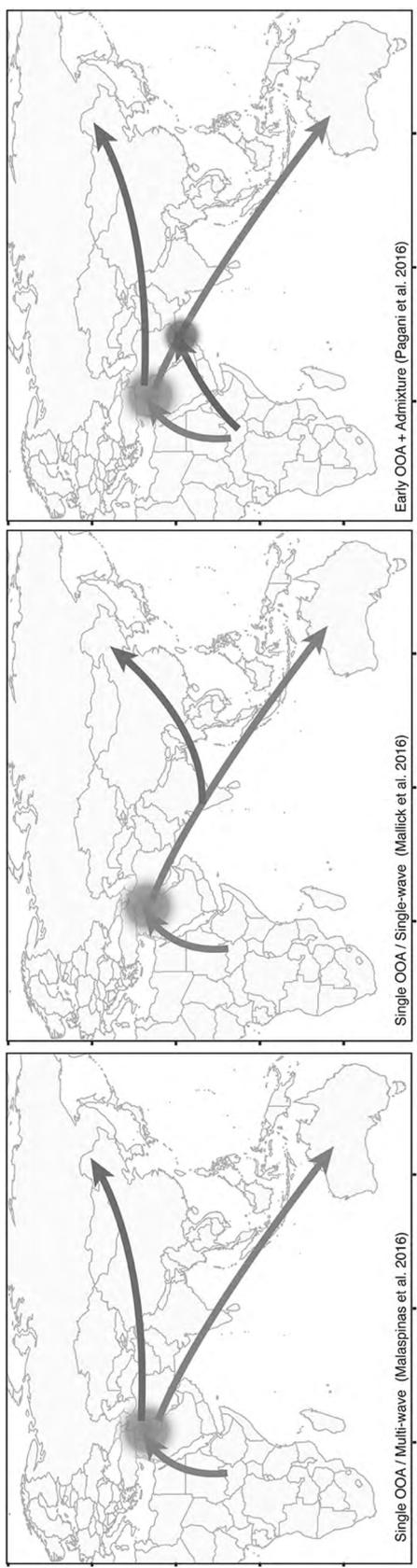
Figure 1. Models for OOA dispersals inferred from whole-genome sequences of modern humans. A color version of this figure is available online.
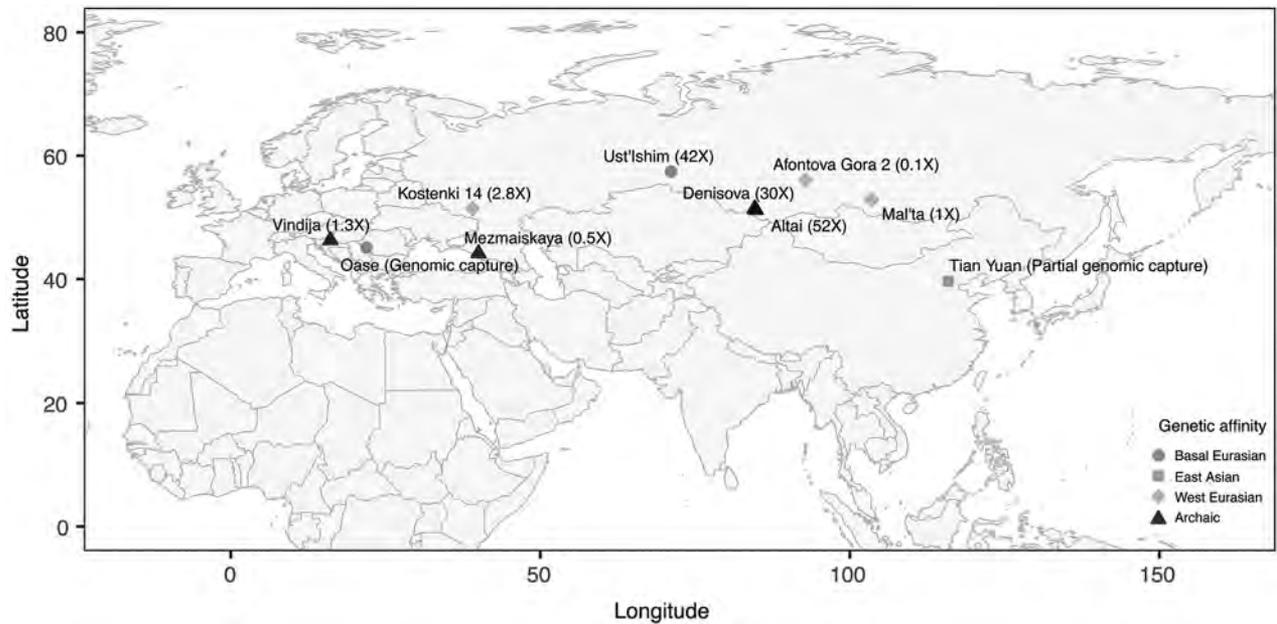
Figure 2. Map showing the location and genome coverage of early Eurasian fossils with ancient DNA data. Plot symbols and colors indicate the respective closest genetic affinities to contemporary populations. A color version of this figure is available online.

in the amount of surviving Neanderthal DNA exist. For example, populations of East Asian descent harbor an excess of ~20% of Neanderthal DNA compared to Europeans (Vernot and Akey 2014). Vernot and Akey showed that this excess is likely explained by an additional pulse of Neanderthal admixture in Asia rather than differences in the efficacy of natural selection between European and Asian populations after the initial shared admixture event (Vernot and Akey 2015). More recently, Vernot et al. (2016) reported evidence for at least three distinct gene flow episodes involving Neanderthals. It is important to note, however, that an alternative explanation of the lower amount of Neanderthal DNA in some populations would be a dilution of Neanderthal ancestry due to admixture with early humans with less or an absence of Neanderthal DNA (Lazaridis et al. 2016; Vernot and Akey 2015).

Present-day Oceanian populations show compelling evidence for additional admixture with a different archaic group represented only by the genome sequence obtained from a finger bone found in Denisova Cave in the Altai mountains of Siberia (Meyer et al. 2012; Reich et al. 2010). Initial studies suggested a contribution of up to 5% of Denisovan DNA to Oceanians, while more recent studies have yielded slightly lower estimates (1%–3%), a consequence of improvements in methods distinguishing Denisova and Neanderthal genomic segments (Sankararaman et al. 2016; Vernot et al. 2016). Subsequent to the publication of its genome, Denisovan ancestry was also reported in some Southeast Asian Island populations as well as at very low levels in mainland East Asian populations. This geographic pattern led Reich et al. (2011) to suggest a model where the gene flow occurred in Southeast Asia itself, implying a wide distribution of Denisovan-like groups across

Asia. More recently, Sankararaman et al. (2016) also found elevated levels of Denisovan ancestry in South Asians, including Tibetan populations that have been shown to harbor an adaptive haplotype of possible Denisovan origin (Huerta-Sánchez et al. 2014; Sankararaman et al. 2016). They also reported the first timing of the admixture event, ranging between 44 and 54 ka. Finally, the divergence between the Siberian and the introgressing Denisovans was also estimated to be relatively old (138–202 ka; Prüfer et al. 2014). These results make it plausible that the hominin species contributing DNA into AMH was actually quite distantly related to the specimen found in Denisova Cave, and possibly with a different geographic distribution. If the distribution of Denisova ancestry among modern human populations were the result of a single gene flow event in either South or Southeast Asia, the earlier inhabitants of those regions would, however, have to have been largely replaced by later migrations. The timing of the admixture and geographic restriction to mostly Oceanian populations also gives additional support to an early dispersal wave through Asia into Oceania, which would have to have diverged already by approximately 50 ka.

A striking result from a reanalysis of the genome of the Altai Neanderthal adds further complexities to early human demography in Asia. The initial analysis of the Altai Neanderthal genome revealed that it shows a closer genetic affinity to African populations than the Denisovan, which was suggested to be due to "superarchaic" gene flow from an unknown archaic hominin into Denisovans (Prüfer et al. 2014). Kuhlwilm et al. (2016) reanalyzed these data together with new partial genomic data from European Neanderthals, finding evidence for additional gene flow of modern human origin into the Altai Neanderthal.

The observed divergence of the introgressed genomic segments from contemporary human genomes suggests that this group represents an early divergence from the ancestors of AMH, even predating the deep divergence of South African hunter-gatherer groups. This opens the intriguing possibility of the presence of an earlier AMH group in Asia, maybe the result of a separate OOA migration that did not leave any descendants among present-day humans. While it is tempting to speculate a possible link to early AMH fossils from the region such as those discovered at Skhul and Qafzeh, only ancient DNA data from those will allow testing this hypothesis.

Other Dispersals through Asia

Early Dispersals into Europe and Siberia

The availability of ancient DNA data of early Europeans and Asians has again yielded surprising new insights into the population history of Asia. The oldest AMH genome sequenced to date was obtained from a 45,000-year-old Siberian individual from Ust'Ishim. Genomic analyses revealed a similar affinity to East Asians and Early Europeans (Fu et al. 2014), implying a basal position prior to their divergence for Ust'Ishim. A similar pattern was seen in an analysis of genomic data of a 37,000–42,000-year-old individual from Peştera cu Oase in Romania (Oase 1), which showed no closer affinity to any ancient or modern non-Africans, including Ust'Ishim (Fu et al. 2015; our fig. 1). Surprisingly, Oase 1 was also found to harbor a larger fraction of Neanderthal DNA than any other modern human individual (6%–9%). An analysis of the lengths of the chromosomal segments derived from Neanderthals suggests that this individual likely had a Neanderthal ancestor as recently as four to six generations before. The results from these studies imply that there were at least two distinct early dispersals through different parts of Asia prior to the arrival of the ancestors of present-day inhabitants. Both of these groups appear to have had negligible genetic contributions to subsequent Eurasians inhabiting their respective geographic regions and can therefore be considered "failed" onward dispersals descending from the initial OOA population (Fu et al. 2014, 2015).

Origins of Contemporary East Asians

The evidence from both modern and ancient DNA studies described in the previous sections suggests that the present-day inhabitants of East Asia predominantly derive their ancestry from a separate, possibly later dispersal than Oceanians. Divergence times obtained from demographic modeling between East Asians and Europeans by and large yield more recent times than the one between Europeans and the Aboriginal Australian genome (62–75 ka). Results from Gravel et al. (2011; 42–54 ka) as well as Schiffels and Durbin (2014; 20–40 ka) suggest a divergence no earlier than 50,000 years ago, whereas only Gronau et al. (2011) report an older divergence (62–76 ka). These timings are mirrored in more recent studies, ranging from ~42 ka

(95% CI 29–55 ka) for the European/East Asian split in Malaspinas et al. (2016) to 19–37 ka in Mallick et al. (2016). More recently, the availability of ancient DNA of well-dated early AMH representing postdivergence populations has allowed providing lower bounds on the divergence time. The 36,000-year-old UP individual Kostenki 14 (Russia) was found to show greater genetic affinity to present-day Europeans than to East Asians, demonstrating that the West Eurasian gene pool had already diverged from the East Asian ancestors by that time (Seguin-Orlando et al. 2014). Furthermore, Fu et al. (2013) recovered partial genomic data from a 40,000-year-old individual from Tianyuan (China) that showed closer affinity to East Asians than to West Eurasians. While the amount of data in this study is limited to a single chromosome, their result does suggest that the ancestors of present-day East Asians had already split from West Eurasians by at least 40 ka.

The Far Northeast and into the Americas

The question of the initial peopling of the Americas has received considerable attention, at the same time also providing insights about modern human presence in far Northeast Siberia. Gutenkunst et al. (2009) estimated the divergence between East Asians and Native Americans at 32–54 ka, whereas Schiffels and Durbin (2014) found evidence for a relatively clean split between East Asians and Native Americans at around 20 ka. A more recent study by Raghavan et al. (2015) investigated the divergence between Native Americans and a variety of East Asian and Siberian groups. They obtain consistent divergence times of ~23 ka for all comparisons, albeit with varying rates of subsequent gene flow. They conclude that ancestors of present-day Native Americans arrived no earlier than 23 ka in far Northeast Siberia. A lower bound on the arrival time can be set from the subsequent divergence between the two main Native American branches, which was estimated at ~13 ka, also supported from ancient DNA data of a 13,000-year-old individual from a Clovis burial site (Rasmussen et al. 2014).

The publication of the genome from a 24,000-year-old UP individual from Mal'ta (Siberia) revealed an unexpected ancient genetic link between Native American and European populations (Raghavan et al. 2014). It was estimated that between 14% and 38 % of the ancestry of Native Americans derives from this group, which is genetically closer to Western Eurasians than to East Asians. This suggests that descendants of early West Eurasians subsequently reached as far as south-central Siberia in their dispersals. Genomic data from another individual dated at 17,000 years ago showed a similar pattern, indicating that their descendants occupied the region throughout the Last Glacial Maximum (LGM; Raghavan et al. 2014). While the present-day occupants of the region show different, mostly East Asian–related ancestry, a recent genomic study on local Bronze Age groups suggests that remnants of these early West Eurasian groups may have still been present in the region until the early Bronze Age (Allentoft et al. 2015).

Another surprising genetic link was discovered more recently, relating some Amazonian groups to peoples from the Andaman Islands and Oceania (Raghavan et al. 2015; Skoglund et al. 2015). It is currently not known whether this contribution derives from a dispersal predating the main migration into northeast Asia and the Americas discussed above or later gene flow resulting in a genetically structured ancestral Native American population. While there is also a possibility of an even later gene flow postdating the main migration, the geographic restriction to indigenous groups from the Amazon region in South America makes this scenario less likely. Regardless of the actual location and timing of the admixture event, these results suggest large-distance dispersals of multiple, deeply diverged groups of AMH across Asia during the Pleistocene.

Open Questions and Future Directions

While the availability of population genomic data from diverse modern and especially ancient samples has led to a wealth of new insights about human population history in Asia and the rest of the world, these data have also opened an array of exciting follow-up questions and directions for future research, some of which are outlined below.

Who Were the Earliest Modern Humans in Asia?

While current evidence from genomic data is favoring a single-wave OOA model for the ancestors of present-day humans, it is not sufficient to resolve the question of how those people relate to the earliest AMH fossils outside of Africa. The ongoing improvements in ancient DNA techniques make a successful extraction of genomic data from early OOA sites in East and Southeast Asia (Bae et al. 2014; Demeter et al. 2012; Liu et al. 2010, 2015; but see Michel et al. 2016) a real possibility. The high levels of genetic differentiation between present-day African and non-African populations should in principle allow addressing this question with even limited amounts of genetic data.

Who Were the Denisovans That Interbred with Modern Humans?

The timing and especially the location of the admixture of Denisovans and modern humans remains essentially unknown. It is reasonable to predict that an increasing amount of genomic data of other archaic hominin fossils from around Asia will become available in the near future, which will allow a much more fine-scale investigation of the interaction between humans and these as of yet enigmatic hominins.

How Many Early Dispersals Were There across Asia, and What Was the Genetic Makeup of the Groups Involved?

While data on ancient West Eurasians is accumulating rapidly, genomic information from early AMH in East Asia is still sparse. So far, the best proxy for an ancestral East Asian population comes from a single chromosome from a 40,000-year-old individual from Tianyuan Cave in China. If ancient DNA retrieval from other nontemperate regions like Southeast Asia is feasible, it will be possible to investigate how many different groups were migrating across the continent and to which extent they contributed to its current inhabitants.

Novel Analytical Methods

Genetic data is a transformative tool for investigating human population history, but like any other tool it suffers from limitations and possibility for biases. To obtain a more complete picture of human demographic history, novel methods are needed that integrate data across multiple fields, combining evidence from diverse sources including genetic, morphological, and paleoclimatic data (Eriksson et al. 2012).

Concluding Remarks

The explosion in population genetic data from both extant and ancient humans has yielded fascinating and unexpected new insights into our past. A major lesson emerging from these studies is a newfound appreciation of the complexities of the history of our species. It is now clear that failed dispersals and large-scale population replacements and admixture, as well as repeated colonization of geographic regions, were likely the norm rather than the exception throughout much of human history (Allentoft et al. 2015; Fu et al. 2015, 2016; Lazaridis et al. 2016). The rapid progress of ancient DNA research in particular will continue to offer us unexpected surprises upending current paradigms. While the speed of this progress can be dizzying and this research is sometimes rife with controversy, it will ultimately reward us with a much richer picture of our history.

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Testing Modern Human Out-of-Africa Dispersal Models Using Dental Nonmetric Data

by Hugo Reyes-Centeno, Hannes Rathmann, Tsunehiko Hanihara, and Katerina Harvati

The mode and timing of the dispersal of modern humans out of Africa and into Eurasia has important implications for the genetic and phenotypic structure of extant human populations. However, no consensus exists on the number, geographic route, and chronology of dispersal events. In this paper, we review competing dispersal models and evaluate their spatial and temporal predictions against geographical distances between population samples and measures of population differentiation derived from nonmetric dental data. The implications of our results for the modern human expansion into Asia are discussed.

The mode and timing of modern human expansion out of Africa continues to be intensely debated, with various competing models proposed for the number, geographical route, and chronology of dispersal events. While substantial efforts have been made to formulate out-of-Africa dispersal models in a multidisciplinary fashion, some lines of evidence often conflict with others, particularly when disparate methods are used. In physical anthropology, skeletal morphometric data has been used to test competing dispersal hypotheses by summarizing the morphological variation between populations and comparing it with the geographical distance between them, as

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would be predicted by different evolutionary and dispersal scenarios (e.g., Hubbe, Neves, and Harvati 2010; Pinhasi and von Cramon-Taubadel 2009; Reyes-Centeno et al. 2014). Some population genetic studies have similarly applied this approach to address competing out-of-Africa hypotheses, summarizing the allele frequency variation between populations and predicted geographical separation along hypothetical out-of-Africa dispersal routes (Ghirotto, Penso-Dolfin, and Barbujani 2011; Reyes-Centeno et al. 2014; Tassi et al. 2015). Work based on both the skeletal and genomic lines of evidence has lent support to a model in which modern humans expanded out of Africa as early as the terminal Middle Pleistocene (MP) and dispersed in two waves into Asia, initially into Australasia along a southern route and later into northern Eurasia along a northern route (Reyes-Centeno et al. 2014). Such a model, however, is in contrast to inferences drawn from phylogeographic models of uniparental genetic loci, namely mitochondrial and Y chromosome DNA studies, which support a single dispersal out of Africa (e.g., Mellars et al. 2013; Oppenheimer 2012).

Studies of competing out-of-Africa dispersal models are mainly based on an evolutionary model in which modern humans experienced "cascading bottlenecks" as populations successively grew and spread across the world, iteratively founding new groups as they dispersed. This demographic process was first hypothesized on the basis of the observation that levels of intrapopulation genetic diversity decreased as a function of geographic distance from Africa—a pattern that was attributed to a loss of diversity after each founding event (Eller 1999; Harpending and Rogers 2000). In such a model, each new founding population represents a subset of the diversity of the ancestral group, in a chain of serial founder occurrences that can be traced back to the exit of anatomically modern humans out of Africa. Various studies have since confirmed this pattern, both from genomic allele frequency

data (e.g., Li et al. 2008; Prugnolle, Manica, and Balloux 2005; Ramachandran et al. 2005) and skeletal morphometric data (Betti et al. 2009; Betti, von Cramon-Taubadel, and Lycett 2012; Manica et al. 2007; von Cramon-Taubadel and Lycett 2008). Thus, skeletal and genomic lines of evidence can provide independent and complementary information on the dispersal pattern of modern humans. Interestingly, the pattern of decreasing intrapopulation diversity with distance from Africa has also been observed for dental nonmetric data (Hanihara 2008). The finding is consistent with early comparative studies of dental nonmetric traits suggesting that archaeological and extant sub-Saharan Africans retain an ancestral plesiomorphic dental morphology relative to other modern human populations and Pleistocene hominins (Irish 1998; Irish and Guatelli-Steinberg 2003).

There are many reasons to use dental evidence for reconstructing population history. Teeth are relatively well preserved in archaeological and paleontological contexts. As such, they are an essential line of evidence for understanding the structure and diversity of modern human variation across time and space, particularly when other skeletal elements are unavailable or poorly preserved (see, e.g., Benazzi et al. 2011; Harvati et al. 2015). Their better state of preservation compared with other skeletal elements results in teeth being recovered in larger numbers and therefore providing larger samples that result in more robust statistical analyses. Furthermore, dental morphology is generally considered to be heritable, selectively neutral, and evolutionary conservative (Hillson 1996; Scott and Turner 2000; but see, e.g., Mizoguchi 2013). According to Scott and Turner (2000), the worldwide variation in human dental morphology was primarily generated by random processes of founder effects and genetic drift. Developmentally, dental crowns form early in the life of an individual; thus, after full formation, they are subject to morphological change only in relation to abrasion or attrition related to diet, behavior, and pathology. Moreover, the heritability of dental nonmetric traits is comparable to that of other cranial regions (Biggerstaff 1970, 1973; Carson 2006; Martínez-Abadías et al. 2009; Mizoguchi 1977; Scott and Yap Potter 1984; Šešelj, Duren, and Sherwood 2015). Dental nonmetric traits have been considered as analogous to genetic alleles to the extent that they vary in frequency across populations (Hallgrímsson et al. 2004; Hanihara 2008), providing an intuitive comparison to genomic data. As with the use of skeletal morphometrics, dental nonmetric traits can therefore provide an additional line of evidence in testing competing out-of-Africa dispersal models. They have previously been used in making inferences on Pleistocene hominin dispersal (e.g., Martinón-Torres et al. 2007) and, more recently, in testing competing models of modern human worldwide expansion (Hanihara 2013).

Utilizing metric and nonmetric dental data, Hanihara (2013) tested competing models of the peopling of East Asia. In doing so, each competing hypothesis was modeled under three dispersal scenarios related to the out-of-Africa expansion preceding the colonization of East Asia. The models differed in whether the out-of-Africa expansion consisted of colonization along a Levantine northern route, an Arabian southern route, or both. The study design consisted of assessing the correlation between intraregional dental variation and geographical distance from Africa as well as the relationship between interregional variation and geographical distance separating populations. The results were ambiguous because the correlations using nonmetric data differed from those using metric data, not clearly supporting any of the models being tested. Despite this, results were consistent in showing stronger support for the models that featured a southern route expansion out of Africa. Interestingly, in the analysis of interregional variation and geographical distance between populations, correlation values were substantially higher for nonmetric data than for metric data. Therefore, in this study, we focus on dental nonmetric data to revisit the test of competing dispersal models out of Africa and into Asia.

We draw from Hanihara's (2008) large nonmetric dental data set, concentrating on populations from Asia and Australia, to help elucidate the colonization of those regions by modern humans. In addition, we extend the evolutionary analytical framework by using genomic data that provide estimates for both the effective population size of ancestral populations and their population divergence time. We compare our results to those of the recent skeletal and genomic studies that apply a similar study design (Reyes-Centeno et al. 2014; Tassi et al. 2015) and discuss our results in light of the anatomically modern human fossils from early Late Pleistocene southern China (Bae et al. 2014; Liu et al. 2015).

Material and Methods

Populations and Dental Nonmetric Data

We selected populations from Africa, Asia, and Australia of a large dental nonmetric traits data set previously collected by one of us (T.H.; Hanihara 2008). Not every dental trait could be scored for each individual because of poor preservation or pathology; thus, our data set has large amounts of missing data. To address this problem, we grouped individual populations into metapopulations in order to have adequate data coverage across all traits. The metapopulations are similar to those used by earlier studies (Hanihara 2008, 2013), with adjustments that allowed us to adequately test the competing dispersal models. In particular, we separated populations from India into northern and southern metapopulations consisting primarily of Indo-European speakers and Dravidian speakers, respectively. Likewise, we separated Southeast Asian populations into a mainland group and an island group. In total, the data set for this study comprised nine metapopulations ($n = 4,303$ individuals; table 1).

Fifteen dental nonmetric traits were scored on the permanent dentition of recent modern human specimens from museum and institutional collections following procedures detailed in Hanihara (2008) by one of us (T.H.). These traits represent the

Table 1. Populations, sample sizes (N), effective population size (N_e), and geographical location

Metapopulation	N	N_e [a]	Local populations[b]	Lat.	Long.
Africa	1,058	11,075	Cameroon (39); Congo (25); Ethiopia (6); Gabon (101); Ghana Ashanti (80); Guinea (3); Kenya (160); Lesotho (2); Liberia (7); Malawi (9); Mozambique (3); Nigeria (25); Nigeria Ibo (153); Rwanda (5); Sierra Leone (5); Somalia (81); South Africa (82); South Africa Khoi-san (33); South Africa Zulu (34); Tanzania (151); Uganda (14); West Africa (40)	9.02	38.47
Australia	371	4,435	Murray River (79); New South Wales (82); Northern Territory (13); Queensland (21); South Australia(138); Victoria (14); Western Australia (24)	−32.56	141.39
India, north	302	8,181	Bengal (135); Bihar (24); Kashmir (3); Nepal (38); Northwest Province (34); Orissa (5); Punjab (63)	27.17	83.19
India, south	165	6,467	Madras (112); Malabar Coast (21); Mysore (15); Sri Lanka (1); Sri Lanka Veddah (16)	11.98	79.49
Melanesia	899	3,581	Fiji (66); New Britain (215); New Caledonia (44); New Guinea (317); New Ireland (55); Solomon (99); Torres Strait (103)	−7.16	150.32
Northeast Asia	356	6,232	Japan (71); Mongolia (224); Northern China (61)	45.76	114.24
Southeast Asia, island	578	3,752	Andaman Islands (85); Borneo (111); Java (92); Nicobar Islands (24); Philippine Aeta and Agta "Negritos" (54); Philippines (171); Sumatra (41)	6.76	110.52
Southeast Asia, mainland	352	5,414	Cambodia (8); Laos (51); Malaysia Peninsula (68); Myanmar (130); Thailand (60); Vietnam (35)	14.10	100.07
West Asia	222	7,469	Bedouin (10); Iraq (45); Israel (38); Lebanon (3); Palestine (67); Syria (22); Turkey (37)	34.16	41.23

[a] Values are point estimates derived from Tassi et al. (2015) and weighted with reference to the sample sizes of the local populations within a metapopulation.

[b] Local population sample size in parentheses.

discrete morphology of dental crowns, including shoveling of the lingual fossa in incisors, accessory cusps in premolars, and crests and cusps in molars (Hanihara 2008; table 2). Most (14 of 15) traits can be related to or directly follow the widely used Arizona State University Dental Anthropology System (ASUDAS; Turner 1991). Dental traits were originally scored in an ordinal, graded fashion and were subsequently dichotomized into categories of presence or absence (see Hanihara 2008 for dichomotization break points). Thus, the final data set consisted of binary numerical information (i.e., 0 = absent, 1 = present) on dental nonmetric traits for each sampled individual. Using binary information reduces potential observer error and simplifies the data set so that the frequencies of the traits can be used in further statistical analyses.

Biological Distance Measure

We calculated the phenotypic distance between populations using the **R** matrix approach, which allows for the assessment of relationships between populations while correcting for the confounding effects of genetic drift. The method was originally developed for gene frequency data (Harpending and Jenkins 1973; Harpending and Ward 1982) and was later modified for use with skeletal morphometric data (Relethford and Blangero 1990; Relethford, Crawford, and Blangero 1997). We applied the **R** matrix method for discrete, nonmetric traits developed by Konigsberg (2006). This procedure consists of first calculating Mahalanobis-type distances between populations, accounting for intercorrelations between traits to avoid overrepresenting variation from characters that co-occur (Bedrick, Lapidus, and Powell 2000; Konigsberg 1990). Correlations are

determined by a matrix of pooled within-population tetrachoric correlation coefficients. The resulting pseudo-Mahalanobis matrix is then translated into a **C** codivergence matrix and from that into an **R** matrix. In addition, we considered a heritability of $h^2 = 0.5$, reflecting the approximate average of various heritability estimates of dental nonmetric traits based on twin and family studies (Scott and Turner 2000). Likewise, we weighted the **R** matrix with estimates of population size to account for effects of genetic drift on small populations (Relethford, Crawford, and Blangero 1997). We used point values of effective population size, N_e, derived from published data of levels of genetic linkage disequilibrium (table 1), considering allele frequencies for up to ~370,000 single-nucleotide polymorphisms (SNPs; Tassi et al. 2015). In deriving N_e values, we first matched the populations sampled by Tassi et al. (2015) with our dental populations. Then, we weighted the N_e value of our metapopulations with respect to the sample sizes of our dental subpopulations. This procedure was particularly important when the metapopulations consisted of subpopulations with a wide N_e range. For example, for the island Southeast Asian metapopulation, the Andaman Islanders population has an N_e point value of 1,521, whereas the Sumatran population has a N_e point value of 4,843. Thus, weighting the subpopulation N_e values provides a more realistic N_e average for our metapopulations. Finally, the **R** matrix was converted into a matrix summarizing the pairwise population distance values while removing the differential effects of genetic drift (Relethford 1996; Relethford, Crawford, and Blangero 1997). These final values, P_{ST}, are analogous to F_{ST} in population genetics, reflecting the apportionment of phenotypic or genetic variation between populations (Leinonen et al. 2013; Roseman and

Table 2. Dental nonmetric data summary

Dental trait	No. individuals scored (% with trait)								
	AFR	AUS	INN	INS	MEL	NEA	SEI	SEM	WAS
Shoveling (UI1)	118 (51.69)	78 (65.38)	43 (58.14)	22 (59.09)	110 (72.73)	129 (98.45)	111 (75.68)	34 (85.29)	24 (41.67)
Double shoveling (UI1)	133 (.75)	83 (1.20)	51 (1.96)	29 (.00)	110 (5.45)	124 (25.00)	108 (8.33)	40 (15.00)	26 (.00)
Shoveling (UI2)	179 (54.19)	131 (64.89)	60 (56.67)	38 (81.58)	165 (73.33)	156 (91.67)	136 (79.41)	44 (79.55)	30 (60.00)
Premolar accessory cusp (UP1)	478 (4.81)	96 (13.54)	106 (3.77)	60 (5.00)	244 (13.52)	190 (39.47)	267 (20.60)	128 (17.97)	75 (6.58)
Premolar accessory cusp (UP2)	468 (7.91)	92 (39.13)	96 (7.29)	55 (5.45)	239 (27.20)	199 (10.55)	254 (12.99)	133 (9.77)	80 (6.25)
Carabelli's cusp (UM1)	821 (17.17)	199 (5.53)	221 (10.41)	106 (14.15)	727 (15.96)	274 (7.66)	487 (15.20)	298 (15.44)	172 (30.81)
Hypocone (UM2)	867 (82.24)	317 (88.33)	240 (71.25)	143 (69.23)	695 (88.20)	250 (72.80)	446 (76.01)	284 (81.69)	182 (67.58)
Central ridge (LP1)	348 (69.83)	84 (91.67)	66 (78.79)	41 (73.17)	173 (86.71)	172 (71.51)	206 (81.07)	75 (82.67)	23 (56.52)
Sixth cusp (LM1)	351 (22.22)	101 (64.36)	90 (6.67)	55 (14.55)	327 (44.34)	169 (32.54)	251 (24.30)	114 (23.68)	31 (9.68)
Seventh cusp (LM1)	461 (34.27)	175 (6.29)	148 (10.14)	75 (8.00)	444 (10.59)	199 (7.04)	305 (8.85)	156 (10.26)	45 (15.56)
Deflecting wrinkle (LM1)	290 (44.83)	84 (65.48)	67 (17.91)	45 (13.33)	284 (54.58)	110 (40.91)	221 (23.08)	94 (38.30)	32 (9.38)
Protostylid (LM1)	395 (1.52)	126 (8.73)	121 (4.13)	62 (3.23)	384 (3.65)	147 (9.52)	253 (9.88)	128 (8.59)	43 (.00)
Distal trigonid crest (LM1)	442 (.68)	137 (1.46)	141 (.71)	68 (1.47)	437 (5.72)	206 (2.43)	295 (3.05)	144 (.69)	44 (.00)
Hypoconulid (LM2)	455 (73.63)	211 (94.79)	124 (50.00)	74 (37.84)	387 (71.83)	174 (79.31)	301 (59.47)	137 (62.04)	40 (35.00)
Sixth cusp (LM2)	360 (14.17)	115 (40.87)	94 (2.13)	65 (3.08)	314 (11.15)	145 (9.66)	277 (11.19)	120 (7.50)	36 (.00)

Note. Dental trait abbreviations are with reference to the tooth type and dental arcade position. AFR = Africa; AUS = Australia; INN = India, north; INS = India, south; LM = lower molar; LP = lower premolar; MEL = Melanesia; NEA = Northeast Asia; SEI = Southeast Asia, island; SEM = Southeast Asia, mainland; UI = upper incisor; UM = upper molar; UP = upper premolar; WAS = Western Asia.

Weaver 2007). All calculations for arriving at P_{ST} were programmed in R, version 3.1.1 (Ihaka and Gentleman 1996).

Geographical Out-of-Africa Dispersal Models

We modeled out-of-Africa dispersal scenarios using geodesic distance, G, between populations along hypothetical dispersal routes (fig. 1). We used previously assigned population latitude and longitude coordinates (Hubbe, Hanihara, and Harvati 2009) in determining a geographical location to each metapopulation. In doing so, we first weighed the latitude and longitude values by the sample size of each subpopulation with respect to the total sample size for the metapopulation (table 1; fig. 1). In the case of the sub-Saharan African metapopulation, the location was set to Addis Ababa, Ethiopia, following previous studies on the expansion out of Africa (e.g., Ramachandran et al. 2005; Reyes-Centeno et al. 2014). In the case of the island Southeast Asia metapopulation, the weighted-averaged location is in present-day sea, within the Sunda continental shelf.

To compare our results to those of previous studies (Reyes-Centeno et al. 2014, 2015), we calculated predicted geographic distance for four dispersal models. The first is an eastern expansion (EE) model, where a single dispersal from Africa into Asia via the Levant follows simple terrestrial migration routes, avoiding major geographic barriers and spanning primarily along a latitudinal axis (Liu et al. 2006; Pagani et al. 2015; Ramachandran and Rosenberg 2011). The second is a "beachcomber" single-dispersal (BSD) model, where expansion into Asia occurs primarily along the Indian Ocean rim (Oppenheimer 2012). The third is a multiple dispersals (MD) model, which stipulates that a first dispersal from Africa was followed by a subsequent dispersal (Mirazón Lahr and Foley 1994). In this model, the first dispersal into Southeast Asia and Australia follows a southern coastal route, while the latter dispersal into northern Eurasia follows a northern Levantine route. The fourth model, multiple dispersals and Australo-Melanesian isolation (MDI), considers a similar geographical scenario, with only extant Australo-Melanesians considered to be descendants of the first dispersal, having remained relatively isolated since the ini-
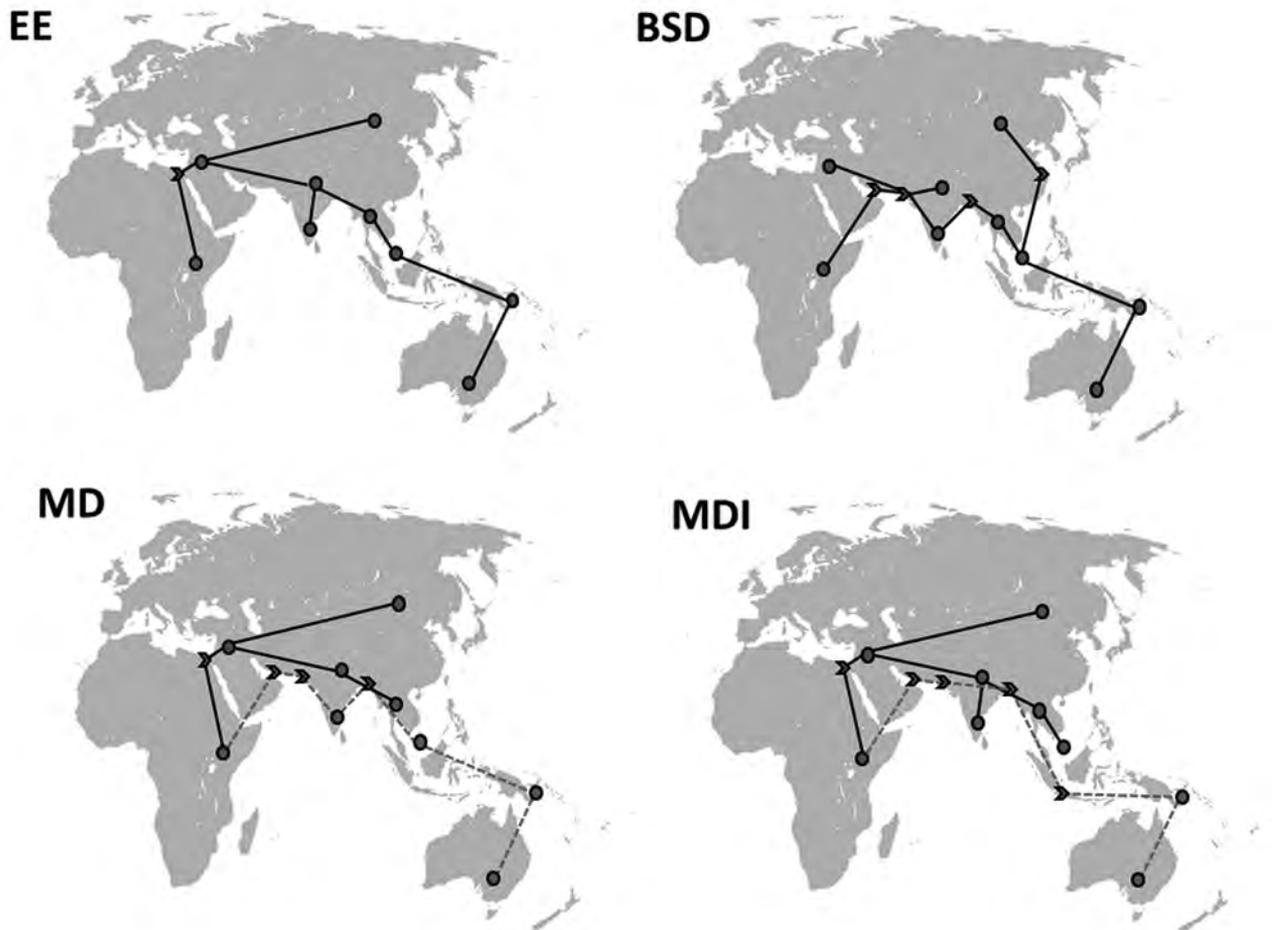
Figure 1. Out-of-Africa dispersal models. Points are assigned geographical locality of metapopulations. Lines indicate hypothetical dispersal routes, and arrows are assigned to waypoints. In models MD and MDI, dashed/blue lines and dots represent an early dispersal. BSD = beachcomber arc single dispersal; EE = eastward expansion single dispersal; MD = multiple dispersals; MDI = multiple dispersals and Australo-Melanesian isolation. A color version of this figure is available online.

tial occupation of the region (Rasmussen et al. 2011). We amended this model to reflect the current consensus that riverine corridors would have served as more likely routes of dispersal through India, rather than a coastal route along the Indian Ocean rim (Boivin et al. 2013; Field and Mirazón Lahr 2005; Field, Petraglia, and Lahr 2007). The models are broadly comparable to those previously tested with this data set (Hanihara 2013).

Pairwise *G* along hypothetical dispersal routes was calculated using the PASSaGE software (Rosenberg and Anderson 2011), assuming a spherical shape for Earth and a radius of 6379.336847 km. Six waypoints (fig. 1) were used to model the specific dispersal routes of each model. Waypoint latitude and longitude coordinates included the following: Cairo (30.6, 31.24), Dubai (25.27, 55.31), Karachi (24.89, 67.03), Dhaka (23.71, 90.41), Jakarta (−6.21, 106.84), and Shanghai (31.23, 121.47). A matrix summarizing the pairwise *G* was constructed for each model. In addition, we constructed a control **G** matrix that connected all populations without regard to hypothetical dispersal routes. In other words, no waypoints were used, and all populations were connected to each other.

Population Divergence and Chronology of Out-of-Africa Dispersal Models

Because each of the dispersal hypotheses differs with respect to the timing of dispersal out of Africa and colonization of Asia, a chronological framework is necessary for testing competing models. We accounted for this using two approaches. The first was a model-independent approach estimating pairwise population divergence time, *T*, from published genomic data. The second was a model-dependent approach whereby hypothetical dates within the geographical space of a metapopulation could be used to construct a dissimilarity matrix of pairwise chronological separation, **C**. In the first approach, we calculated *T* on the basis of N_e estimates (table 1) and averaged genetic distance F_{ST} values, as reported in Tassi et al. (2015). This calculation assumes that differentiation of two populations, as represented by F_{ST}, is directly proportional to the time, *T*, elapsed since their separation and inversely proportional to their effective population sizes, N_e (Reyes-Centeno et al. 2014; Tassi et al. 2015). A pairwise **T** matrix was constructed in units of generations, rep-

resenting the pairwise divergence time of our metapopulations. In the second approach, we compiled from the literature approximate dates on hypothetical dispersal out of Africa and occupation in the geographical regions of our metapopulation samples according to each model (see table 3 for dates and references). We calculated the Euclidean distance between dates and constructed a chronology matrix of pairwise *C* values. To explore how the model-dependent dates correspond to the genomic-derived estimates of population divergence, we calculated pairwise *T* in calendar years. We used an intergenerational time of 29 years, following an approximation across sexes in recent hunter-gatherer societies (Fenner 2005).

Testing Out-of-Africa Dispersal Models

In testing the competing dispersal models, we used the aforementioned P_{ST}, **G**, **T**, and **C** matrices for statistical analyses using Mantel tests (Mantel 1967). First, we evaluated the significance of the association between the P_{ST} and **G** matrices in a simple Mantel test. Then, we tested the association between the P_{ST} and **G** matrices while holding either the model-independent **T** or the model-dependent **C** matrices constant in a partial Mantel test (Smouse, Long, and Sokal 1986). The Mantel test procedures were conducted in the XLSTAT commercial software (Addinsoft SARL) with 10,000 permutations to assess correlation significance in all cases. When evaluating our results, we applied a Bonferroni correction accounting for multiple models testing ($\alpha = 0.01$). We applied a Dow-Cheverud test (Dow and Cheverud 1985) to statistically assess whether the dispersal models were better associated to dental nonmetric variation than was the control model.

Results

Table 4 reports the results of our **R** matrix and corresponding P_{ST} matrix values. Positive pairwise values in the **R** matrix indicate population pairs that are more similar to each other than on average, relative to all the population samples. Negative values indicate population pairs that are less similar to each other than on average. Values along the diagonal reflect how distant each population is from the centroid of the pooled samples. In this case, the Australian and Northeast Asian meta-

Table 3. Dispersal models chronology

Model	Chronology, ka									Reference
	AFR	AUS	INN	INS	MEL	NEA	SAI	SAM	WAS	
EE	56	40	45	45	40	36	40	40	45	Liu et al. (2006)
BSD	75	55	65	70	55	40	60	65	72	Oppenheimer (2012)
MD	80	55	30	70	60	25	65	30	45	Lahr and Foley (1994)
MDI-MP	130	50	45	45	50	40	40	45	45	Petraglia et al. (2010)
MDI-LP	68.5	50	31.5	31.5	50	25	30	31.5	38	Rasmussen et al. (2011)

Note. AFR = Africa; AUS = Australia; BSD = beachcomber arc single dispersal; EE = eastward expansion single dispersal; INN = India, north; INS = India, south; LP = Late Pleistocene; MD = multiple dispersals; MDI = multiple dispersals and Australo-Melanesian isolation; MEL = Melanesia; MP = Middle Pleistocene; NEA = Northeast Asia; SEI = Southeast Asia, island; SEM = Southeast Asia, mainland; WAS = Western Asia.

Table 4. Population differentiation

	Pairwise **R** matrix and P_{ST} values by metapopulation								
	AFR	AUS	INN	INS	MEL	NEA	SAI	SAM	WAS
AFR	.072	.007	−.009	−.014	−.028	−.065	−.031	−.024	.011
AUS	.214	.147	−.023	−.031	.069	.001	−.002	−.008	−.072
INN	.194	.189	.031	.013	−.017	−.027	−.004	−.008	.019
INS	.199	.191	.047	.035	−.010	−.024	.003	−.013	.027
MEL	.227	.061	.115	.096	.080	.026	.009	.001	−.039
NEA	.456	.259	.258	.240	.163	.158	.036	.051	−.054
SAI	.206	.122	.064	.046	.050	.117	.026	.019	−.012
SAM	.221	.151	.093	.094	.078	.097	.023	.040	−.022
WAS	.176	.316	.074	.058	.191	.354	.116	.159	.068

Note. Values along the diagonal and above the diagonal are **R** matrix values. Values below the diagonal are pairwise P_{ST} values. AFR = Africa; AUS = Australia; INN = India, north; INS = India, south; MEL = Melanesia; NEA = Northeast Asia; SEI = Southeast Asia, island; SEM = Southeast Asia, mainland; WAS = Western Asia.

populations are most distant from the centroid. Since all values along the diagonal of the **R** matrix are positive, similarity in dental nonmetric traits is greater between pairs of individuals than between individuals in different populations. P_{ST} values ranged between 0.023 for the island Southeast Asia and mainland Southeast Asia metapopulation pair to 0.456 for the African and northeast Asian metapopulation pairs. The former represents the metapopulations most similar to each other, whereas the latter represents the most dissimilar. Table 5 reports the population divergence estimates in units of generation and transformed into calendar years. The largest values are for the Africa-Melanesia pair, followed by the Africa-Australia pair.

In testing the competing dispersal models, the first Mantel test analysis between the **P**$_{ST}$ and **G** matrices resulted in statistically significant correlation values for the control, EE, and BSD models (table 6). A Dow-Cheverud test of the control model against all of the other models was significant only for the BSD model ($r = -0.361, P = .044$). In the second analysis, the Partial Mantel tests using either the model-independent **T** or model-dependent **C** matrices resulted in statistically significant correlation values for only the BSD model, following Bonferroni correction (table 6).

Discussion

In testing competing dispersal models for the colonization of Asia and Australia, our analysis yielded support for the BSD model. This is in agreement with Hanihara's (2013) previous analyses, where a model that consisted of a single dispersal out of Africa and into Asia along coastal routes had a higher correlation to dental nonmetric traits than did other dispersal models. These results, on the other hand, are in conflict with recent studies supporting the MDI-MP model when applying a similar methodological framework to genomic and cranial phenotype data (Reyes-Centeno et al. 2014, 2015). They are also contrary to various other recent genome-wide, autosomal DNA data sets that suggest multiple waves of dispersal into Asia (e.g., Di, Sanchez-Mazas, and Currat 2015; Rasmussen et al. 2011). Nevertheless, our results agree with various genetic studies of uniparental loci. Indeed, the BSD model was mainly constructed from uniparental genetic data and especially from the well-resolved typology of mitochondrial DNA (mtDNA) haplogroups (Oppenheimer 2012). Notably, a single dispersal hypothesis is also consistent with interpretations of studies on mtDNA retrieved from fossil Eurasian specimens (Fu et al. 2013; Posth et al. 2016). Our results must therefore be

Table 5. Population divergence time

	Pairwise divergence values								
	AFR	AUS	INN	INS	MEL	NEA	SAI	SAM	WAS
AFR	0	3,450	2,508	2,300	3,829	3,123	2,859	2,878	2,368
AUS	100,049	0	1,533	1,290	695	1,580	1,383	1,493	1,595
INN	72,738	44,451	0	44	55,560	28,520	24,674	20,926	167
INS	66,696	37,403	1,289	0	44,139	25,776	22,246	19,506	209
MEL	111,032	20,152	1,916	1,522	0	1,735	44,442	1,750	1,920
NEA	90,554	45,828	983	889	50,322	0	6,514	4,815	1,156
SAI	82,915	40,116	851	767	1,532	225	0	74	1,033
SAM	83,466	43,307	722	673	50,762	166	2,133	0	919
WAS	68,686	46,261	4,841	6,059	55,686	33,522	29,964	26,641	0

Note. Values above the diagonal are in units of generations. Values below diagonal are in calendar years (BP), assuming an intergenerational time of 29 years. All values are rounded to the nearest whole number. AFR = Africa; AUS = Australia; INN = India, north; INS = India, south; MEL = Melanesia; NEA = Northeast Asia; SEI = Southeast Asia, island; SEM = Southeast Asia, mainland; WAS = Western Asia.

Table 6. Mantel test results

Matrices	*r* (*P*), by dispersal model				
	Control	EE	BSD	MD	MDI
P$_{ST}$ – G	.545 (<.001)*	.525 (.002)*	.745 (<.001)*	.083 (.631)	.167 (.330)
P$_{ST}$ – G, T	.302 (.083)	.361 (.042)	.641 (<.001)*	.100 (.553)	.084 (.624)
P$_{ST}$ – G, C	...	.407 (.020)	.554 (.001)*	.001 (.983)	.256 (.130)[a]
					−.029 (.864)[b]

Note. Mantel test values are Pearson correlation coefficient, *r*, rounded to the third decimal place and two-tailed probability, *P*, after 10,000 permutations. Simple Mantel tests are of empirical population distances derived from dental nonmetric data, P$_{ST}$, and geographical distances, *G*, between populations. Partial Mantel tests are of pairwise P$_{ST}$ and *G*, while controlling for either empirical population divergence, *T*, or hypothetical population divergence, *C*. BSD = beachcomber arc single dispersal; EE = eastward expansion single dispersal; MD = multiple dispersals; MDI = multiple dispersals and Australo-Melanesian isolation.

[a] MDI Middle Pleistocene model.
[b] MDI Late Pleistocene model.
* Statistical significance after Bonferroni correction (α = 0.01).

interpreted with regard to their correspondence to uniparental markers and apparent discordance with some genomic autosomal data.

Out-of-Africa dispersal models derived from uniparental data are based on the geographical distribution of haplogroups and population divergence time estimates, providing a chronological and spatial framework for the evolution and diffusion of these loci (reviewed in Underhill and Kivisild 2007). While they have been influential in the reconstruction of modern human migration patterns, mitochondria and Y chromosome molecules are nonetheless single loci that are subject to large stochastic variation and which may not provide a realistic representation of the natural history of populations (Balloux 2010; Underhill and Kivisild 2007; Wall and Slatkin 2012). Perhaps more problematically, mitochondria are thought to reflect factors of natural selection to a greater degree than neutral genetic drift (Balloux 2010; Balloux et al. 2009; Mishmar et al. 2003; Wallace 2015). While intrapopulation genetic diversity in mtDNA decreases with distance from Africa, as would be expected under a serial founder effect, such correlation has been found to be lower than for autosomal markers in the same populations (Balloux et al. 2009). It also appears to be lower than the correlation found for cranial shape in another set of populations (Betti et al. 2009; von Cramon-Taubadel and Lycett 2008). Moreover, climate temperature variables have been found to correlate significantly with mtDNA diversity but not with autosomal DNA diversity at neutral markers, suggesting that natural selection mediated by climate has contributed to the distribution and variation of mtDNA in modern humans (Balloux et al. 2009). It should perhaps not be surprising that a neutral evolutionary model would apply to a lesser extent to mitochondria in comparison with neutral regions of the autosome, given that approximately 93% of the mitochondrial genome consists of genes involved in functional regulation and physiology (Kivisild 2015; Wallace 2015). Crucial to the interpretation of our results, therefore, is the question of whether dental nonmetric variation is primarily mediated by neutral evolutionary forces.

While the direct association of phenotypic variation and neutral genetic variation between extant populations has been

quantified in several studies of cranial shape (Harvati and Weaver 2006; Reyes-Centeno, Ghirotto, and Harvati 2017; Smith 2009; von Cramon-Taubadel 2009), such an approach remains to be applied to dental nonmetric traits at a global scale. At a local scale, Hubbard, Guatelli-Steinberg, and Irish (2015) studied the association of paired genetic and dental nonmetric data sets from four contemporary Kenyan populations. They found a moderate (*r* = 0.5) correlation that was statistically nonsignificant (Hubbard, Guatelli-Steinberg, and Irish 2015), perhaps due to the study's relatively small sample size. In comparison, statistically significant correlations as high as ~72% (*r* = 0.85) have been found for cranial shape variation and neutral genetic variation between modern human populations sampled from across the globe (von Cramon-Taubadel 2009). Until large-scale studies on the association of dental variation and neutral genomic variation are systematically studied, it will remain unclear to what extent the former is useful in reconstructing global population history, particularly in comparison to other skeletal elements.

Human evolutionary studies have shown increasing interest in understanding the association between different genomic and anatomical markers. While most efforts have concentrated on the association between genetic markers and skeletal phenotype to infer drift and natural selection (e.g., Harvati and Weaver 2006; Roseman 2004; Smith 2009; von Cramon-Taubadel 2009), more recent work (e.g., Evteev and Movsesian 2016; Herrera, Hanihara, and Godde 2014; Ricaut et al. 2010) has sought to assess how different genetic markers correlate with the skeletal and dental phenotype. These latter studies have pointed to the nuances in the differential association between skeletal and dental markers, on the one hand, and different molecular markers, on the other hand. For example, Herrera et al. (2014) found that, for a sample of populations in the Bering Strait region, craniometric data were highly correlated with mtDNA but not with Y chromosome DNA. By contrast, cranial nonmetric data were found to be highly correlated with Y chromosome DNA but not with mtDNA. To our knowledge, there are currently no studies that have explored these differential associations for dental traits.

In terms of the chronology of dispersal, the divergence date of African and non-African populations from uniparental data is often taken to indicate the maximum dates for a single out-of-Africa event (Fu et al. 2013; Green and Shapiro 2013). Recent fossil calibrations would place this in a Late Pleistocene framework, between ~54 and 95 ka (Fu et al. 2014; Rieux et al. 2014). However, from an autosomal DNA perspective, separation of African and non-African populations may be as early as the terminal MP, between ~90 and 130 ka (reviewed in Scally and Durbin 2012). Estimates for the separation of Africans and Australo-Melanesians tend to be older than those for the separation of Africans from other Eurasians and have been cited as support for an early dispersal out of Africa and a southern route into Asia (Rasmussen et al. 2011; Reyes-Centeno et al. 2014; Tassi et al. 2015; Pagani et al. 2016). Several studies have found that, even when accounting for admixture with other hominins, genomic evidence indicates that Australo-Melanesians diverged earlier from Africans in comparison with other Eurasian populations (Pagani et al. 2016; Tassi et al. 2015; Vernot et al. 2016). This point is indeed reflected in the population divergence estimates in our study and, to a lesser degree, our chronology distance estimates.

Reconciling support for different dispersal models is not straightforward but may be associated to the ways in which different anatomical and genetic loci reflect different evolutionary processes. As discussed above, disentangling the association between different anatomical and genetic markers will provide additional insights. One potentially reconciling view is that the separation of Africans and non-Africans was a gradual process involving population movements between Africa and Eurasia during the early Late Pleistocene (Groucutt et al. 2015; Li and Durbin 2011; Reyes-Centeno 2016; Scally and Durbin 2012; Schiffels and Durbin 2014). A delayed expansion into Eurasia by modern humans has also been proposed (Xing, Watkins, Hu, et al. 2010; Xing, Watkins, Shlien, et al. 2010), with the ancestors of extant non-Africans remaining restricted to the Middle East and possibly North Africa during the early Late Pleistocene. However, it is also possible that anatomically modern humans made eastward excursions into Asia (reviewed in Reyes-Centeno 2016).

Many of the critical paleontological discoveries relevant to the out-of-Africa dispersal debate are dental remains from Southeast Asia. Recent discoveries include anatomically modern teeth from Luna (Bae et al. 2014) and Fuyan (Liu et al. 2015) caves in Southern China. As inferred from stratigraphic associations and dating of flowstones, these findings suggest that modern humans were present in the region ~70 ka and as early as ~127 ka. The evidence could be in line with other paleontological discoveries in the region, including the mandible from nearby Zhiren Cave, retrieved from a stratigraphic context dated to between 116 and 106 ka (Cai et al. 2017; Liu et al. 2010), as well as the fossil remains from the Tam Pa Ling site in Laos, directly dated to ~63 ka (Demeter et al. 2012, 2015). Both the Zhiren and Tam Pa Ling skeletal remains exhibit a mosaic of anatomically modern and premodern traits. More

controversially, an isolated premolar associated with the Indonesian Punung fauna, retrieved from breccia dated to ~120 ka, has been considered to exhibit anatomically modern morphology (Storm et al. 2005; Westaway et al. 2007), although this assessment has recently been questioned (Polanski, Marsh, and Maddux 2016). Together, these findings have opened the possibility of modern human occupation in Southeast Asia during the early Late Pleistocene.

Applying the analytical framework used in our study to fossil samples may help clarify the mode and timing of dispersal of anatomically modern humans out of Africa and into Asia during the Pleistocene, particularly in light of ancient population replacements. Under the assumption that the dental nonmetric traits we sampled indeed reflect modern human population history, support for the BSD model in this study implies that the early Southeast Asian settlers represented by the Luna, Fuyan, Zhiren, and possibly Punung fossils could be members of lineages with little or no contribution to the modern human gene pool, as was also found on the basis of genomic analysis for some of the earliest Eurasian fossils thus far sequenced, including the Peştera cu Oase 1 (Romania) and Ust'Ishim (Russia) specimens, which represent extinct lineages (Fu et al. 2014, 2015).

In addition to including only recent human population samples in the study of Pleistocene dispersals processes, our study is limited by some other factors. For example, although our data are exceptional in terms of sample size, they have relatively limited coverage in terms of the dental nonmetric traits analyzed. Specifically, we may not have sufficiently sampled traits characteristic of a plesiomorphic condition in ancestral African populations. Several aspects of dental root traits not sampled here have been shown to occur at higher frequency in extant sub-Saharan African populations and are shared with Plio-Pleistocene hominins (Irish and Guatelli-Steinberg 2003). Furthermore, we caution that other untested models are also plausible. For example, we have not considered how dental traits may reflect admixture between modern humans and premodern hominins. Turner (1992), for example, hypothesized that within an out-of-Africa framework, dental affinities between African, Indian, and Southeast Asian populations could be the result of admixture between local archaic populations and expanding modern humans. His reasoning was based on the observation that the dental morphology of extant Southeast Asians could be considered intermediate between African and northern Eurasian dental morphology.

In summary, three interpretations can be offered in light of the results of our analyses and in comparison with previous studies. The first is that variation in dental nonmetric traits may follow variation in uniparental markers more closely and potentially reflect nonneutral evolutionary processes to a greater degree than other skeletal elements. This view implies that the models supported here do not necessarily reflect population history accurately. The second is that a BSD model may in fact be a better representation of the modern human dispersal process out of Africa and into Asia. This view would be in contrast

to the chronological framework of autosomal DNA estimates and the spatial dispersal patterns previously supported by some studies of skeletal and genomic evidence. The third is that admixture between modern humans and other hominins differentially affects craniodental morphology, resulting in the discrepancy between the present analyses and earlier studies of the cranial phenotype.

Recently, it has been proposed that the patterns used to explain the serial founder effect may be compatible with not only an evolutionary scenario of neutral evolution but also with one in which natural selection and admixture play a bigger role (Pickrell and Reich 2014). Although this hypothesis remains to be tested, it has served to highlight the limitations of using extant and recent human populations as proxies for the first inhabitants of their respective geographic regions and calls for the use of fossil evidence. Indeed, the BSD hypothesis suggesting a coastal dispersal around the Indian Ocean rim was modeled on the observation that the distribution of mtDNA haplogroup M is found at high frequency in extant South and Southeast Asian populations (Macaulay et al. 2005; Oppenheimer 2012). However, mtDNA haplogroup M has also been identified in Late Pleistocene European fossils and not in extant Europeans (Posth et al. 2016), which suggests that it was not exclusive to a coastal Late Pleistocene expansion into Southeast Asia but rather that it was largely replaced in other regions more recently. It has been suggested that such extensive population movements and partial replacements during the Late Pleistocene were more common than suspected by recent ancient DNA work (e.g., Fu et al. 2016; Posth et al. 2016).

Our results highlight productive areas for further research. First, it is necessary to test at a global scale whether and to what extent the patterns of variation for dental nonmetric data are correlated with patterns of variation for neutral regions of the autosome and sex chromosomes and, therefore, population history as well. Second, association with environmental variables, including climate and diet, would in turn provide some indication as to the adaptive component of dental nonmetric variation. Third, the integration of fossil dental data as well as additional dental features may serve to clarify our results and those from earlier studies. More broadly, continued study of the fossil record and ancient DNA is necessary to better understand the origins and dispersal of modern humans. Likewise, clarifying how different parts of the genome are related to each other and how these, in turn, are associated to skeletal phenotype will lead to a deeper understanding of the evolutionary processes that have shaped the genomic and phenotypic structure of modern humans.

Acknowledgments

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Archaic Hominin Populations in Asia before the Arrival of Modern Humans

Their Phylogeny and Implications for the "Southern Denisovans"

by Yousuke Kaifu

Our traditional scheme during the twentieth century was that *Homo erectus* had thrived on the vast terrain of eastern Asia since the Early Pleistocene, followed by the appearance of a more advanced but still primitive form of *Homo* in China during the mid-Middle Pleistocene. Recent discoveries or (re-)recognitions of other archaic hominins, such as *Homo floresiensis* from an Indonesian island, Neanderthals and the "Denisovans" from southern Siberia, as well as an extremely robust mandible from Taiwan, now open up a different view. By incorporating these latest discoveries, this paper intends to offer a phylogenetic model of diverse archaic Asian hominins distributed from southern Siberia to Southeast Asia and India. On the basis of this new model, I discuss how paleoanthropological data inform the taxonomic identity of the Denisovans and the admixture event with modern humans.

The general acceptance of the Recent African Origin theory for modern humans around the turn of the last century has sparked new studies on the process of global dispersal by *Homo sapiens*. Asia is not an exception in this regard. Hotly debated issues in this region include timing, routes, and the number of dispersal waves of early modern humans (Kaifu, Izuho, and Goebel 2015), but recent advancements in ancient genetic studies also raise another intriguing possibility: admixture between indigenous archaic (premodern) hominins and dispersing modern humans (Green et al. 2010; Malaspinas et al. 2016; Mallick et al. 2016; Reich et al. 2010). To provide useful paleoanthropological background for such studies, this paper synthesizes paleoanthropological evidence to infer evolutionary relationships among archaic hominin populations in eastern Asia (East and Southeast Asia).

Major issues to be discussed here are (1) the degree of genetic isolation among regional populations, (2) continuity or discontinuity in each population lineage, and (3) whether there was significant genetic contribution from the populations in western Eurasia or Africa. For these purposes, I review published evidence concerning the spatiotemporal variation in craniodental morphology of Asian hominins. I also report my own new analysis of craniometric variation using a large cranial sample from Asia. The primary focus of this paper is on the relationships among the late Middle Pleistocene and Late Pleistocene hominins. However, my discussion extends as far back as the Early Pleistocene Asian *Homo erectus* to reconstruct the possible phylogeny of late archaic hominins in Asia.

For the purpose of this paper, I call fossils from Java as well as from Chinese early Middle Pleistocene sites (e.g., Zhoukoudian Locality 1) *H. erectus* following the traditional manner, but I call a series of post-*erectus*-grade premodern hominins (Dali, Jinniushan, and so on) "late archaic *Homo*" rather than use controversial taxonomic names, such as *Homo daliensis*, *Homo mabaensis*, *Homo heidelbergensis*, or archaic *Homo sapiens* (Bae 2010). The major purpose of this synthesis is to draw a reasonable scheme about paleodemes (p-demes; Howell 1999) and the phylogeny of archaic Asian hominins on which a meaningful taxonomy should be based in the future. I also use the new information to interpret the recent claim of significant gene flow from the "Denisovans" to modern humans in Oceania (Malaspinas et al. 2016; Prüfer et al. 2014; Reich et al. 2011).

Diversity of *Homo erectus* and Related Populations in Eastern Asia

Homo erectus is a paleospecies that can be broadly defined as having relatively small cranial capacity, large basicranial platform, a low cranial vault that is maximally broad at the level of the supramastoid crests, strongly flexed occipitals, and projecting faces (Rightmire 2013). Asian representatives of this species, or *H. erectus* sensu stricto, have been traditionally recognized from sites in Java (e.g., Trinil, Sangiran, Mojokerto, Sambungmacan, and Ngandong) and China (e.g., Zhoukoudian, Nanjing, Yunxian, and Yiyuan). The evolutionary rela-

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tionship between these two regional groups, however, is vague at best.

One popular view is that *H. erectus* was a polymorphic species widely distributed over the region between northern China and Java (or a greater part of Eurasia and Africa, depending on how we define the species). This view predicts the presence of a morphocline between the paleodemes in northern China and Java, like we see today in *Homo sapiens*, but there is no empirical evidence to support such an expectation. This is primarily because suitable fossil materials from the intervening mainland Southeast Asia are lacking (fig. 1). In this section, I review the current evidence relevant to the variation in archaic Asian hominins.

Regional Continuity of *H.* erectus *in Java*

Several sites in Central and East Java have yielded hominin fossils that are classified as *H. erectus* by most researchers. Among them, those from the Early Pleistocene contexts of Sangiran, Mojokerto, and probably Trinil (Kaifu et al. 2010) represent the early phase of *H. erectus* evolution in Java from ≥1.2 to 0.8 Ma (Hyodo et al. 2011; Kaifu et al. 2005, 2010; Larick et al. 2001; fig. 2).

Late Middle and Late Pleistocene archaic hominins of Java are represented by the fossils from Ngandong, Sambungmacan, and Ngawi. In this paper, I collectively refer to them as "late Javanese *H. erectus*." These fossil remains are often re-
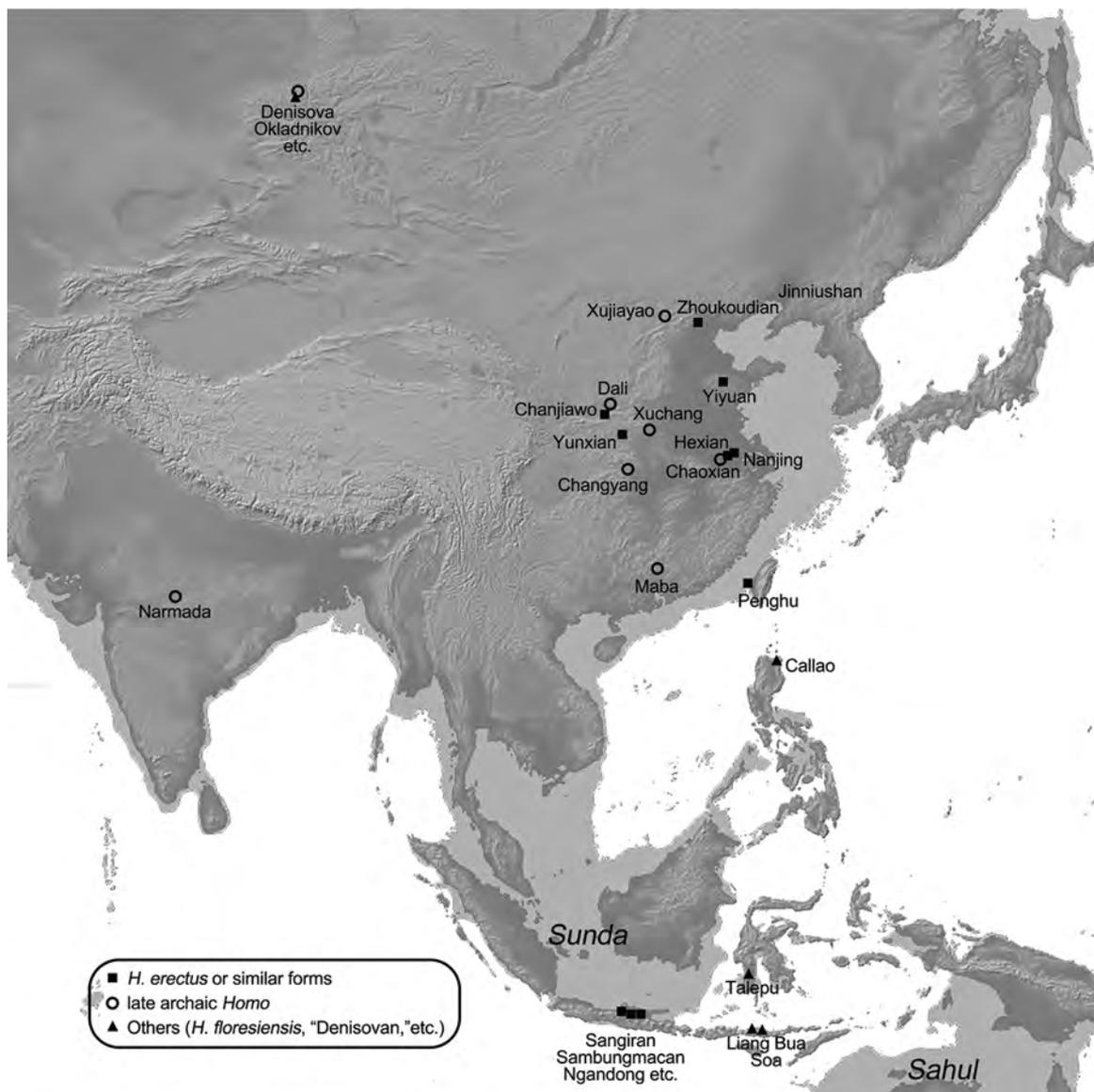
Figure 1. Map of the fossil localities discussed in this paper. The light gray areas are the continental shelves 0–100 m below sea level. The base map was created using the GeoMapApp software (http://www.geomapapp.org/). A color version of this figure is available online.
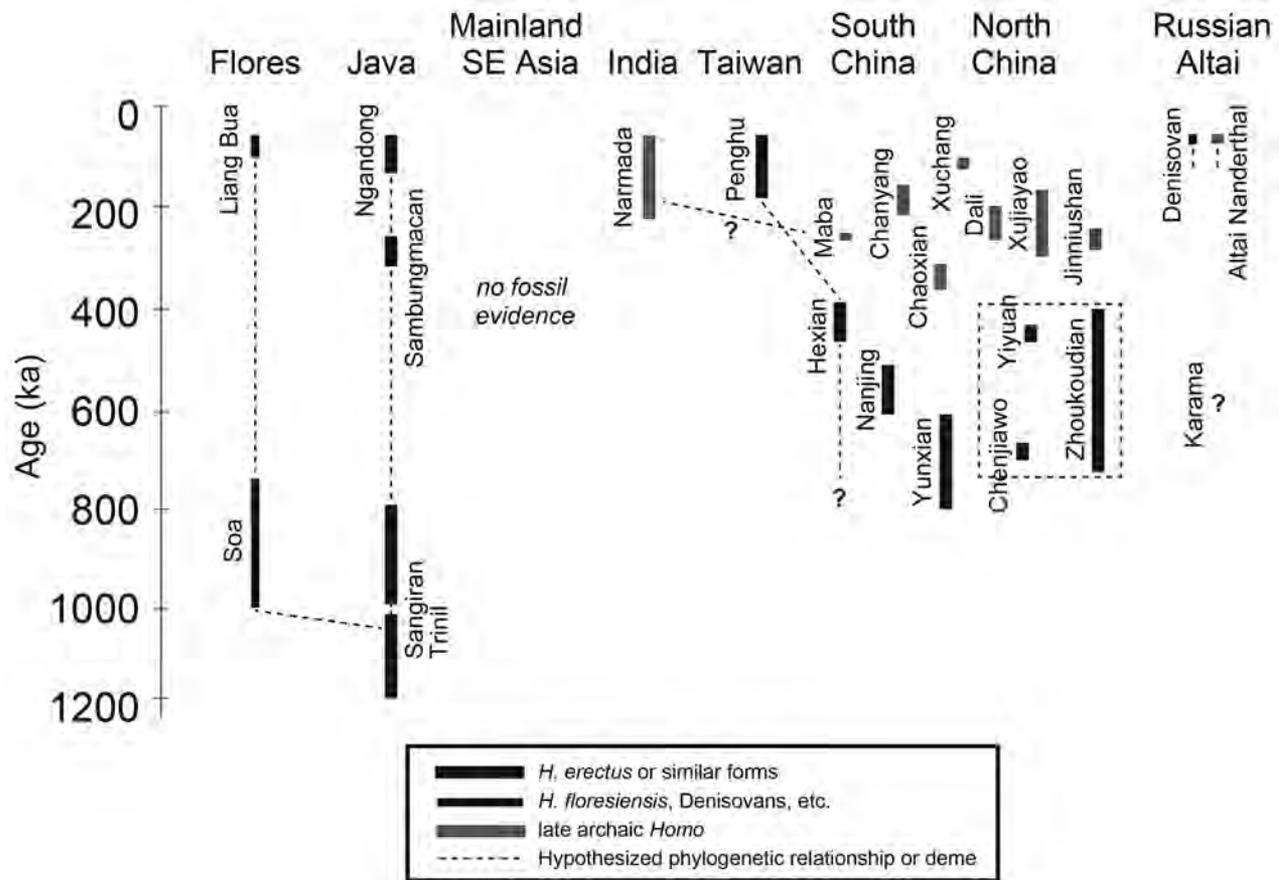
Figure 2. Chronology of the archaic Asian fossils discussed in this paper with their hypothesized relationships. Probable time ranges are indicated for the Sangiran, Zhoukoudian, and Flores hominins as well as Denisovans, whereas the other bars reflect uncertainties of the reported ages. See the text for the sources of the chronological data.

garded as contemporaneous within the time range of 70–30 ka (Antón 2003; Yokoyama et al. 2008). However, this is an unwarranted assumption, mainly because of the uncertain stratigraphic association between the dated materials and the *H. erectus* remains (Grün 1997; Indriati et al. 2011). From a geological perspective, the Sambungmacan *H. erectus* fossils should be chronologically older than the Ngandong assemblage, because the latter was excavated from the terrace deposits formed along the present Solo River (Hoffman et al. 2010), whereas the former apparently derived from the fluvial deposits formed by the ancient Solo River. More recently, Indriati et al. (2011) suggested that the Ngandong terrace may be as old as ~546 ka if the pumice samples that they dated were not reworked materials. If so, the course of the river has not changed for more than 500,000 years, at least in this location. In my opinion, this contradicts the evidence for a high-energy depositional environment that resulted in the accumulation of many large mammalian fossils within the terrace.

The relationship between the above early and late Javanese *H. erectus* is the focus of this section. Researchers agree that cranial samples from these groups are morphologically differ-

ent, but there is controversy about what this difference reflects (Baab 2010; Baab and Zaim 2017; Kaifu et al. 2008, 2015c; Zeitoun et al. 2010). Some researchers suppose the variation was a result of anagenetic local evolution, whereas others suppose discontinuity of the evolutionary lineage and thus replacement of the *H. erectus* population by another species, *Homo soloensis*.

In my opinion, this disagreement derives from the different analytical methods and samples used by the different researchers. First, published morphometric analyses are useful and informative but do not capture some of the known important features to describe cranial variation in Java. For example, development of the laterally thickened supraorbital torus (fig. 3), disappearance of postglenoid process of the mandibular fossa (fig. 4), and manifestation of a notch at the posterior foramen magnum (opisthionic recess) are unique to the late Javanese *H. erectus*, but they have been neglected in morphometric studies. In this sense, a "traditional" nonmetric approach is useful to comprehensively analyze the cranial variation in Java. However, the usefulness of the cladistic analysis based on "123 morphological and 345 metrical features" (Zeitoun et al. 2010)
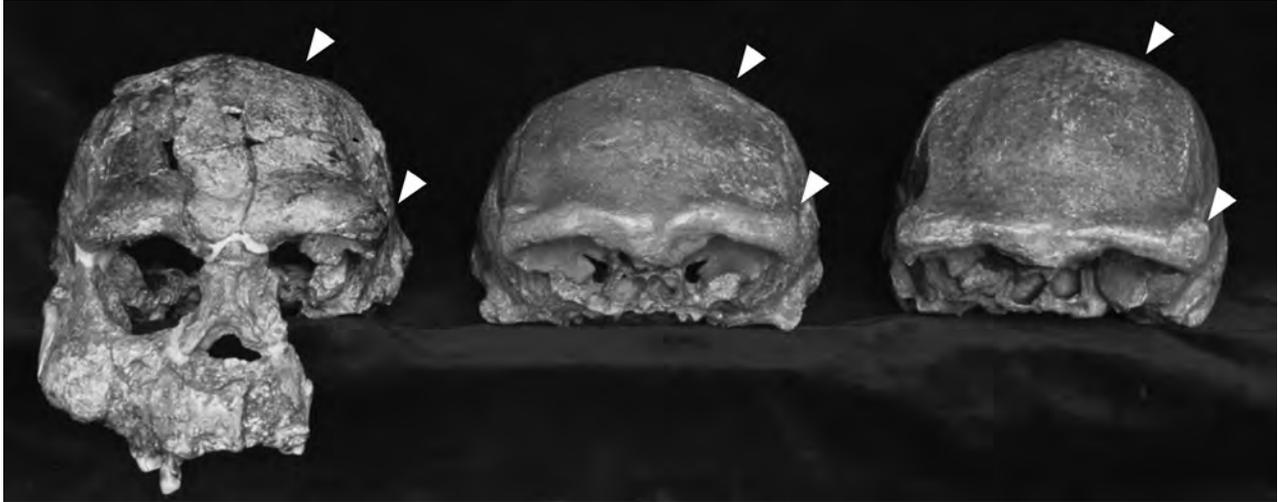
Figure 3. Examples of the development of peculiar cranial features in the chronological series of Javanese *Homo erectus*. *Left*, Sangiran 17 (0.8 Ma); *center*, Sambungmacan 4 (∼0.27 Ma); *right*, Ngandong 12 (∼0.1 Ma?). Sambungmacan 4 exhibits a laterally thickened supraorbital torus and rounded parietals (indicated by the arrowheads), two of many characteristic features of Ngandong *H. erectus*, while it retains a primitive low cranial vault morphology similar to that of Sangiran/Trinil *H. erectus*. A color version of this figure is available online.

is questionable, because this study did not consider possible correlations among the examined characters, a potentially significant source of error in this method.

The second issue is the samples used. In a series of detailed craniometric and nonmetric comparisons made with use of the nearly maximal sample of the existing cranial specimens from Java, my colleagues and I made the following observations: (1) Some of the chronologically younger *H. erectus* crania from Sangiran (1.0–0.8 Ma) exhibit several features characteristic of Ngandong *H. erectus*, such as tendencies toward laterally thickened supraorbital torus, wider frontal squama, vertically set occipital plane, and some details of the occipital torus morphology in Sangiran 17 (Kaifu, Aziz, and Baba 2013), as well as a series of features that probably related to the anterior shift of the posterior limit of the temporal muscle in Skull IX and Bukuran (Kaifu et al. 2011*b*); (2) Some of the cranial specimens from Sambungmacan (Baba et al. 2003; Kaifu et al. 2008) and Ngawi (Kaifu et al. 2015*c*) exhibit features that are intermediate between the conditions of the Sangiran/Trinil and Ngandong series. For example, Sambungmacan 4 is similar to Ngandong *H. erectus* in most cranial surface features, but the former has a primitive low cranial vault (as in Sangiran *H. erectus*) and shows a slightly curved roof of the mandibular fossa (intermediate morphology between the Sangiran and Ngandong conditions; Baba et al. 2003; figs. 3, 4). The Ngawi specimen also exhibits varying similarities to the Sangiran condition in the smaller cranial size, the supraglabellar depression, and the mandibular fossa morphology (Kaifu et al. 2015*c*).

There is general agreement that the morphological differences between the Sangiran/Trinil and Sambungmacan/Ngawi/Ngandong cranial series are relatively large, but this is not sur-

prising given the chronological gap of ∼0.5 million years between them (fig. 2). If a large fossil sample is analyzed comprehensively using both metric and nonmetric methods, there is no evidence of abrupt temporal variation. In agreement with this view, Antón (2002:319) noted that "despite a great temporal range, the Indonesian lineage is morphologically consistent through time, with earlier and later Indonesian fossils more similar to one another than either is to the temporally intermediate Chinese material." In summary, as has been suggested by many researchers (Antón 2002, 2003; Baba et al., 2003; Kidder and Durband 2004; Weidenreich 1943; Wolpoff 1999), the hominin fossil record from Java strongly suggests gradual evolution of Ngandong-like cranial morphology (if not in a linear way, as claimed by Baab and Zaim 2017) and long-term evolutionary continuity of the *H. erectus* lineage in the geographically isolated environment at least after 1.0 Ma and probably from its beginning ∼1.2 Ma.

H. Erectus *from Northern China*

The 40-m-thick sediments at Zhoukoudian Locality 1 in northern China record the occupation history of *H. erectus* from about 0.75 to 0.4 (?) Ma (Shen et al. 2009). The six well-preserved crania of Zhoukoudian *H. erectus* show remarkable morphological homogeneity (Etler 1996; Weidenreich 1943; Wu and Poirier 1995), although some researchers suggest a slight degree of morphological change through the stratigraphic sequence (Wolpoff 1999; Wu and Dong 1985; Wu, Schepartz, and Norton 2010; see Pope 1992 for an opposing view).

The unique cranial features of Zhoukoudian *H. erectus*, compared with the Javanese representative of the species, have been
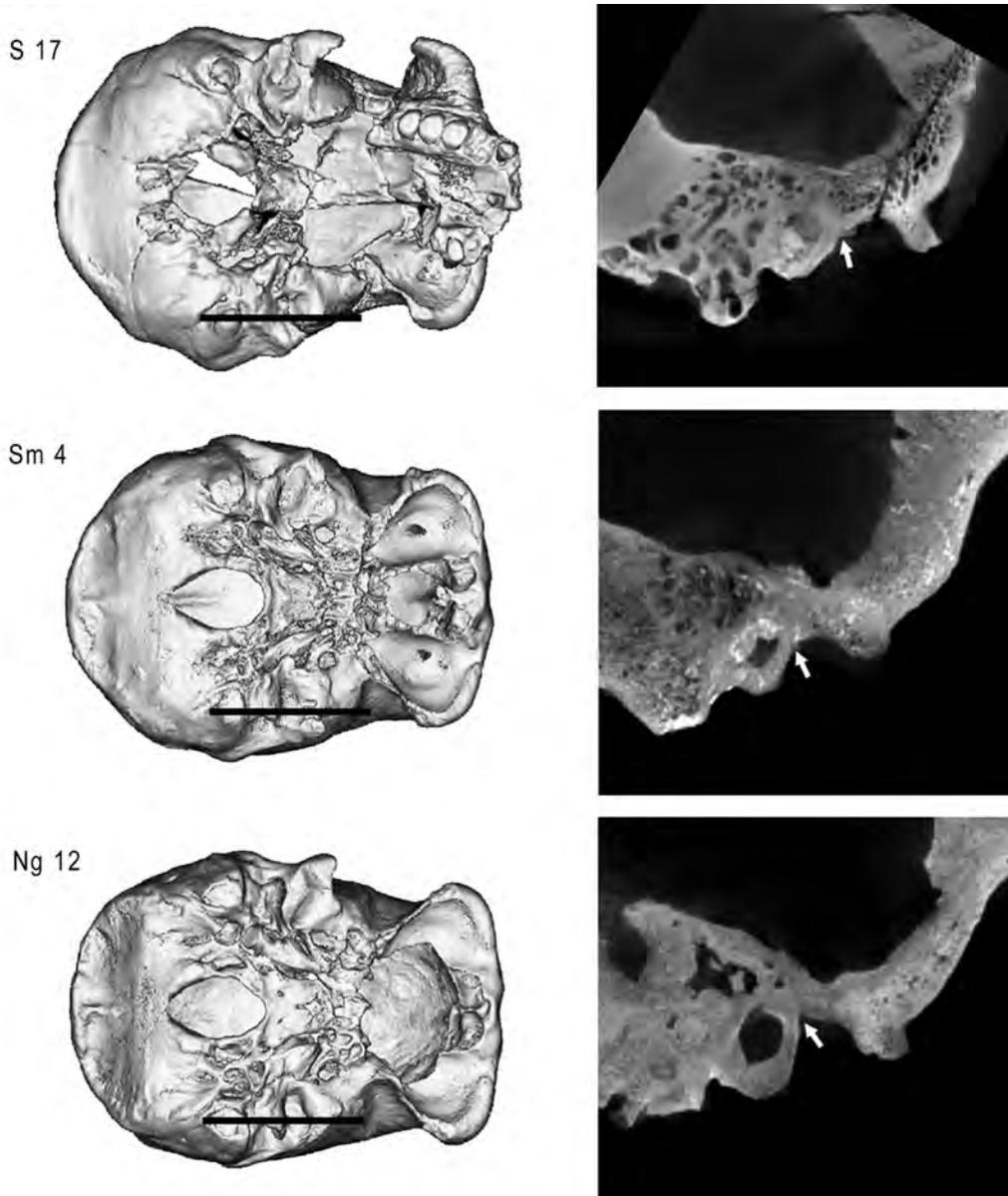
Figure 4. Development of peculiar mandibular fossa morphology in the chronological series of Javanese *Homo erectus*. The locations of the sagittal micro–computed tomography sections are indicated in the images on the left. Each cranium is oriented according to the Frankfurt Horizontal. Arrows indicate the position of the squamotympanic fissure, the position of which shifts superiorly in chronologically later crania. The figure is not to scale. S 17 = Sangiran 17; Sm 4 = Sambungmacan 4; Ng 12 = Ngandong 12.

noted from the early stage of its research history, and these observations remain valid after the recent increase in the fossil sample. Such unique features of Zhoukoudian include a more marked supratoral sulcus, a steeply rising frontal squama with salient tuberosities, a narrow occiput, a laterally projecting suprameatal crest, and markedly inclined temporal walls (Antón 2002; Baab 2010; Kidder and Durband 2004; Santa Luca 1980; Weidenreich 1943, 1951). Regional differences between northern China and Java are also demonstrated by more recent craniometric comparisons, despite the varying analytical methods

and samples used (Antón 2002; Baab 2008, 2010; Baba et al. 2003; Cui and Wu 2015; Durband 2006; Durband, Kidder, and Jantz 2005; Grimaud-Herve et al. 2012; Kaifu et al. 2011*a*, 2011*b*; Liu, Zhang, and Wu 2005; Rightmire 2013; Zeitoun et al. 2010).

Detailed interpretation of these observations differs among the researchers, however. A small number of researchers claim that the Zhoukoudian Locality 1 *Homo* is distinct and merits its own species, "*Homo pekinensis*" (Cameron and Groves 2004; Zeitoun et al. 2010), whereas others suppose more closely related genetic relationship among regional populations of Asian

H. erectus. In general support of the latter view, Baab (2010) noted "imperfect distinction between the Zhoukoudian and Sangiran fossils" in her three-dimensional geometric morphometric analysis of cranial shape and suggested that "isolation between the two regions did not occur until the Middle or Late Pleistocene or that the Sangiran hominins are morphologically close to the common ancestor of the Zhoukoudian and later Javanese *H. erectus*."

However, the study by Baab (2010) was based on a very limited sample that included only two Early Pleistocene Javanese specimens (Sangiran 2 and 17) and two Chinese specimens (Zhoukoudian 11 and 12). An analysis using a larger sample is required to more clearly demonstrate the actual pattern of regional variation in Asia (see below). Furthermore, some of the above-noted cranial features of Zhoukoudian *H. erectus* (a marked supratoral sulcus, steeply rising frontal squama with salient tuberosities, and markedly inclined temporal walls) are not captured in most craniometric analyses published so far. In fact, cranial morphological differences between Zhoukoudian and Javanese *H. erectus* are so obvious (Antón 2002) that an experienced researcher can easily sort out these cranial specimens without making a metric examination. Importantly, these regional differences cannot be explained by allometric scaling effects, because the cranial size is similar between the two groups.

In summary, Zhoukoudian and Javanese *H. erectus* are morphologically distinguishable from each other. However, the two regions are physically separated by about 5,000 km. The biological relationship between the two regional populations of *H. erectus* has to be examined by observation of the region between the two, and this is the next issue to be looked at.

Other Fossil Evidence from East Asia

In the vast area intervening between Zhoukoudian and Java, the Middle Pleistocene Chinese sites of Yiyuan, Chenjiawo (Lantian), Yunxian, Hexian, and Tangshan (Nanjing) yielded cranial and other specimens usually attributed to *H. erectus* (fig. 1). In addition, there are a few Early Pleistocene sites from where hominin cranial or dental remains were discovered (Gongwangling [Lantian], Yuanmou, and Jianshi). Many of these specimens are unfortunately fragmentary or heavily distorted, and their morphological assessments are, at present, difficult or controversial. For example, some researchers conclude that a partial cranium from Nanjing is similar to Zhoukoudian *H. erectus* (Antón 2002; Etler 1996; Wu and Li 2002), whereas others suggest that they are metrically different (Cui and Wu 2015; Liu, Zhang, and Wu 2005; Vialet et al. 2010). Some progressive features or morphological reflections of possible western genetic influence are suggested for Yunxian (Li and Etler 1992; Pope 1992; Wu and Poirier 1995), but these remain elusive because of substantial postdepositional crushing and deformation of the two crania from there (cf. Vialet et al. 2005, 2010).

For this reason, we here focus on less controversial or more complete fossils from Yiyuan, Chenjiawo, and Hexian as well

as another newly discovered mandible from Taiwan. The recently found partial cranium from Salkhit, eastern Mongolia, is excluded from this discussion, because it probably belonged to a modern human individual (Kaifu and Fujita 2012; see also Lee 2015) rather than an archaic hominin, as originally proposed (Coppens et al. 2008; Tseveendorj, Batbold, and Amgalantogs 2006; Tseveendorj et al. 2016).

Yiyuan and Chenjiawo (northern China). Fragmentary hominin cranial, postcranial, and dental remains from the mid-Middle Pleistocene site at Yiyuan are yet to be described fully (Sun et al. 2014), but according to Etler (1996), these are the only Chinese hominin materials that show "pervasive, all-around similarity" to Zhoukoudian *H. erectus*. A well-preserved mandible from the early Middle Pleistocene site at Chenjiawo in Shaanxi Province is also similar to the Zhoukoudian mandibles in overall dimensions, shape, and detailed surface morphology (Woo 1964). These fossils probably demonstrate that the southern range of the Zhoukoudian *H. erectus* paleodeme extended to at least around the Yellow River in northern China during the early-middle Middle Pleistocene.

Hexian (southern China). The hominin collection from Longtandong (Dragon Pool Cave), Hexian Country, includes a well-preserved calvaria, a fragmentary mandible, and isolated teeth (Wu and Dong 1982; Wu and Poirier 1995; Xing et al. 2014). The most recent combined electron spin resonance/U-series analysis concluded that these remains are 412 ± 25 ka (Grün et al. 1998), although other studies suggest dates as young as 150 ka (Chen et al. 1987).

Most studies agree that this specimen is more or less unique in the existing Asian *H. erectus* collection (Antón 2002; Cui and Wu 2015; Durband, Kidder, and Jantz 2005; Etler 1996; Kidder and Durband 2004; Pope 1992; Wolpoff 1999). For example, the occipital bone of Hexian is broad and lacks one of the peculiar characteristics of Zhoukoudian *H. erectus*, a narrow occipital (Antón 2002; Cui and Wu 2015; Durband, Kidder, and Jantz 2005). Although my own observation of the original specimen made me realize that the originally reported occipital (biasterionic) breadth of Hexian of 142 mm (Wu and Dong 1982) is an overestimate, my own measurement of 131 mm is still significantly broader than the range exhibited by the Zhoukoudian *H. erectus* (113–117 m). The earlier suggestion that Hexian exhibits some "progressive" cranial features in the fossil record of Chinese *H. erectus* (Wu and Dong 1985) is also in question, because no diachronic trends have been established within the Zhoukoudian cranial collection (Pope 1992), and the youngest cranium from there (Zhoukoudian 5) is not necessarily most similar to Hexian (Cui and Wu 2015).

A current controversy surrounding the Hexian *H. erectus* is whether this population supports the presence of a north to south morphocline of Asian *H. erectus*. Researchers agree that the Hexian calvaria is not a perfect intermediate between Zhoukoudian and Javanese *H. erectus*, and this makes the interpreta-

tion of cranial variation ambiguous (Antón 2002; Cui and Wu 2015; Durband, Kidder, and Jantz 2005).

In my view, the dentognathic evidence is of at least equal importance as the cranial evidence in this controversy. The single mandibular fragment from Hexian is notable in its thick corpus, and the existing incisor, premolar, and molar teeth are considerably larger than 1.0–0.75 Ma *H. erectus* fossils from Zhoukoudian and Java (Chang et al. 2015; Pope 1992; Xing et al. 2014). This is significant because the dental and mandibular robusticity tends to decrease through Pleistocene *Homo* evolution, and this trend is demonstrated even in the late Early Pleistocene of Sangiran, Java (Kaifu 2006; Kaifu et al. 2005; Zanolli 2013). Therefore, the robust mandible and teeth from the ~0.4 Ma site of Hexian is contrary to the hypothesis of a north to south morphocline of Asian *H. erectus*. In view of this general evolutionary trend, the presence of an apparently primitive, robust mandible and teeth in the region between Zhoukoudian and Java suggests the presence of another distinct regional population of *H. erectus*, one whose evolutionary origin is currently unknown.

Penghu (Taiwan). The recent discovery from Taiwan strongly supports the above view. In 2009, a fossilized archaic *Homo* mandible (Penghu 1) was recognized among the rich faunal collection dredged by fishing nets from the 60- to 120-m-deep Penghu submarine channel, 25 km off the western shore of Taiwan (Chang et al. 2015). The specimen is an almost complete right side of the mandible. Its original stratigraphic context is

unknown. Radiocarbon dating failed because of a lack of collagen, and laser-ablation U-series dating had limited success because of uranium overprint in the seawater. However, its general contemporaneity with other faunal remains, including spotted hyena (*Crocuta crocuta ultima*), was demonstrated by chemical analyses of the bone samples. This biostratigraphic evidence strongly suggests that Penghu 1 postdates *H. erectus* from Zhoukoudian, Hexian, and Sangiran and is probably younger than 190 ka (Chang et al. 2015).

A surprising aspect of Penghu 1 was its robust dentognathic morphology, which is comparable to the Hexian condition (fig. 5). In fact, its mandibular corpus robusticity index (width : height ratio) was the greatest among the known fossil *Homo* mandibles throughout the Pleistocene, and its molar size was as large as those of the >1.0 Ma *Homo*. Although Chang et al. (2015) were cautious about the taxonomic classification for Penghu 1, its similarities to the Hexian specimens are apparent (Liu et al. 2017). The persistence of such apparently primitive morphologies in the late Middle or even in the Late Pleistocene suggests survival of another, previously unrecognized evolutionary lineage of archaic *Homo* in Asia.

Hominins on Wallacean Islands

Currently, skeletal remains of *Homo floresiensis* are known only from the Late Pleistocene deposits at the Liang Bua cave on the Flores Island in eastern Indonesia. The excavated skeleton and other isolated bones and teeth all belong to small-bodied indi-
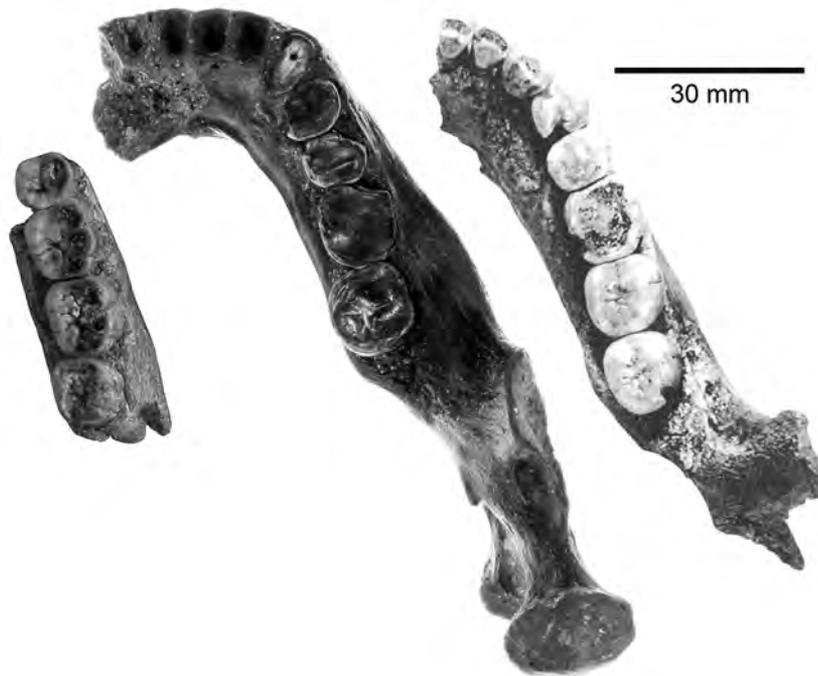

Figure 5. Penghu 1 (*center*) compared with 0.8–0.75 Ma *Homo erectus* mandibles from Java (Sangiran; *left*) and China (Zhoukoudian; horizontally flipped image from Weidenreich 1936; *right*). The new Taiwan mandible is more robust than the *H. erectus* specimens despite its younger age (fig. 1). A color version of this figure is available online.

viduals with estimated stature of ~105 cm. The endocranial volume is at the level of *Australopithecus* but is comparable to that of *Homo habilis* when scaled to body size (Kubo, Kono, and Kaifu 2013). The recently found hominin mandible and teeth from So'a Basin, Flores, suggest a deep evolutionary root of this diminutive species, at least as far back as ~0.7 Ma (Brumm et al. 2016; van den Bergh et al. 2016*a*). Archaeological evidence from this open-air site implies that the ancestors of *H. floresiensis* arrived on the island as early as 1.0 Ma (Brumm et al. 2010).

The previous claims that *H. floresiensis* is very primitive and was closely related to ~2.0 Ma African *H. habilis* or even *Australopithecus* are problematic in many ways (see discussion in Kaifu et al. 2011*a*). For example, the reported primitive aspects of the mandibles and teeth (Brown and Maeda 2009) are unreliable according to later reexaminations (Kaifu et al. 2011*a*, 2015*b*). A series of more recent, detailed analyses of the cranium and teeth, the most diagnostic elements in evolutionary systematics of the genus *Homo*, shows that *H. floresiensis* is derived compared with *H. habilis* and has its closest affinities with early Javanese *Homo erectus* dated to 1.2–0.8 Ma (Kaifu et al. 2011*a*, 2015*a*).

Combined with other evidence, such as geographic proximity and the oldest known date for the hominin presence on Flores (~1.0 Ma at So'a Basin on the same island; Brumm et al. 2010), the ancestor of *H. floresiensis* was most likely early Javanese *H. erectus* or its related form. Because *H. floresiensis* lacks a series of cranial features unique to late Javanese *H. erectus* from Sambungmacan and Ngandong, it is clear that the former evolved in isolation in the insular setting (Kaifu et al. 2011*a*). Other islands, such as Luzon (Callao Cave: Mijares et al. 2010) and Sulawesi (Talepu: van den Bergh et al. 2016*b*), may also have hosted archaic hominins, although the identities of these island hominins are yet to be demonstrated.

More Modern Forms of Asian Archaic *Homo*

Late Archaic *Homo* from China

Non-*erectus* late archaic hominin fossils are known from Chinese sites, such as Jinniushan (partial skeleton), Dali (cranium), Xujiayao (cranial fragment and teeth), Maba (partial cranium), Chaoxian (cranial fragment, maxilla, and teeth), and Changyang (maxilla and teeth). Useful reviews of these fossils are available in Bae (2010), Brown (2001), Etler (1996), Pope (1992), and Wu and Poirier (1995), so these are not repeated here. Li et al. (2017) recently reported several new cranial fossils from Xuchang, Henan Province. Below, I summarize the issues directly relevant to their phylogenetic relationships.

Dating of these specimens is challenging, but there is general agreement that all of these are from late Middle Pleistocene contexts, in the range of approximately 360–100 ka (fig. 2; see also Ao et al. 2017; Tu et al. 2015; Yin et al. 2011). The morphology of these specimens has been variously described and compared, but most of the earlier studies are descriptive or based solely on univariate metric comparisons, except for some cases (Li et al. 2017). Within this limit, the published studies agree on some issues but disagree on others.

Continuity or Discontinuity. The above Chinese fossils are more derived compared with *Homo erectus* and show a suite of cranial characters related to brain expansion (e.g., rounded cranial bones, arched squamosal suture, and expanded occipital plane). It is uncertain whether this is the result of in situ evolution from local *H. erectus* or reflects an eastward dispersal of African or European late archaic *Homo* (Bae 2010; Wu and Athreya 2013). For example, Rightmire (2008) noted that fossils like Dali display many of the same features that characterize African and European Middle Pleistocene archaic *Homo* and prefers to include all of these specimens in the same species, *Homo heidelbergensis* (Rightmire 2004). Other researchers claim that the apparent persistence of some "regional" craniodental characters supports evolutionary continuity between *H. erectus* and late archaics in China, allowing for some degree of gene flow from western Eurasia to the latter (Etler 1996; Li et al. 2017; Pope 1992; Wolpoff 1999; Wu 2014).

Among such claimed regional characters, a few appear to be significant. Perhaps the most convincing is a distinctly shorter upper face in Chinese *H. erectus* (Zhoukoudian, Nanjing) and late archaic *Homo* (Dali, Jinniushan) as compared with contemporaneous Afro-European *Homo* (Bodo, Kabwe, Petralona, Arago, and Atapuerca; Pope 1992; Wu and Athreya 2013; Wu and Brauer 1993). Elsewhere, I have shown that Javanese *H. erectus* (Sangiran 17 and IX) also shares this character with Chinese hominins, and these Asian hominins together display distinctly narrower upper facial breadths (Kaifu et al. 2011). This regional difference in facial height is also reflected in the mandible. Chang et al. (2015, see fig. 4k, 4l) demonstrated that the height of the mandibular ramus is greater in African Middle Pleistocene *Homo* (Tigehnif 2 and 3, KNM-BK 67) than in contemporary Asian mandibles (Sangiran 21, Zhoukoudian G1 and H1, Penghu 1). The evolutionary origin of such "Asian features" is unclear, but the regional persistency observed in northern China at least makes it unlikely that a total replacement model would explain the transition from *H. erectus* to late archaic *Homo*.

Morphological diversity. Many researchers note substantial morphological diversity within the cranial sample of Chinese late archaic *Homo* (Howell 1999; Pope 1992; Wu 2014), but the biological meaning of this diversity is difficult to elucidate. Some researchers suggest that the robust and gracile cranial morphology seen in Dali and Jinniushan, respectively, is ascribed to sexual dimorphism in the same population (Wolpoff 1999), but others suggest that they belonged to different demes (Howell 1999). Recent detailed analyses of the cranium from Xuchang (Li et al. 2017) and the mandible (Wu and Trinkaus 2014) and teeth (Xing et al. 2015) from Xujiayao emphasize their unique mosaic of primitive and derived morphological characters, which makes their taxonomic statuses unclear.

One intriguing question in this regard is the position of the Maba cranium, whose markedly round orbital shape and prominent nasal saddle are unique among the Chinese fossils. Building on the earlier observation (Wu and Wu 1985), Pope (1992) noted that these and other cranial features present in Maba are "totally consistent with Neanderthal morphology." He further suggested genetic influence from these western late archaic hominins. Other researchers are dubious about this proposal (Howell 1999; Wolpoff 1999), although we now have genetic evidence that Neanderthals were actually present in eastern Asia at least north of the Tibetan Plateau (Krause et al. 2007; Prüfer et al. 2014). Apart from the question of Maba's relationship with Neanderthals, its uniqueness remains a key issue to solve the question of the morphological diversity of Chinese late archaic *Homo* (see "Late Archaic *Homo* from India"). Also, on a related note, Bailey and Liu (2010) reported that the maxillary dentition from Chaoxian, another site in southern China, lacks uniquely derived features of European Neanderthals. Recently, some researchers have suggested that the suprainiac fossa in the occipital bone of Xuchang 2 and semicircular canal morphology in Xuchang 1 and 2 as well as Xujiayao 15 reflect influence from Neanderthals (Li et al. 2017). However, caution against the use of individual Neanderthal features for documenting population affinities has been raised by the same research group elsewhere (Wu et al. 2014).

Late Archaic Homo from India

The partial hominin cranium from Hathnora in the Narmada Valley, India, is the single unquestionable archaic hominin fossil currently known from southern Asia. The specimen was discovered from a conglomerate layer containing reworked mammalian fossils that are variously dated to between ~48 and >236 ka (Cameron, Patnaik, and Sahni 2004; Patnaik et al. 2009). Although it was originally identified as an "advanced" *H. erectus* (de Lumley and Sonakia 1985), the globularity and other cranial features seen in the Narmada specimen support its allocation to some taxon within post-*erectus*-grade *Homo* (Athreya 2010; Cameron, Patnaik, and Sahni 2004; Kennedy et al. 1991).

As such, the question that should be asked is what are its morphological affinities with other late archaic *Homo* specimens from Africa, Europe, and Asia. Most studies agree that Narmada resembles other Middle Pleistocene *Homo* (Athreya 2010; Cameron, Patnaik, and Sahni 2004; Kennedy et al. 1991), and some emphasize its closer affinities with European Middle Pleistocene hominins, such as Steinheim, or more broadly *H. heidelbergensis* (Cameron, Patnaik, and Sahni 2004; Kennedy et al. 1991).

On the other hand, Howell (1999) found "fundamental" similarity between the crania from Maba and Narmada and put them together to propose the Maba/Hathnora paleodeme. This hypothesis sounds reasonable given their relative geographic proximity and latitudinal similarity (fig. 1) as well as the claimed European affinities of Maba (Pope 1992; Wu and

Wu 1985). Unfortunately, however, Maba is missing in the previous comparative studies of the Narmada cranium.

Russian Altai

Since 2007, ancient DNA extracted from bones excavated from caves in the Russian Altai, southern Siberia (e.g., Okladnikov and Denisova), have confirmed the earlier prediction by paleoanthropologists and archaeologists that Neanderthals once occupied this mountain range in the Late Pleistocene (Krause et al. 2007; Prüfer et al. 2014). Additionally, mitochondrial DNA (mtDNA) and nuclear DNA retrieved from a finger phalanx from the Denisova cave was found to be different from that of both modern humans and Neanderthals and was used to propose another unknown archaic hominin group, named "Denisovans" (Krause et al. 2010; Meyer et al. 2012; Reich et al. 2010). More recent studies identified Denisovan DNA from two fossil molars from the same site, which suggested Denisovans used the cave over a long period, from >100 ka to around 50 ka, with probable interruption(s) by Neanderthals (Reich et al. 2010; Sawyer et al. 2015). Morphological analyses of the two Denisovan isolated molars (M^2 or M^3) emphasized their large size and features that are unique compared with those of modern humans, Neanderthals, and Asian archaic *Homo* in general (Reich et al. 2010; Sawyer et al. 2015). In addition, archaeological evidence suggests that the Altai Mountains had been occupied by unidentified hominins since the early Middle Pleistocene (Derevianko and Shunkov 2005).

Craniometric Variation in Asian Archaic Homo

With a few exceptions (e.g., Rightmire 2013), the previous craniometric studies of Asian premodern *Homo* (including *Homo erectus*) are based on variously incomplete samples that do not include some important, well-preserved specimens. To understand cranial shape variation on the basis of the maximally available sample, I conducted the following principal component analysis (PCA) using size-adjusted linear measurements.

The materials included were all the well-preserved Asian *H. erectus* specimens (Sangiran, Sambungmacan, Ngandong, Zhoukoudian, and Hexian) and *Homo floresiensis* (LB1) as well as one of the few relatively complete crania of late archaic Asian *Homo* (Dali). Unfortunately, metric data for Jinniushan were not available. Comparative specimens included African Early-Middle Pleistocene *Homo* (*Homo habilis* sensu lato), *Homo ergaster*, "*Homo rhodesiensis*"), and another early *Homo* group from Dmanisi. The inclusion of *H. habilis* and Dmanisi *Homo* is to establish character polarity. Only fully adult specimens were analyzed (i.e., subadult specimens, such as KNM-WT 15000 and D2700, were excluded).

The focus of this analysis was the neurocranium, including the upper face. Eight linear measurements were chosen to capture the overall cranial vault architecture and to maximize the sample size: these are maximum cranial length (grabella-opisthocranion

length; GOL), porion-bregma height (PBRH), breadths across the supraorbital torus (SOTB) and the cranial vault (frontal squama [postorbital breadth; POBB], parietals [squamosal suture breadth; SQSB], and occipital [biasterionic breadth; ASB]), as well as those that largely represent breadths of the mid (biradicular breadth; BRAB) and posterior (supramastoid breadth; SMCB) cranial base. The size adjustment was done by dividing these measurements by the "size variable" for each specimen, which was defined as the geometric mean of the cranial length (GOL), the average of the six breadths (SOTB~SMCB), and height (PBRH). The PCA was conducted using the variance-covariance matrix of the eight size-adjusted linear measurements.

As shown in table 1, most measurements were taken from the original specimens by myself or other researchers. Some were taken from casts with corrections for the estimated shrinkage (usually ~1% in a resin cast), and others were based on the computed tomography given in the literature (D3444, D4500). These are potential sources of probably minor errors.

The scores for principal component (PC1 and PC2) that cumulatively explain 61% of the total variation (table 2) are plotted in figure 6. In PC1, specimens with relatively wider upper face (SOTB) and cranial base (BRAB, SMCB) are loaded positively, and those with relatively wider frontal squama (POBB), occipital (ASB), and higher cranial vaults (PBRH) are loaded negatively. Specimens with higher PC2 scores tend to have narrower upper facial breadth (SOTB) relative to the brain case widths (SQSB, ASB, and SMCB).

Interesting chronological and regional trends are observed in this PC space. First, the samples from Africa and Java are clearly separated from each other with no overlap, but they display similar trajectories of chronological changes from the upper-right corner to the lower-left corner (Sangiran → Sambungmacan → Ngandong in Java; Turkana *H. ergaster* → OH9/Daka → Kabwe in Africa). Second, Zhoukoudian *H. erectus* is similar to Turkana *H. ergaster* and is separated from Javanese *H. erectus* with little overlap; the former is closer to more primitive Dmanisi *Homo* and *H. habilis* than the latter. Third,

Table 1. Measurements used for the principal component analysis

	GOL	SOTB	POBB	SQSB	ASB	BRAB	SMCB	PBRH	Data source
KNM-ER1470	168	115	82	120	104	136	140	94	K&B
KNM-ER1813	145	99	69	103	94	113	114	80	K&B
KNM-ER3733	182	119	92	131	119	131	142	96	K&B
KNM-ER3883	182	120	88	134	115	131	141	93	K&B
OH9	206	*135*	100	*139*	123	135	146	*99*	R13, W91
Daka	180	125	95	129	116	130	139.5	101	A08
Kabwe	207	139	104	144	125	136	148	108	K&B
D2280	177	*113*	*86*	*118*	104	132	136	*93*	R13
D3444	163	104[a]	78	115[a]	104	120	132	89[a]	R13
D4500	165	112[a]	76[a]	118[a]	92[a]	132[a]	135[a]	75[a]	L13
Sang2	183	104	84	138	123	126	142	94	K&B
Sang17	207	125	101	144	134	148	161	104	K&B
Bukuran	194	113	88	139	126	133	153	98	K&B
SangIX	186	111	87	132	117	126	142	93	K
Sm1	199	118	107	146	126	138	151	107	K&B
Sm3	178	114	101	138	120	136	146	98	K&B
Sm4	199	122	116	146	133	138	156	102	K&B
Ng6	221	122	108	149	128	141	155	112	K&B
Ng7	192	121	106	142	124	136	147	103	K&B
Ng10	202	124	110	152	127	143	159	109	K&B
Ng11	203	132	114	151	128	141	160	112	K&B
Ng12	201	124	107	138	126	136	151	108	K&B
Ngawi	187	114	101	140	127	136	147	102	K&B
ZKD10	199	*119*	98	138	116	*147*	150	106	W43
ZKD11	192	*113*	93	135	120	*137*	145	94	W43
ZKD12	195.5	*118*	95	139	118	*151*	147	101.5	W43
Hexian	191	114	101	146	131	139	160	97	K
Dali	206.5	*125*	*106.4*	*149*	115	141	150.5	102.5	W&A13
LB1	139	88	71	110	92	105	114	75	K&B

Note. Italic typeface indicates data obtained from a cast. A08 = Asfaw, Gilbert, and Richards 2008; ASB = biasterionic breadth; BRAB = biradicular breadth; GOL = grabella-opisthocranion length; K = Kaifu et al. 2011*b*; Y. Kaifu, unpublished data; K&B = Kaifu et al. 2008; Y. Kaifu and H. Baba, unpublished data; L13 = Lordkipanidze et al. 2013; PBRH = porion-bregma height; POBB = postorbital breadth; SMCB = supramastoid breadth; SOTB = supraorbital torus breadth; SQSB = squamosal suture breadth; R13 = Rightmire 2013; W43 = Weidenreich 1943; W91 = Wood 1991; W&A13 = Wu and Athreya 2013.

[a] Data based on computed tomography.

Table 2. Component loadings of the principal components (PC) analysis based on eight linear cranial measurements

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
GOL	.085	−.090	−.711	.661	−.113	−.170	−.031	.006
SOTB	.621	−.499	.324	.313	.402	.039	−.011	.001
POBB	−.605	−.024	.621	.328	−.317	−.195	−.021	.001
SQSB	−.133	.754	.128	.423	−.077	.454	−.082	.001
ASB	−.408	.703	.030	−.076	.515	−.188	−.178	.001
BRAB	.915	.222	.099	−.127	−.239	−.066	−.161	.001
SMCB	.563	.736	.122	.068	.055	−.110	.327	.001
PBRH	−.387	−.373	.251	−.780	.005	.179	.080	.019
Percentage	37	24	12	11	9	4	2	0
Cumulative percentage	37	61	74	85	94	98	100	100

Note. ASB = biasterionic breadth; BRAB = biradicular breadth; GOL = grabella-opisthocranion length; PBRH = porion-bregma height; POBB = postorbital breadth; SMCB = supramastoid breadth; SOTB = supraorbital torus breadth; SQSB = squamosal suture breadth.

the small northern Chinese sample also aligns with the above temporal trajectories (Zhoukoudian *H. erectus* → Dali), but the position of the southern Chinese specimen (Hexian) is away from the intermediate zone between the Javanese and northern Chinese samples.

These observations support the above-discussed genealogical independence of the Javanese *H. erectus* population lineage as well as the absence of a regional morphocline between

northern China and Java. Hexian is never an intermediate form between the two regional groups of Asian *H. erectus*. Also, figure 6 suggests that the cranial shape of Zhoukoudian *H. erectus* falls closer to the ancestral form (Dmanisi and *H. habilis*) than does the early Javanese *H. erectus*. In addition, the type specimen of *H. floresiensis* (LB1) is most similar to early Javanese *H. erectus* from Sangiran, as previously demonstrated (Kaifu et al. 2011a; see also Baab, McNulty, and Harvati 2013).
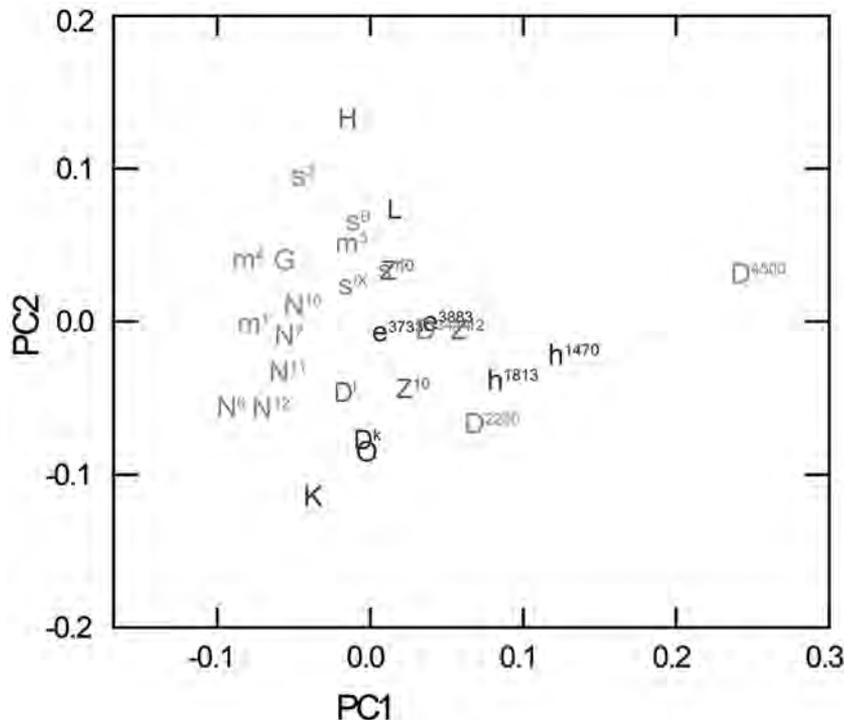
Figure 6. Plot of the principal component (PC) scores. Africa: D^k = Daka, e = Turkana *Homo ergaster*, h = *Homo habilis* sensu lato, K = Kabwe, O = OH9; Flores: L = Liang Bua *Homo floresiensis*; Java: G = Ngawi, m = Sambungmacan, N = Ngandong, s = Sangiran; Georgia: D = Dmanisi *Homo*; China: D^l = Dali, H = Hexian, z = Zhoukoudian. The superscripts denote the specimen numbers or names. A color version of this figure is available online.

A New Model of Archaic Hominin Phylogeny in Asia

The evidence reviewed and reported above offers the following working hypothesis about evolutionary relationships of archaic Asian hominins (see also fig. 2). (1) In Java, a regional group of *Homo erectus* had experienced gradual, slow, continuous evolution from the Early through Late Pleistocene. A series of time-successive demes can be defined within this population lineage, but here I refer to them collectively as "Javanese *H. erectus* p-deme." This view is reasonable given the geographic setting. Throughout the Pleistocene, Java experienced episodic range contraction and fragmentation as glacial cycles recurred, and it has been relatively isolated from the Asian mainland (Antón 2002). During the episodes of glacial low sea levels, Java was the southernmost constituent of Sundaland, a huge peninsula extending from the present-day Malay Peninsula to Borneo (Kalimantan) and Bali, whereas it was an island during the warm interglacial epochs, as is today (fig. 1). The past geographic range of the Javanese *H. erectus* p-deme on the Sundaland or Asian mainland is unclear at present because of the lack of fossil specimens outside Java. (2) The lineage of *Homo floresiensis* goes back to ∼1.0 Ma on the Flores Island. The species originated from a population with early Javanese *H. erectus* affinities and evolved in total isolation from the Middle-Late Pleistocene *H. erectus* populations in Java, in the isolated island setting. (3) The situation in mainland Southeast Asia (the area excluding southern China) is unknown due to the poor fossil evidence from this region. (4) In northern China, a *H. erectus* paleodeme represented by the fossil collection from Zhoukoudian Locality 1 was present during the earlier Middle Pleistocene (Zhoukoudian p-deme). Its geographic range extended southward at least around the region of the Yellow River. (5) In southern China, there is currently no evidence to support morphocline or interaction between the northern Chinese and Javanese demes of *H. erectus*. Instead, the fossils from Hexian and Penghu strongly suggest the presence of another deme that had its own evolutionary history (Hexian/Penghu p-deme). (6) The divergence time of the lineages leading to the Javanese *H. erectus* p-deme and the Zhoukoudian p-deme is unclear, but it can be hypothesized as sometime between Dmanisi *Homo*, the most primitive Eurasian hominins (1.77 Ma; Lordkipanidze et al. 2013) and the minimum age for the earliest Javanese *H. erectus* (1.2 Ma). The evolutionary origin of the Hexian/Penghu p-deme is unclear, but it also has deep roots back to the Early Pleistocene if their robust dentognathic morphology was not a product of evolutionary reversal. (7) Late archaic *Homo* in northern China (Dali, Jinniushan, Xuchang, and Xujiayao) may or may not belong to the same p-deme. Their genealogical relationship with the Zhoukoudian p-deme and influence from Afro-European late archaic *Homo* are debated. At least the extreme hypothesis of complete replacement is unlikely. (8) It is possible that Maba and Narmada formed their own p-deme of southern Asian late archaic *Homo* with some relationship with the genetic pool in western Eurasia. (9) Genetic evidence shows eastward dispersal of Neanderthals into the Russian Altai (Okladnikov and other sites) in the late Pleistocene.

It should be noted that, unlike genetic studies, paleoanthropology has no power to detect subtle introgression between extinct hominin groups. I propose the above model acknowledging this limitation, but with the hope that it serves as a useful guide to infer genetic relationships among the extinct hominin populations in Asia.

This model is radically different from the classic model that Asian *H. erectus* was a single evolutionary entity that exhibited clinal geographic variation across the continent from Indonesia to northern China (Antón, 2002; Kidder and Durband, 2004; Wolpoff, 1999; see the phylogenetic scheme illustrated in figure 9.8 of Rightmire 2001) but is more or less similar to the recent scheme illustrated by Stringer and Barnes (2015), where each population lineage is treated as relatively independent from each other.

Discussion: Denisovans on the Southern Dispersal Route of Early Modern Humans

Among the many unanswered questions about the Denisovans, I here discuss the issue of admixture with modern humans. There is evidence of gene flow from the Denisovans to modern humans, but the observed proportion of the Denisovan genetic component in each extant population shows an unexpected geographic pattern. It was substantially higher in Oceania (particularly New Guinea and Australia, or Sahul) and the eastern Indonesian islands (up to ∼5% of the genomes), but it was minimal in Sunda, mainland Asia, and the Americas (∼0.2%) and was absent in Europe and Africa (Prüfer et al. 2014; Reich et al. 2011). One explanation for this finding is that archaic Denisovans lived over "an extraordinarily broad geographic and ecological range, from Siberia to tropical Asia" and that the Denisovan gene flow occurred not in southern Siberia but in Southeast Asia (Reich et al. 2011). Cooper and Stringer (2013) even suggested that the Denisovans crossed the ocean and later admixed with early modern humans on the islands between the Sunda and Sahul lands (fig. 1).

Although there is ongoing controversy about the timing and routes taken by early modern human populations who dispersed from Africa deep into Asia, there is little doubt that the initial colonizers of Sahul were descendants of populations who migrated using the routes south of the Himalaya Mountains in the Late Pleistocene (Kaifu, Izuho, and Goebel 2015). Therefore, Denisovan admixture detected from the extant Australo-Melanesian populations must have occurred somewhere along this route in South or Southeast Asia. Two fundamental questions emerge: (1) Did the "southern Denisovans" belong to the same p-deme as the original Siberian Denisovans? (2) Who was present in South and Southeast Asia when modern humans first entered this region during the Late Pleistocene?

As for the first question, there is currently no empirical fossil evidence to suggest the presence of a single morphotype that was distributed across the extensive region between Siberia and Southeast Asia (I call this the "Greater Denisovan hypothesis"). More specifically, the two existing Denisovan molars, particularly the more recently reported Denisova 8, are morphologically unique among the known fossil collections from Asia (Sawyer et al. 2015). In my view, the phylogenetic model illustrated in figure 2 points to a rather patchy distribution of several distinct hominin groups (e.g., the Zhoukoudian and Hexian/Penghu p-demes) in each region of Asia. For these reasons, we may need to think of a scenario different from the Greater Denisovan hypothesis.

The alternative scenario we should consider is that the donor of Denisovan DNA to the Australo-Melanesians belonged to its own p-deme but shared a substantial portion of DNA with the Siberian Denisovans because of their shared ancestry. Another hypothesis that is compatible with this is that the "Siberian Denisovan" had no taxonomic reality, but it was a Neanderthal population admixed with another local primitive hominin. Namely, the reported occurrence of both the Denisovan and Neanderthal DNAs in the same Denisova cave (and possibly even in the same stratigraphic unit in it) does not mean alternating occupations by different p-demes (Sawyer et al. 2015) but is ascribed to individual genetic variation within the same population: some of the members inherited unmixed Neanderthal nuclear DNA but others did not, and the more ancient mtDNA identified for the three Denisovan individuals derived from the other archaic population. The unidentified occupants from the Lower Paleolithic open-air site of Karama near the Denisova cave (Derevianko and Shunkov 2005) may or may not represent such a non-Neanderthal local population in the Altai.

In either case, the above discussion raises a possibility that the morphotype of the "southern Denisovan" is not necessarily similar to the original Siberian Denisovan, and the former may be represented in the already-known fossil samples from South or Southeast Asia.

With these predictions in mind, we turn to the second question, which is the original occupants on the southern dispersal route by early modern humans. The phylogenetic model illustrated in figure 2 suggests the presence of at least three distinct p-demes on this route in the Late Pleistocene: a late archaic *Homo* (the Maba/Hathnora p-deme) in the region of India and the mainland Southeast Asia, late *H. erectus* (Ngandong p-deme) in Java, and *H. floresiensis* (Liang Bua p-deme) on Flores. On the basis of this observation, I discuss the following different scenarios with regard to the possible donor of the Denisovan DNA, mainly from the perspective of the Asian hominin fossil record.

A. *The Maba/Hathnora p-deme.* The divergence time of this hypothetical deme from the lineage leading to *Homo sapiens* is unknown, but it was probably sometime in the Middle Pleistocene if this deme was related to African or European Middle

Pleistocene *Homo.* This date is consistent with the estimated divergence time of autosomal DNA between the Siberian Denisovans and modern humans (550–765 ka; Prüfer et al. 2014). However, the lack of Denisovan DNA in present-day South and mainland Southeast Asian populations contradicts the hypothesis that the Maba/Hathnora p-deme was the source of the Denisovan DNA seen in present-day Oceania (Cooper and Stringer 2013; Reich et al. 2011).

B. *Javanese* Homo erectus. The past geographic range of this long-lasting lineage is unclear, but it is quite possible that it was widespread across the Sunda region (fig. 1). This is probably why Stringer and Barnes (2015) referred to this lineage as "Sunda *H. erectus.*" If so, the migrating ancestral population of Australo-Melanesians must have come across them, giving a chance of introgression. The divergence time between Javanese *H. erectus* and *H. sapiens* is probably much older than 1.2 Ma, but the inconsistency with the reported divergence time between the Siberian Denisovans and modern humans may not be a problem if the former was an admixed population between the local primitive hominins and Neanderthals as discussed above. If this *H. erectus* deme was the source of the Denisovan DNA found from Oceania, this event might explain some *H. erectus*–like cranial characters in fossil and extant aboriginal Australians, as noted before by proponents of the multiregional hypothesis of modern human origins (e.g., Hawks et al. 2000; Wolpoff and Lee 2015). The absence of Denisovan DNA in the present-day populations of Sunda can be explained by the later expansion of farming communities from the north and resultant genetic overprinting (Matsumura, Oxenham, and Lan Cuong 2015).

C. Homo floresiensis. Flores, the home of *H. floresiensis*, is on the way from Sunda to Sahul. So early *H. sapiens* probably encountered this diminutive, small-brained, archaic hominin. However, I doubt whether they substantially interbred with each other, primarily because signatures of such admixture are not evident in the skeletal morphology of Australo-Melanesians.

Concluding Remarks

The existing Asian fossil record is admittedly scant, but it is always productive to intensively review what we can and cannot say on the basis of the available materials. Contrary to the classic scheme, the accumulating fossil evidence suggests the presence of regionally different evolutionary lineages or p-demes of archaic *Homo* in Pleistocene Asia with no clear geographic morphoclines (fig. 2). The current paleoanthropological evidence is also useful to question some aspects of the existing hypotheses regarding Denisovan introgression to modern humans, which derived from the genetic data. In particular, I found that the "Javanese *Homo erectus* as the southern Denisovans hypothesis" is tenable and worth further investigation. Of course, it is possible that the fossils of the southern Denisovans are yet to be discovered or still remain unrecognized in

existing fossil collections. However, closer scrutiny of other possible scenarios is needed before we reach this conclusion.

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Homo sapiens in the Eastern Asian Late Pleistocene

by María Martinón-Torres, Xiujie Wu, José María Bermúdez de Castro, Song Xing, and Wu Liu

Online enhancement: appendix

Recent fossil and genetic data poses new questions about the degree of variability of the Late Pleistocene fossils from China and the possible interaction of modern humans with other archaic hominins. This paper presents a general overview of the variability of the dental fossil record from some key Late Pleistocene localities in China. Our study reveals that despite having similar chronologies, not all the samples present the same suite of derived traits. This finding may reflect complex demographic dynamics with several migrations and dispersals and/or a degree of population substructure similar to that described for the African continent. Simple and linear models to explain the origin and dispersals of *Homo sapiens* seem to be progressively outdated by the new fossil, demographic and genetic evidence. In addition, we warn about genetic admixture as a possible source of morphological variability and we hypothesize that some skeletal features of *Homo floresiensis* and Denisovans could be related to their hybridization with other hominin groups.

Recent studies suggest that the variability of the hominin Asian fossil record, particularly for the Middle to the Late Pleistocene is larger than expected (e.g., Curnoe et al. 2012, 2015; Liu et al. 2017; Martinón-Torres et al. 2016; Xing et al. 2016). New fossil and genetic data suggest that along with "classic" *Homo erectus*, Asia has witnessed the early arrival and/or evolution of *Homo sapiens* (Kuhlwilm et al. 2016; Liu et al. 2015; Shang and

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Trinkaus 2010), Denisovans (Reich et al. 2010; see Buzhilova et al. 2017; Sawyer et al. 2015; Stringer and Barnes 2015), "archaic" or "post-*erectus*" hominins (Buck and Stringer 2014; Stringer 2012; Stringer and Barnes 2015), *Homo floresiensis* (Brown and Maeda 2009; Brown et al. 2004; Kaifu et al. 2015), and some other specimens of uncertain taxonomical attribution (Curnoe et al. 2012, 2015; Li et al. 2017; Xing et al. 2015b). So far, there are no Neanderthal fossils east of the Altai Mountains in Siberia (Prüfer et al. 2014). However, some Chinese specimens display features that were defined as typically Neanderthal (Li et al. 2017; Martinón-Torres et al. 2007; Wu and Bruner 2016; Wu and Trinkaus 2014; Wu et al. 2014), and genetic studies reveal that Neanderthals and *H. sapiens* may have interbred outside Africa as early as 100 ka (Kuhlwilm et al. 2016; Prüfer et al. 2014; Reich et al. 2010; Simonti et al. 2016; Vernot et al. 2016; but see Fu et al. 2015; Sankararaman et al. 2012).

This paper aims to present a general overview of the dental morphological variability in early Late Pleistocene China and poses new questions derived from the contemporaneity and possible interaction of *H. sapiens* with other archaic hominins. The notion that genetic exchange has occurred several times, among different species, throughout the Late Pleistocene (Kuhlwilm et al. 2016; Prüfer et al. 2014; Simonti et al. 2016; Vernot et al. 2016) adds a possible source of morphological variability that needs to be considered when analyzing the fossil record (see Ackermann, Mackay, and Arnold 2016; Ackermann, Rogers, and Cheverud 2006). To this purpose, we will first briefly present some of the key Pleistocene human fossil localities that

currently support the presence of *H. sapiens* in China before 50 ka. Then we will discuss the degree of hominin morphological variability within China during the early Late Pleistocene and the degree of variability of China compared to that of Africa during the same period. Finally, we will address the weight of genetic admixture as potential source of anatomical variability by reviewing the cases of Denisovans and *H. floresiensis*.

We will focus on the dental evidence, as it is the most abundant and well-preserved record in all periods and geographical locations, and it allows a deeper and wider assessment of the variability of the hominins at that time, including the "elusive" Denisovans whose anatomical evidence consists of three teeth and a finger bone (Sawyer et al. 2015). Due to their high component of genetic expression, teeth have been considered the "safe box" of the genetic code, becoming an ideal proxy to infer phylogenetic relationships (Guatelli-Steinberg and Irish 2005; Irish and Guatelli-Steinberg 2003). The frequency and degree of expression of many of the discrete traits of the crown and the root have distinct patterns of variation among different hominin populations, becoming a valuable source of information to infer the relationship among human groups (Irish and Guatelli-Steinberg 2003; Pilbrow 2006*a*, 2006*b*; Scott and Turner 1997; Turner, Nichol, and Scott 1991).

Early Late Pleistocene Human Evidence from China

Currently, there are more than 40 localities in China with Late Pleistocene hominin fossils (fig. 1; table 1; Dennell 2014; Keates 2010; Wu and Poirier 1995). Until recently, the earliest unambiguous evidence of *Homo sapiens* eastward of the Arabian Peninsula was found at Tianyuan Cave (Shang and Trinkaus 2010); Niah Cave, Borneo (Barker et al. 2007); Tam Pa Ling, Laos (Demeter et al. 2012, 2017); and Lake Mungo, Australia (Bowler et al. 2003), all of them dated to 40–50 ka. The Fuyan Cave in Daoxian (South China; Liu et al. 2015) and the recently redated human fossils from Zhirendong (South China; Cai et al. 2017; Liu et al. 2010*a*) have refueled the hypothesis that *H. sapiens* was in China 30–60 kyr earlier than the classic Recent Out of Africa hypothesis predicted. Other lines of evidence, such as archaeological, environmental, chronological, and genetic data (Armitage et al. 2011; Bae 2017; Blinkhorn and Petraglia 2017; Boivin et al. 2013; Bretzke and Conard 2017; Kuhlwilm et al. 2016; Reyes-Centeno et al. 2014) also point to the possibility that modern humans were in Asia during the first half of the Late Pleistocene (but see Michel et al. 2016; Norton and Jin 2009; Shen and Michel 2007).

Among these sites, Fuyan (Daoxian) Cave, Luna Cave, Zhirendong Cave, and Huanglong Cave are currently considered as the best evidence in support of the early presence of *H. sapiens* in China, based on a clearer chronostratigraphic context and a more diagnostic morphology. There are other sites such as Ganqian (Tubo; Shen et al. 2001), Tongtianyan (Liujiang; Shen et al. 2002; Yuan, Chen, and Gao 1986), Dingcun (Chen, Yuan, and Gao 1984; Pei 1985), and Jimuyan (Wei et al. 2011) that we consider of interest to assess the evolution of modern

humans in China. However, because of the more ambiguous morphology of the fossils and/or uncertainties about their antiquity they are considered less unequivocal than those from Fuyan Cave, Luna Cave, Zhirendong Cave, and Huanglong Cave. These additional sites are presented in the appendix, available online. We may note that this study only includes dental evidence that has been dated to the first half of the Late Pleistocene, so the number of sites with evidence in support of an early *H. sapiens* dispersal is indeed larger than discussed here (see fig. 1; table 1).

Fuyan (Daoxian) Cave

In 2015 we provided what we feel is the strongest fossil evidence in support of the presence of fully modern humans in China in the early Late Pleistocene (Liu et al. 2015). The sample consists of 47 human teeth (fig. 2) that can be unambiguously attributed to *H. sapiens* and that are dated between 80 and 120 ka through a multidisciplinary approach that includes high-precision multicollector inductively coupled plasma mass spectrometric (MC-ICP-MS) techniques, ^{14}C measurements on fauna, biostratigraphy, paleomagnetism, and a detailed geological and stratigraphic study (see Liu et al. 2015 for details). Morphometrically, the attribution of the Daoxian teeth to *H. sapiens* is unequivocal (Liu et al. 2015). Apart from proving the presence of *H. sapiens* considerably earlier than was previously thought (but see Michel et al. 2016), the Daoxian teeth bring along new questions and evolutionary scenarios that need to be tested in the coming years. The Daoxian teeth are more derived than other contemporaneous populations from Africa and Europe and closer in morphology to contemporary modern humans and late Late Pleistocene samples. Within the Late Pleistocene hominins, the teeth from Daoxian are more derived than those from Qafzeh despite having similar chronologies, not only by presenting smaller dimensions but also in the lack of buccal/labial grooves in their anterior dentition and in the modern-like relative cusp size of upper first molars compared to Qafzeh (Liu et al. 2015). In our opinion, these differences point to the possibility that the Levantine and the early Late Pleistocene Chinese *H. sapiens* represent two different demes (see the discussion below).

Zhiren Cave

The Zhiren Cave in South China has provided a human mandible and two associated teeth (likely one M_2 and one M_3) that were presented as the earliest *H. sapiens* fossils in China (Liu et al. 2010*a*). Initially U-series dating on overlying flowstone attributed these human fossils to the very early Late Pleistocene (100–113 ka BP). The associated faunal sample was interpreted as typical of the late Middle or early Late Pleistocene (Liu et al. 2010*a*). The claim of the "earliest *H. sapiens*" was not fully accepted by the scientific community because of some uncertainties on the correlation between the fossils and the dated flowstones (Dennell 2010; Kaifu and Fujita 2012) and because
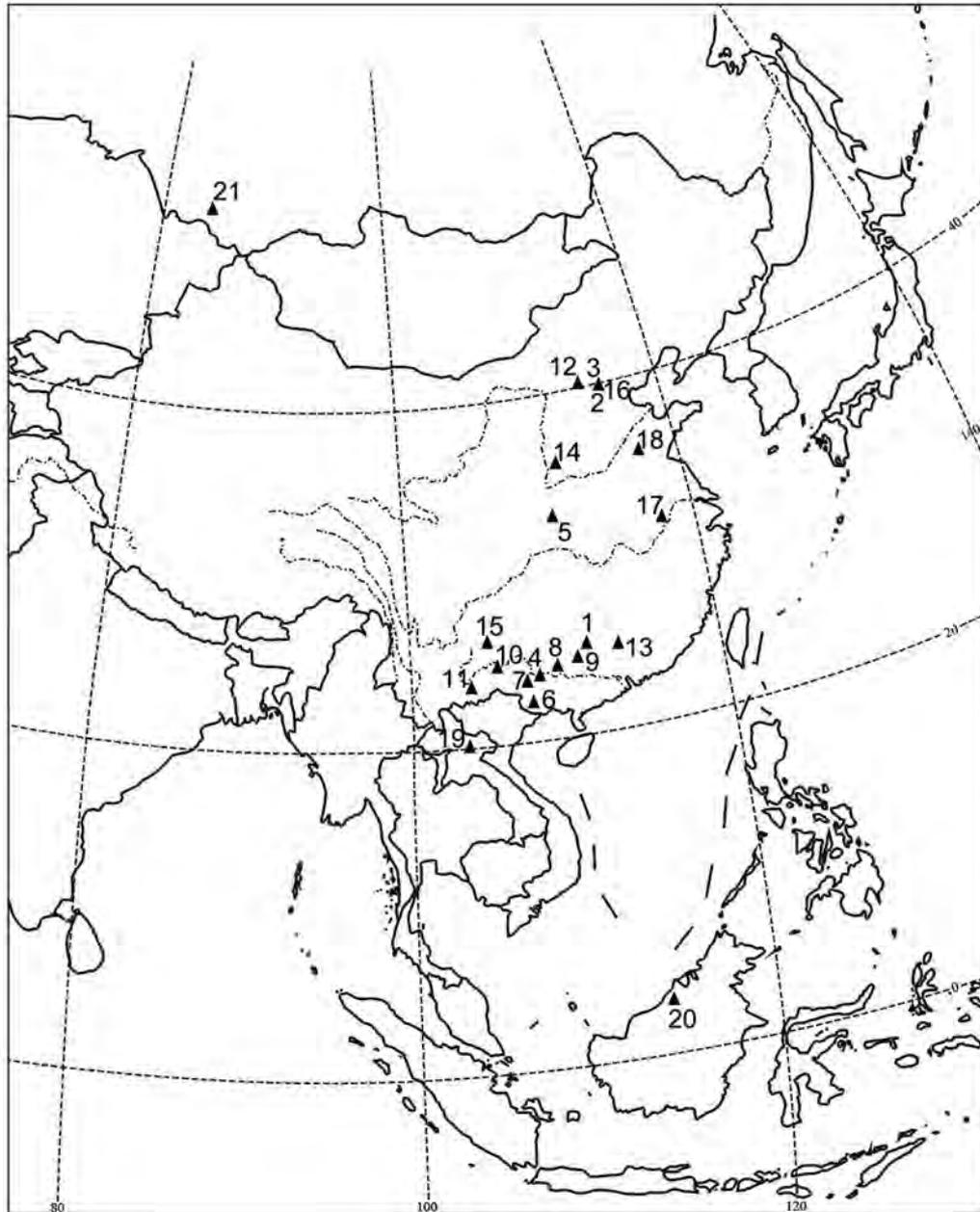
Figure 1. Map of eastern Asia with the location of Daoxian and other sites that have yielded late archaic or early modern human remains. 1 = Daoxian; 2 = Tianyuan Cave; 3 = Upper Cave; 4 = Liujiang; 5 = Huanglong Cave; 6 = Zhiren Cave; 7 = Luna Cave; 8 = Tobo Ganqian Cave; 9 = Jimuyan; 10 = Longlin; 11 = Maludong Cave; 12 = Xujiayao; 13 = Maba; 14 = Dingcun; 15 = Panxian Dadong; 16 = Zhoukoudian Locality IV; 17 = Hexian; 18 = Yiyuan; 19 = Pa Ling; 20 = Niah Cave; 21 = Denisova.

of the expression of some archaic features on the mandible that were obscuring its taxonomic assignment (Dennell 2010, 2014). Recently, paleomagnetic, stratigraphic, and optically stimulated luminescence (OSL) dating methods have been applied to the cave sediments, allowing a more precise bracketing of the human remains between 106 and 110 ka and apparently clearing the doubts related to the chronology of the Zhirendong deposits (Cai et al. 2017).

Regarding the taxonomy of the fossils, the mandible presents all the primary anterior symphyseal elements of a modern human chin such as a projecting tuber symphyseos, distinct mental fossae, modest lateral tubercles, and a vertical symphysis (Liu et al. 2010*a*), a combination that is considered as typical and possibly exclusive of *H. sapiens*. However, Liu and collaborators (2010*a*) highlight that the corpus robustness of Zhirendong places the fossil close to later Pleistocene archaic

Table 1. Summary of the main Middle and Late Pleistocene sites in China with human fossils mentioned in this paper and their ages

Specimen	Preservation	Dating (ka)	References
Daoxian	47 isolated teeth	120–80	Liu et al. 2015
Tianyuan Cave	Partial mandible and most of postcranial	42–39	Shang and Trinkaus 2010
Liujiang	1 complete cranium and some postcranial bones	~67	Yuan, Chen, and Gao 1986
		111–139	Shen et al. 2002
Huanglong Cave	7 isolated teeth	44–34	Liu et al. (2010*b*
		103–79	
		101–81	Shen et al. 2013
Zhiren Cave	Partial mandible, a small piece of alveolar bone around the second or third right mandibular molar, and a single right mandibular second or third molar	100–113	Cai et al. 2017; Liu et al. 2010*a*
Luna Cave	2 isolated teeth	127–70	Bae et al. 2014
Xujiayao	1 maxilla, 1 temporal bone, 1 ramus of mandible, 3 isolated teeth, 2 occipital bones, 12 parietal bones	125–104	Chen, Yuan, and Gao 1984; Chen et al. 1982
		220–160	Tu et al. (2015
Longlin	Partial cranium with left I^1–M^1; right I^2, fragment of M^1, partial mandible with left I$_1$, canine, P$_3$, M$_2$–M$_3$; right I$_1$–I$_2$, canine, P$_3$–P$_4$ and M$_2$, several isolated tooth fragments, almost complete left half of axis (vertebra C2), proximal ulna fragment, and several rib fragments	11.5	Curnoe et al. 2012
Maludong Cave	1 cranium and 2 mandibles	~14	Curnoe et al. 2012
Tobo Ganqian Cave	17 isolated teeth	>100	Shen et al. 2001
Dingcun	3 isolated teeth and 1 immature parietal bone fragment	114–75	Pei 1985
		160–200	Chen, Yuan, and Gao 1984
Jimuyan	5 isolated teeth	Late Pleistocene	Wang et al. 2011
Panxian Dadong	4 isolated teeth	300–130	Jones et al. 2004; Shen, Liu, and Jin 1997
Zhoukoudian Locality IV	1 left upper third premolar	175–135	Chen, Yuan, and Gao 1984
Hexian	1 cranium, a mandibular fragment, and 10 isolated teeth	412	Grün et al. 1998; Liu et al. 2017; Xing et al. 2014;
Yiyuan	7 isolated teeth	420–320	Han et al. 2015
Upper Cave	3 skulls, 3 skull fragments, 4 mandibles, isolated teeth, vertebrae, and some postcrania	~34	Chen, Hedges, and Yuan 1992
Maba	Most of a right cranium with right orbital and partial nasal bone	135–129	Yuan, Chen, and Gao 1986

humans. This apparent mosaic pattern of mandibular morphologies could be suggestive of a modern human emergence scenario for East Asia with assimilation or population continuity with gene flow between *H. sapiens* and a more archaic population. Even in the hypothetical case that Zhirendong hominins represent a hybrid between *H. sapiens* and a late-surviving *Homo erectus*, this would still mean that *H. sapiens* was present in China around 100 ka to allow the gene flow to occur. In addition, little is known about how to recognize a human hybrid in the fossil record (see the discussion below). Other researchers have pointed out the possibility of the Zhirendong mandible representing a "gracile *H. erectus*" (Dennell 2010, 2014). However, none of the "archaic" traits are diagnostic of *H. erectus* s.s. Beyond variable degrees of symphysis projection also documented in present-day populations, the Zhirendong mandible presents the characteristic lower border protrusion of *H. sapiens* (see, e.g., Pampush 2015; Thayer and Dobson 2013). In addition, despite the high degree of wear, it is possible to identify clear *H. sapiens*–like dental features. By

microscopic inspection of the original specimens we certify that Zhiren 1 molar shows a + type of occlusal groove pattern and that the middle and distal trigonid crests, the C6 and the C7, are absent. The roots are slender and display a high bifurcation. This constellation of crown and root features, together with the small dimensions (Liu et al. 2010*a*), are typical of *H. sapiens* and outside of *H. erectus* s.s. variation (e.g., Martinón-Torres et al. 2016; Xing et al. 2014, 2016; but see Zanolli 2013 and the discussion below). Zhiren 2 has strongly parallel roots with high bifurcation, although a taphonomical alteration of the root surface prevents a proper morphological assessment. The crown does not show signs of middle or distal trigonid crest or of anterior fovea, fitting the typical pattern of *H. sapiens* (Bailey 2002; Irish and Guatelli-Steinberg 2003; Martinón-Torres et al. 2007; Scott and Turner 1997). Finally, it is noteworthy that socket shape indicates dental winging for its lower central incisors. Interestingly, to our knowledge, winging (see Scott and Turner 1997 for definition) has been only documented in *H. sapiens*.
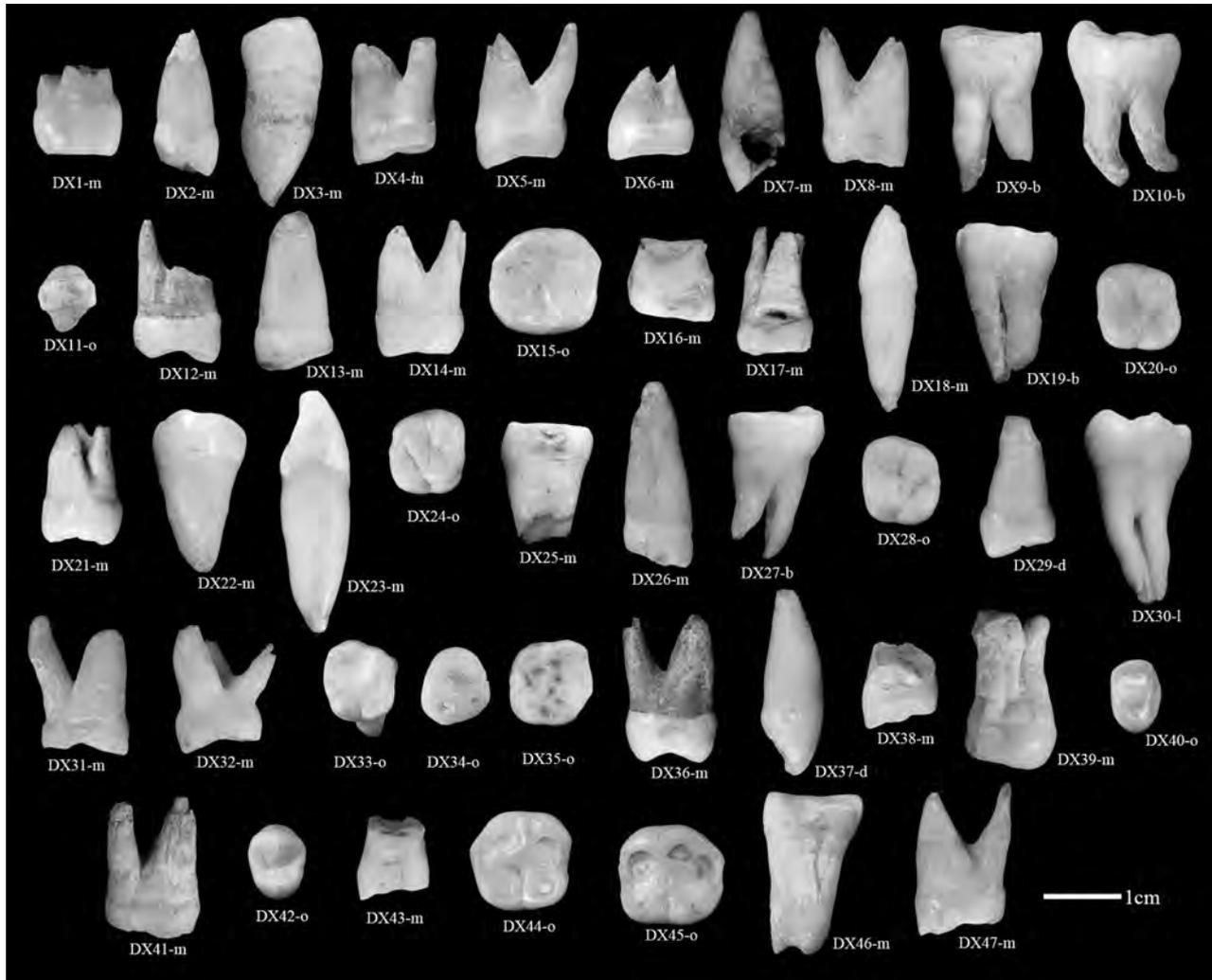
Figure 2. Daoxian teeth (o = occlusal; b = buccal; m = mesial; l = lingual; d = distal). A color version of this figure is available online.

Luna Cave

Luna Cave in the Guangxi Zhuang Autonomous Region in southern China has provided only two human teeth (Bae et al. 2014), so the morphological information they can provide is limited. It is important to highlight that these fossils are found in situ in a stratified deposit in association with flake tools. No direct dating of the fossils or fauna has been attempted to date. However, the U-Th dating of apparently stratigraphically well-constrained speleothems in close association with the human remains suggests a secure minimum age of 70 ka for these teeth (Bae et al. 2014). In our opinion, the Luna Cave teeth also present features typically found in modern humans (but see *Homo floresiensis* discussion below) such as simplified occlusal surfaces, strongly reduced hypocone and a four-cusped lower molar. Yet, the M_2 roots are more robust than those found in Daoxian and Zhiren caves (Liu et al. 2010a, 2015). This, together with the small sample size, renders the Luna teeth less

strong evidence for attribution to *H. sapiens* than that from Daoxian.

Huanglong Cave

The excavation at Huanglong Cave, in the Hubei Province in central China, has uncovered seven human teeth together with dozens of stone and bone artifacts and possible burned sediments (Liu et al. 2010b). A multidisciplinary chronological approach was undertaken with electron spin resonance (ESR), U-series on associated fauna and speleothems and the identification of an "*Ailuropoda-Stegodon*" faunal unit in association with the hominins. These methods provided apparently diverging ages ranging between 34 and 44 ka (ESR) to 79–103 ka (U-series). Recent U-series dates on localized thin flowstone formations bracket the hominin specimens between 81 and 101 ka (Shen et al. 2013). Regarding the taxonomic assignment,

Liu et al. (2010*b*) provided a detailed description and comparison of the Huanglong teeth, concluding that most of the features were typical of modern *H. sapiens*, though they also highlighted a more pronounced root robustness than in other contemporaneous populations. Here we ratify the taxonomic assignment to *H. sapiens* and particularly highlight that Huanglong I¹ presents a double-shovel shape, a feature that is likely autapomorphic of *H. sapiens* (Bailey and Hublin 2013; Irish 1998*a*, 1998*b*; Liu et al. 2013; Martinón-Torres et al. 2007). Overall, relying on a more precise chronostratigraphy and a better understanding of the fossil record variability (e.g., Bae et al. 2014; Curnoe et al. 2012, 2015; Li et al. 1984; Liu et al. 2010*a*, 2010*b*; Xing et al. 2015*b*), we consider that the Huanglong Cave fossils represent robust evidence of the presence of *H. sapiens* in China during the early Late Pleistocene.

Discussion

Variability of Northern versus Southern Asia

The study of both dental and cranial evidence from China (e.g., Liu et al. 2010*a*, 2010*b*, 2015; Wu and Trinkaus 2014; Wu et al. 2014; Xing et al. 2015*b*) points to differences in the geographic distribution of sites with modern human remains. Early Late Pleistocene localities with fossil teeth that can be reasonably attributed to *Homo sapiens* tend to be restricted to southern China (Bae et al. 2014; Liu et al. 2015; Martinón-Torres et al. 2016). In contrast, the earliest unequivocal *H. sapiens* fossils from northern China are not older than ca. 40 ka (Shang and Trinkaus 2010; Wei et al. 2016). The hypothesis that during the same period southern China was inhabited by more derived populations than central and northern China could stretch back to the Middle Pleistocene. The Panxian Dadong fossils (Liu et al. 2013) are more derived than other Middle Pleistocene groups such as those coming from Zhoukoudian, Hexian, Yi-yuan, or Xujiayao (Bailey and Liu 2010; Liu et al. 2017; Martinón-Torres et al. 2016; Xing 2012; Xing et al. 2014, 2015*b*, 2016).

The differences between the hominin populations from northern and southern China are relevant for the study of the pattern and routes of hominin dispersals (Liu et al. 2015; Martinón-Torres et al. 2016). Climatic instability and the fluctuating extension of deserts (Boivin et al. 2013; Dennell 2013*a*, 2013*b*) could have favored a pattern of fragmentation and isolation within China, resulting in the persistence of more primitive hominin lineages in northern latitudes while more derived lineages arrive and/or evolve in the south.

In addition, the early Late Pleistocene samples from China may present some biological and cultural affinities that could shed light on the first dispersals of *H. sapiens* into the region. Teeth from Daoxian present obvious caries during a period when they are considered infrequent, and that could potentially cast doubts on their antiquity. However, the same type of cavities have been found in Zhirendong and Tubo. This could mean that the first modern humans that arrived to Asia shared the same change in immune susceptibility that made them more prone to develop caries. Alternatively, the relatively higher incidence of caries may reflect a change of diet in these populations. This is particularly important in the light of studies suggesting that modern humans may have exploited rainforest resources in southern and southeast Asia earlier than usually assumed (e.g., Demeter et al. 2012; Roberts et al. 2015, 2016; Westaway et al. 2007). The earliest dispersal of modern humans outside Africa may be related to the development of new ecological adaptations that allowed *H. sapiens* to disperse into new territories. In turn, the exploitation of new ecosystems may be potentially related with the finding of new resources for consumption that may make these populations more prone to suffer caries, although this theory needs further research.

Finally, it is worthy to note that some teeth from Daoxian and Huanglong Cave (Liu et al. 2010*b*, 2015; Wu et al. 2006) present certain activity-related wear marks such as elongated wear facets at the cement-enamel junction or strongly oblique occlusal planes (Smith 1984). These marks could exemplify some cultural complexity or behavioral innovations in these groups, potentially allowing them to settle in the southern part of Asia.

Variability of Late Pleistocene Asia versus Africa

The analysis of the Late Pleistocene dental samples from China reveals that the combination of primitive and derived features does not follow a temporal gradient, and samples that are roughly contemporaneous may show a different combination of traits. Previous studies pointed to the presence of more primitive populations in northern China by the time when more derived groups had already inhabited the southern latitudes (Liu et al. 2013, 2015; Martinón-Torres et al. 2016; Xing et al. 2015*b*). Based on a range of genetic, anatomical, and ecological analyses, some researchers pointed to the terminal Pleistocene and early Holocene in Southwest China as a complex period with several human migrations throughout different routes (Curnoe et al. 2012, 2015; Ji et al. 2013; Zhong et al. 2011) as well as population admixture. Recently, Curnoe et al. (2012) studied the fossil assemblages recovered at the Longlin and Maludong localities in Southwest China, dating to ca. 11.5 ka cal BP and 14.3 ka cal BP, respectively. These hominins expand the range of morphological variability known for this period as they combine a high number of ancestral features with some unusual traits such as the strong alveolar prognathism and the broad flat midface (Curnoe et al. 2012). According to Curnoe and colleagues (2012) there are two possible hypotheses. One is that these hominins represent a late-surviving archaic population similar to what may have occurred in North Africa with the Aterian populations (see below) or that East Asia may have been colonized during multiple waves, "with the Longlin-Maludong morphology possibly reflecting deep population substructure in Africa prior to modern humans dispersing into Eurasia" (Curnoe et al. 2012:1). In both hypothetical scenarios, the demographic story of East Asia does not seem lineal and suggests deep geographic subdivisions and population substruc-

ture, perhaps similar to what is being identified in Africa (Curnoe et al. 2012; Stringer 2016; and discussion below).

Our research would support the notion of complex population dynamics during the Pleistocene-Holocene transition in China and obliges us to abandon lineal narratives to explain the origin and evolution of *H. sapiens*. Similar conclusions were reached by other researchers after analyzing the African record (e.g., Gunz et al. 2009; Stringer 2016). The chronological overlap between modern and more primitive morphs in the late Middle Pleistocene/early Middle Stone Age fossil record from Africa suggests that the appearance of *H. sapiens* in the continent cannot be seen as a simple linear progression toward the typical present-day populations (Stringer and Barnes 2015). According to Stringer (2016:8), "there was never a single centre of origin, and despite later homogenization," some ancient substructure could have persisted in Africa (see also Gunz et al. 2009). This idea is supported by the new fossils and dates from the Jebel Irhoud site in Morocco (Hublin et al. 2017; Richter et al. 2017). The presence of a pre-*sapiens* population in northern Africa by 300 ka suggests that evolutionary processes behind the emergence of *H. sapiens* have not been confined to sub-Saharan Africa (Hublin et al. 2017; Stringer and Galway-Witham 2017).

As we discuss below, even in the context of an Out of Africa hypothesis, the idea of a single unidirectional dispersal seems to be progressively outdated by new fossil, demographic, and genetic evidence. The revelation that human genomes contain DNA introgressed through interbreeding with archaic hominins outside Africa obliges us to revisit the original formulation of the Out of Africa model (Groucutt et al. 2015; Stringer 2011) and to discuss alternative models. One of the alternatives is the multiregional with hybridization model (Wu 2004), which states that the origin of modern humans can be explained by local continuity with minor degree of interpopulation gene flow. Another key alternative is the assimilation model, which assumes African origin for our species but suggests that subsequent spread involves genetic admixture with local archaic humans rather than replacement (Smith, Falsetti, and Donnelly 1989; Smith, Janković, and Karavanić 2005; Smith et al. 2016; Trinkaus 2005).

Unfortunately, the dental fossil record from the late Middle to early Late Pleistocene is not large enough to provide details of early occurrences of *H. sapiens*. Even among those who defend an African origin for *H. sapiens* (see Wu 2004 for discussion), the specific geographical origin of the source population of present-day humans is still debated. Some scholars have suggested that the populations that inhabited sub-Saharan Africa are good candidates to represent the source for present-day humans in the world (e.g., Grine 2000; Grine and Henshilwood 2002; Grine, Henshilwood, and Sealy 2000; Grine, Klein, and Volman 1991; Grine et al. 2007; Irish and Guatelli-Steinberg 2003). In contrast, other researchers point to North Africa as a key area to explore the origin of the earliest *H. sapiens* outside Africa, especially if we take into account its proximity to the Levantine region where Qafzeh and Skhul are located (Hublin

and Tillier 1981; Hublin et al. 2012, 2017). Here we review the dental evidence from both aforementioned regions.

In North Africa, the richest Middle and Late Pleistocene hominin samples come from Morocco (Hublin et al. 2012, 2017). The Aterian human populations are represented by the dental evidence from Dar es-Soltan, Grotte des Contrebandiers, and El Harhoura localities (Hublin et al. 2012), dating to between 35 and 90 ka. They are characterized by remarkably large and robust postcanine dentitions, falling well outside the range of variation of Upper Paleolithic *H. sapiens* and frequently outside Neanderthals and the Middle Paleolithic samples of Qafzeh and Skhul. Lower teeth are comparatively smaller than upper teeth but are still larger than in Neanderthals and Upper Paleolithic modern humans. As highlighted by Hublin et al. (2012), these dentitions are characterized by the expression of well-developed accessory ridges in upper premolars, high frequencies of Carabelli's trait, the nonreduction and even exceptionally large (and subdivided) hypocones, and a large mesial accessory marginal tubercle in one of the specimens. Hublin and colleagues (2012) interpret these traits as primitive and reminiscent of the anatomically modern humans from the Levant and the ca. 40 ka fossils from Peștera cu Oase in Romania (Trinkaus et al. 2003). Thus, they suggest that the Aterian groups could be linked to the first dispersal of *H. sapiens* into Eurasia.

Later genetic analyses revealed that the Peștera cu Oase individual contains 6%–9% of Neanderthal genes (2% more than any living human today) and that this population did not contribute substantially to later Europeans (Fu et al. 2015). If Aterians are somehow related to the anatomically modern humans from the Levant and Romania, then the Peștera cu Oase fossils would expand the northern limit of the so-called failed dispersal (sensu Mellars 2006; Oppenheimer 2009) of Skhul and Qafzeh hominins, in the sense that this first dispersal neither significantly expanded beyond its geographical origin nor contributed significantly to extant modern human populations.

In our opinion, the dental morphology of the Aterian groups is remarkably different from most Late Pleistocene populations in southern China. Interestingly, this pattern of morphological "giantism" is similar to the pattern observed in other northern and eastern African groups predating the Aterians such as those from Rabat, Jebel Irhoud, and Tighenif (Bermúdez de Castro et al. 2007; Hublin 1985; Hublin and Tillier 1981; Hublin et al. 2017; Vallois and Thoma 1977). The late Middle Pleistocene teeth from Jebel Irhoud have been described as "modern-like" due to the absence of typically Neanderthal traits (Hublin et al. 2017). However, and like the Aterian samples, these teeth have very large crowns and roots, and their molars have been described as morphologically complex. This would reinforce the idea that North Africa may have not worked well as a population source but as a sink (see Dennell, Martinón-Torres, and Bermúdez de Castro 2011 for a definition of sources and sinks). However, the association of the Jebel Irhoud fossils with Middle Stone Age lithics like those found in eastern and southern Africa leaves open the possibility that hominins and their tech-

nologies may have migrated across the continent (Stringer and Galway-Witham 2017).

Besides the North African groups, the Late Pleistocene fossil record roughly contemporaneous to the Daoxian samples is mostly restricted to the South African localities of Klasies River Mouth (90 ka; Rightmire and Deacon 2001), Die Kelders (60–80 ka; Grine 2000), and Blombos Cave (65–70 ka; Grine, Henshilwood, and Sealy 2000). In general, these samples are described as "essentially modern," small in size when compared to penecontemporaneous archaic populations from Eurasia and mostly similar to South African living populations. The Die Kelders teeth present most of the morphological variants displayed by recent sub-Saharan Africans (Irish 1997, 1998*a*, 1998*b*), although some of these features are plesiomorphic (Stringer, Humphrey, and Compton 1997) and do not necessarily signify a close and regional evolutionary relationship between both. In general, the morphological and metric features of the sub-Saharan groups are closer to the southern China populations than to the North African ones (see Irish 1997, 1998*b* for detailed dental characterization of sub-Saharan populations). Whether closer similarities between Daoxian and the sub-Saharan groups are reflecting a closer relationship or are merely evincing regional variation needs further study and evidence.

In summary, the high degrees of morphological variability of the Late Pleistocene populations from both Africa and Asia may be indicative of deep population substructure and highlight the need to look for less lineal and anagenetic models to explain the origins of *H. sapiens*.

The Hybrid "Mess"

Recent genetic data have revealed a degree of admixture between *H. sapiens* and the indigenous populations that were already settled in Asia during the Late Pleistocene. This genetic exchange adds an important contributing factor to the morphological variability of the East Asian Late Pleistocene human groups (Ackermann, Mackay, and Arnold 2016; Harvati, Gunz, and Grigorescu 2007; Trinkaus 2005; Weaver and Roseman 2005; Wolpoff et al. 2001). As pointed out by Harvati, Gunz, and Grigorescu (2007), the earliest *H. sapiens* fossils outside Africa are key evidence to search for the phenotypic signal of interbreeding. It is often assumed that a human hybrid should display intermediate morphologies between the two parental populations or a "mosaic" of features inherited from each (e.g., Bräuer 1992; Frayer et al. 1993; Trinkaus 2005). It is not clear, however, how balanced is the weight that each parent has in the resulting phenotype, and it is also possible that the hybrid fits the morphotype of one of the parents with only one or two nonmetric features of the other (Soficaru et al. 2007). Yet the phenotypic expression of hybridization may be even more complex.

Recent studies on extant primates have provided interesting insights into the way we could potentially trace hybridization in the fossil record (see Ackermann, Rogers, and Che-

verud 2006; Harvati, Gunz, and Grigorescu 2007). Ackermann, Rogers, and Cheverud (2006) point out several skeletal manifestations that could be suggestive of inbreeding. According to these authors, genetic admixture frequently leads to evolutionary innovation (Ackermann, Rogers, and Cheverud 2006; Rieseberg et al. 2003). In this case, the hybrid could fall outside the range of parental forms (transgressive hybrids; Seehausen et al. 2014). The expression of novel phenotypes would obviously complicate tracing the ancestry of the admixture. The second feature is that hybrid skeletons of extant primates tend to display an increase or decrease in size, called "heterosis" and "dysgenesis," respectively. Third, hybrid populations are also characterized by high degrees of individual variability that may exceed the combined variation of both parental groups (Ackermann, Rogers, and Cheverud 2006; Harvati, Gunz, and Grigorescu 2007). Finally, we should expect a high frequency of rare osteological alterations, particularly supernumerary sutures and nonmetric dental anomalies (Ackermann, Rogers, and Cheverud 2006; Harvati, Gunz, and Grigorescu 2007; Schillaci et al. 2005). The majority of dental anomalies that Ackermann, Rogers, and Cheverud (2006) identified in their hybrid baboon sample were supernumerary teeth and tooth crowding or misalignment, particularly at the premolar region. As an example, 50% of the first-generation (F_1) olive and yellow hybrid males showed a supernumerary tooth, and 90% of these were bilaterally expressed, an anomaly that is below 5% in humans and other primates (Rajab and Hamdan 2002). According to these authors (Ackermann, Rogers, and Cheverud 2006), the individual expression of dental and osteological anomalies, particularly if they are uncommon, such as bilateral anomalies, could be good indicators of genetic admixture, even better than changes in size. These pathologies are usually interpreted as signs of developmental instability. It has been shown that even when the hybridizing populations have diverged as recently as 160 ka—as is the case of the yellow and olive baboons studied by Ackermann, Rogers, and Cheverud (2006)—interbreeding can result in an obvious breakdown in the coordination of development of their hybrid offspring. Although it is difficult to extrapolate these results to the hominin fossil record, evidence of heterosis and similar nonmetric anomalies in primate hybrids (Schillaci et al. 2005; Smith and Scott 2005) and in other animals such as recent and Late Pleistocene ground squirrel hybrids (Goodwin 1998) could prove useful to investigate the potential mixed ancestry of some hominin fossils (Harvati, Gunz, and Grigorescu 2007).

In the sections below, we take a closer look to *Homo floresiensis* and Denisovans through the prism of hybridization.

Homo floresiensis as a Potential Hybrid. Since it was first named (Brown et al. 2004), *H. floresiensis* has caused great debates between those who recognize its taxonomic distinctiveness and those who propose that it is a dwarfed and/or pathological individual (see Aiello 2010, 2013 for reviews). In our opinion, the possible contemporaneity of *H. sapiens* with *H. floresiensis* (Brown et al. 2004; Brumm et al. 2016) raises the

need to consider genetic exchange as a possible source of the anatomical variability of this group. Although the new dates on the Liang Bua locality (50–100 ka according to Sutikna et al. 2016) narrow the window of time for a possible admixture between *H. floresiensis* and *H. sapiens*, the evidence suggests that an overlap between both hominin groups should not yet be discarded (Demeter et al. 2012, 2017; Morley et al. 2016). Similarly, with minimum ages of ca. 143 ka for the Solo hominin remains (Indriati et al. 2011) the contemporaneity of *H. sapiens* and *H. floresiensis* with *H. erectus* still needs to be proven. However, the time gap is narrow enough to keep open the possibility that they may have overlapped in the region.

The dentition of *H. floresiensis* has been described as unique (Kaifu et al. 2015) due to the combination of features that has not been observed in any other hominin species. We agree with Kaifu et al. (2015) that *H. floresiensis* dentition cannot be simply explained as a scaled-down version of earlier hominins such as *Australopithecus*, *H. habilis* or *H. erectus*. Although it is not the purpose of this paper to review in detail the *H. floresiensis* teeth, we would like to focus on a few "peculiar" traits that could be potentially interpreted as signs of hybridization (see Ackermann, Rogers, and Cheverud 2006; Harvati, Gunz, and Grigorescu 2007).

Morphological novelties. In our opinion, *H. floresiensis* P_3 is anomalous/unusual both in terms of shape and absolute and relative size with regard to other elements of the dentition. Kaifu et al. (2015) "failed to find a single specimen with comparable morphology" for the Liang Bua P_3. Thus, this uniqueness could represent a morphological novelty in the context of genetic drift, speciation, or, as we would like to suggest, hybridization. In addition, the shape of lower molars is also atypical (as also shown by Kaifu et al. 2015). Beyond the expression of a midtrigonid crest, the pattern of additional crests at the enamel-dentine junction (Kaifu et al. 2015) does not fit any of the patterns described so far in extinct and extant humans (e.g., Bailey, Skinner, and Hublin 2011; Martínez de Pinillos et al. 2014; Martinón-Torres et al. 2014).

Dental pathologies. The specimen LB1 from Liang Bua presents full-sized bilateral rotated P^4's (Brown et al. 2004; Kaifu et al. 2015). According to Ackermann (2010), this is quite an unusual anomaly worthy of consideration as a possible sign of hybridization. In addition, LB1 also presents unilateral congenital absence of the right P_4 and right M^3 (Brown et al. 2004) and an aberrant occlusal wear pattern (Kaifu et al. 2009) that could be related to its hotly debated cranial and facial asymmetry (Argue et al. 2009; Baab, McNulty, and Harvati 2013; Eckhardt and Henneberg 2010; Kaifu et al. 2009). Interestingly, craniofacial asymmetry also has been interpreted as an indicator of developmental instability in the frame of hybridization (Ackermann 2010).

High level of intrapopulation variability. The shape analysis of the Liang Bua dental crowns (Kaifu et al. 2015) reveals that there is not a clear pattern of affinities with any of the comparative groups and specimens from the same dental class. Teeth from the same individual fall inside and outside of the ranges of variation of *H. sapiens*, *H. erectus*, and/or *H. habilis*. Although the sample is too small to properly assess intrapopulation variability ($n = 1$ or $n = 2$ depending on the dental class), it is worthy to note that P_3's plot relatively separated from each other. This could be reflecting high degrees of individual variability. However, more findings are needed to confirm this.

Although the debate about *H. floresiensis* has been fruitlessly polarized between those who defend a dwarfed *H. habilis* or *H. erectus*–like hominin (e.g., Argue et al. 2017; Baab, McNulty, and Harvati 2013; Brown and Maeda 2009; Brown et al. 2004; Kaifu et al. 2015; van den Bergh et al. 2016) and those who defend a pathological *H. sapiens* (e.g., Dalton 2008; Eckhardt and Henneberg 2010; Henneberg and Thorne 2004; Hershkovitz, Korneich, and Laron 2007; Jacob et al. 2006; Obendorf, Oxnard, and Kefford 2008), in light of the evidence presented here we suggest a third scenario. *Homo floresiensis* could indeed represent a primitive hominin, a dwarfed *H. erectus*–like group with some degree of introgression from *H. sapiens*, although input from a different species cannot be ruled out. This would explain the dental, cranial, and postcranial anomalies that have long been used to question its taxonomic status (see Aiello 2010, 2013 for reviews), reflecting a degree of developmental instability linked to genetic admixture.

The advanced molar features of Liang Bua (like the four-cusped lower molars) could be the result of space constraints in the mandibles of *H. floresiensis*, as suggested by Kaifu and colleagues (2015). Alternatively, they could be the result of gene flow from *H. sapiens*. Importantly, we would like to highlight that the derived molar traits of *H. floresiensis* also have been identified in a late Early/early Middle Pleistocene sample from Sangiran reported by Zanolli (2013). This *H. erectus* sample is remarkably different from the rest of the Early/Middle Pleistocene assemblages recovered from the Kabuh formation (Grine and Franzen 1994) in showing a significant decrease of MD dimensions, high frequency of four-cusped molars, and non-Y groove patterns. This derived combination is rare in Early and Middle Pleistocene fossils (except for those from Atapuerca–Sima de los Huesos; see Bermúdez de Castro and Nicolás 1995; Martinón-Torres et al. 2012) and confirms a high morphodimensional variability in the Sangiran material. In our view, this high variability is beyond the degree of time-related structural reduction in Javanese *H. erectus* (Martinón-Torres et al. 2016) and suggests more complex scenarios including the possibility of frequent population exchanges between continental and insular Asia. The similarities between *H. floresiensis* and this particular Sangiran deme with regard to the molar morphology could be an indicator of their biological affinity.

The recent discovery of a mandibular fragment and five teeth in the Mata Menge site (Flores, Java), dated to 700 ka and close to the Liang Bua locality (van den Bergh et al. 2016), indicates that humans were inhabiting Flores as early as the early Middle Pleistocene. This possibility was already raised after the discovery of stone tools dating to ca. 1 Ma in the Flores island (Brumm et al. 2010). While the Mata Menge fossils could be used as an argument to discredit the idea that Liang Bua fos-

sils are simply pathological versions of modern humans (see Gomez-Robles 2016), we think that more data is needed to suggest that both samples belong to the same species. After taking a closer look at the dental evidence, we agree with van den Bergh et al. (2016) that the Mata Menge teeth present morphological affinities with post-*habilis* grade *Homo* specimens. Apart from the continuous midtrigonid crest, we think that also the morphology of the I^1, with the moderate labial convexity and the pronounced but smooth basal eminence, falls within the range of variation of the Early to Middle Pleistocene populations from Asia (Martinón-Torres et al. 2007). However, even if it is logical to think that two small hominins found in the same small geographical area must be related, the current evidence is not specific or diagnostic enough to assume that Mata Menge and Liang Bua can be linked in an ancestor-descendant sequence. Beyond their small size, likely due to insular dwarfism, both samples do not share taxonomically distinctive traits to allow such an assumption. Although geographically close, these fossils are separated by more than 500,000 years, hence considering the Mata Menge fossils direct ancestors of the *H. floresiensis* from Liang Bua assumes more than half a million years of evolution in a small geographical area with likely high levels of isolation and inbreeding. This, together with the effects of an apparently rapid insular dwarfism (van den Bergh et al. 2016), renders a developmentally viable population difficult to envisage. Alternatively, Mata Menge may represent evidence of one of the several episodes of occupation of the Flores and nearby islands, confirming the complex nature of intermittent exchanges that may have occurred between continental and insular Southeast Asia throughout the Pleistocene (Dennell et al. 2014; Louys and Turner 2012; Martinón-Torres et al. 2016; Zanolli 2013).

In summary, the identification in the Liang Bua fossils of several features that have been posed as possible indicators of hybridization (see Ackermann, Mackay, and Arnold 2016; Ackermann, Rogers, and Cheverud 2006; Harvati et al. 2015) may support a conciliating hypothesis between the "two sides" of the debate, as it acknowledges a likely non-*sapiens* nature for the Liang Bua hominins but also recognizes obvious pathological features. As suggested by Ackermann, Rogers, and Cheverud (2006), even a small amount of evolutionary divergence among populations, over relatively short time periods, can result in the breakdown in the coordination of development in their hybrids. However, we should not forget that developmental anomalies in this sample also could be attributed to the rapid development and manifestation of insular dwarfism, genetic drift, inbreeding, and/or other developmental abnormalities (Ackermann 2010). More data would be necessary to confirm the hybrid status of *H. floresiensis*.

Denisovans: What Do They Look Like? Recent paleogenetic studies have identified a type of extinct hominin that shares a common ancestor with anatomically modern humans and Neanderthals (Buzhilova, Derevianko, and Shinkov 2017; Krause et al. 2010; Prüfer et al. 2014; Reich et al. 2010; Sawyer et al. 2015; Vernot et al. 2016) and whose DNA can be found in some living populations, particularly in Melanesia and northern Australia (Kuhlwilm et al. 2016; Meyer et al. 2013; Reich et al. 2010; Vernot et al. 2016). Although the skeletal evidence of this group is limited to three teeth and a finger bone, its genetic distinctiveness from Neanderthals and modern humans has led the scientific community to refer to them as "Denisovans." However, it is not clear yet whether they deserve specific distinction or may be represented by many Late Pleistocene human samples that we already know from the Asian fossil record (Li et al. 2017; Martinón-Torres et al. 2016; Stringer and Barnes 2015).

Mitochondrial DNA of Denisovans reveals that this group diverged from Neanderthals and modern humans at about 1 Ma (Krause et al. 2010). These results contrast with those obtained by the analysis of the nuclear DNA (Meyer et al. 2013, 2016; Reich et al. 2010), which suggests that Denisovans diverged from Neanderthals about 380–473 ka and from modern humans between 550 and 765 ka (Meyer et al. 2016). The genetic data also suggest that Denisovans interbred with modern humans, Neanderthals, and a third unknown archaic hominin lineage, possibly a late-surviving *H. erectus*, although its identity remains unclear (Prüfer et al. 2014; Sawyer et al. 2015). Given their mixed genetic legacy, we may expect that fossil candidates to represent Denisovans could display some of the phenotypic traits that have been linked with hybridization (Ackermann 2010; Ackermann, Mackay, and Arnold 2016; Harvati, Gunz, and Grigorescu 2007).

Teeth from Denisovans are characterized by their remarkably large size and their primitive morphological traits (Krause et al. 2010; Sawyer et al. 2015). Despite the close phylogenetic relationship between Denisovans and Neanderthals, the Denisovan molars do not show any typical Neanderthal traits. These teeth fall within the range of variation of Early to Middle Pleistocene fossils from East Asia in the buccolingually expanded mesial cusps, the tapering distobuccal corner, and the divergent and stout roots (Kaifu 2006; Kaifu, Aziz, and Baba 2005; Kaifu et al. 2005; Xing et al. 2015b, 2016). This morphology could be interpreted as late survival of a typically Asian pattern or as the result of genetic interbreeding with an unknown hominin species (perhaps a late-surviving *H. erectus*). In addition, Denisovans' dental size falls within the range of Pliocene and Early Pleistocene hominins, potentially evincing a case of heterosis, a phenotypic consequence of genetic hybridization (Ackermann 2010; Ackermann, Rogers, and Cheverud 2006).

Recently, some of us suggested that the Xujiayao fossils from northern China (Wu and Trinkaus 2014; Xing et al. 2015b) could be a good candidate to represent the Denisovans in the fossil record (Martinón-Torres et al. 2016). According to Tu et al. (2015) their age corresponds to around 160–220 ka; however, a revised age estimate (260–370 ka) was published recently (Ao et al. 2017). Like Denisovan molars, the Xujiayao posterior teeth are characterized by their large size and primitive morphology. However, the Xujiayao anterior teeth (incisor and canine) show traits that have been classically con-

sidered as typical of the Neanderthal lineage (Xing et al. 2015*b*), although the perikymata number seems to be closer to that of modern humans than to Neanderthals or early *Homo* (Xing et al. 2015*a*). Based on the robust morphologies of parietal, occipital, and temporal bones, earlier studies suggested that the Xujiayao hominins would fall somewhere between Zhoukoudian *H. erectus* and modern humans and should be classified as archaic *H. sapiens* (Wu and Poirier 1995). In recent years, a series of studies on the Xujiayao crania, mandible, temporal labyrinth, dental morphology, and dental development (Wu and Trinkaus 2014; Wu et al. 2014; Xing et al. 2015*a*, 2015*b*) point to a combination of features never documented in the fossil record before. The study of the nasal floor reveals that Xujiayao has a bilevel nasal floor, which is also identified in other East Asian *Homo* members (Sangiran 4, Chaoxian 1, and Changyang 1; Wu et al. 2012). Previous studies indicate that a bilevel nasal floor has its highest frequency among the western Eurasian Neanderthals. Early modern humans, in contrast, tend to feature a level (or sloping) nasal floor. The Xujiayao mandibular ramus exhibits a mosaic morphological pattern with respect to the Pleistocene *Homo* and recent human comparative samples (Wu and Trinkaus 2014). Its wide ramus and asymmetrical mandibular notch have higher frequencies in Eurasian archaic *Homo* members. The lateral mandibular notch crest and an open mandibular foramen are dominant among modern humans. It is noteworthy that two features of Xujiayao mandible (an enlarged superior medial and pterygoid tubercle and a retromolar space) bring this sample close to the Neanderthal lineage (Wu and Trinkaus 2014). As previously mentioned, such mixture of both primitive and derived morphologies is also found in the Xujiayao hominin teeth. The updated age of the Xujiayao fossils and their Neanderthal-like features render them good candidates to represent early Denisovans (Ao et al. 2017; Martinón-Torres et al. 2016).

Besides the morphological features outlined in the previous section, the Xujiayao teeth are characterized by their remarkable size, clustering with the Early and Middle Pleistocene specimens from East Asia and even exceeding their dimensions in some cases (Xing et al. 2015*b*). In addition, the immature individual presents two dental pathologies, a pitted enamel defect evident on the buccal surface of premolars and a deep groove that surrounds the crown, particularly pronounced in the lingual and distal aspects of the tooth. If we speculate that the Xujiayao specimen may be a Denisovan, the large dental size, the dental pathologies, and the unique mosaic of morphological traits in their skull, mandible, and dentition could fit the expectations for a hominin with mixed ancestry.

There are other hominin samples that could potentially represent Denisovans (Stringer and Barnes 2015), such as the Penghu 1 mandible from Taiwan (Chang et al. 2015) described as a late-surviving archaic hominin. Data in favor of Penghu representing a hybrid would be its unusually large dental size (potential heterosis) and two dental pathologies/anomalies, such as M_3 agenesia and a five-rooted M_2 (Chang et al. 2015). We are aware of the speculative nature of these suggestions

and hope that subsequent genetic analyses will help clarify the status of Penghu 1. Other populations tentatively representing Denisovans are those called archaic or post-*erectus* hominins (Stringer and Barnes 2015). Among those we highlight the Maba cranium which was recently described as presenting some typical Neanderthal traits (Wu and Bruner 2016), a morphology that would be congruent with the genetic proximity of Denisovans and pre-Neanderthal populations (Meyer et al. 2013, 2016). Finally, the identification of a mosaic of *H. erectus*–like and Neanderthal-like features in the ca. 120 ka crania from Xuchang in China (Li et al. 2017) points to yet another candidate to help us understand what Denisovans could look like.

Concluding Remarks

The study of *Homo sapiens* fossil dental samples from Late Pleistocene China reveals that not all the populations present the same suite of derived traits. This finding may reflect complex demographic dynamics with several migrations and dispersals (Wang 2017) and/or a degree of population substructure similar to that described for the African continent (Gunz et al. 2009; Hublin et al. 2017; Stringer 2016; Stringer and Galway-Witham 2017).

In addition, the fact that *H. sapiens* coexisted and interbred with other Late Pleistocene hominins in Asia adds an important source of morphological variability that is difficult to trace but should not be underestimated when analyzing the evolutionary meaning of the variation in the fossil record from Late Pleistocene Asia. As a case in point, we have hypothesized here the possibility that some skeletal features of Denisovans and *Homo floresiensis* may elate to their genetic admixture with other paleodemes.

Acknowledgments

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Not Just a Crossroad

Population Dynamics and Changing Material Culture in Southwestern Asia during the Late Pleistocene

by Knut Bretzke and Nicholas J. Conard

Southwestern Asia plays an essential part in all models that have been developed to explain how and when modern humans colonized Eurasia. Given the rich record of Southwestern Asia and the long history of research, it is not surprising that the region provides an enormous wealth of information on the lifeways and population dynamics of prehistoric human groups. We argue here that many archaeological models oversimplify the processes of human dispersals and contractions by underestimating the importance of archaeological and paleoenvironmental records on the regional scale. Based on our surveys and excavations in southwest Syria, the Zagros Mountains, and southeast Arabia, we conclude that the different regions provide distinct records of population dynamics during the Late Pleistocene. This led us to conclude that dispersal processes should not be understood as simple unidirectional movements during well-defined windows of opportunity but rather as complex changes in human biogeography with different effects in different regions at different times. We see more promise for research on human dispersals by facing up to this complexity instead of simplifying the problem for the sake of achieving striking results of only schematic value.

Research over the past decades has revealed that *Homo sapiens* evolved in Africa and successively colonized the entire globe. The timing and spatial patterning of the expansion process are hotly debated topics in human evolution. Geneticists, biological anthropologists, and archaeologists contribute data from a variety of perspectives using records with different advantages and weaknesses for research on human dispersals. Genetics and paleoanthropology provide valuable insight into phylogeny (Forster and Matsumura 2005; Hublin and Klein 2011; Kivisild et al. 2004; Klein 2008; Rasmussen et al. 2011; Stringer 2002), which is critical for tracing human dispersals. However, the small number of fossils and sequenced fossil DNA raises questions about how well morphologic and genetic diversity of Pleistocene populations is understood. Moreover, the scarcity of hominin fossils over large parts of the world hinders deciphering regional details of dispersal processes. While developing chronological frameworks for Pleistocene dispersal processes based

on genetic data has limitations (Endicott et al. 2009; Scally and Durbin 2012), this is a strength of archaeological research. Accuracy varies with technique and context of the dated samples, but chronometric dating of human fossils and archaeological finds often provides reliable estimates for the timing of hominin activities in a regional context.

Compared with the genetic and paleoanthropological records, the archaeological record provides the best evidence for the timing and spatial patterns of the presence of humans in the different parts of the world. This is largely due to the durability of stone tools and their high potential for entering the archaeological record. One weakness of the archaeological record in this context is the difficulty researchers have determining which hominin taxon produced the artifacts (Conard 1990; Lieberman and Bar-Yosef 2005).

Despite this weakness, researchers often use the archaeological record to develop hypotheses about human dispersal processes. The underlying rational is that the technology used to produce stone tools is passed from one generation to the next. This argument forms the cornerstone for developing hypotheses about the relationship between spatially and chronologically separated assemblages. Accepting models about the timing, geographic origin, and direction of modern human dispersals based on fossil and genetic data, archaeologists often link key regions by comparing broadly synchronous assemblages. Although archaeological sites are numerous in general, their number declines when we focus on well-dated and typo-technologically well-described assemblages in specific regions.

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Archaeological dispersal models thus often rely on few assemblages and selected characteristics of the lithic material culture (Foley and Lahr 1997; Mellars 2006; Mellars et al. 2013; Rose et al. 2011).

We argue here that approaches searching for cultural similarities in spatially distant assemblages disregard too many factors related to geographic range expansion of biological populations and oversimplify the undoubtedly complex process of human dispersal. The problem is exacerbated by the fact that there is abundant evidence for technological convergence in many archaeological contexts (Shea 2006; Will, Mackay, and Phillips 2015). In this paper we use data from our surveys and excavations in Syria, Iran, and the United Arab Emirates (UAE) and examine the archaeological records from these regions with regard to expansion processes of modern humans out of Africa.

Some Thoughts on the Study of Human Dispersals

Important basic questions in the context of human dispersal processes include the following: What causes expansions and contractions of human populations? What are the costs and the benefits of dispersals? What are the limiting factors for a successful expansion? Ecological research shows that animal dispersal depends on multiple factors including the size and quality of habitats, the size of the local population, and competition for essential resources and mates (Dobson and Jones 1985). Given a range of taxa in a circumscribed area, competition and population size are related to the characteristics of the habitat and thus to environmental and climatic conditions. While dispersals can lead to a number of benefits, such as increased fitness of the individual by reducing competition for resources and mates, dispersals also carry costs (Bonte et al. 2012). The new and unfamiliar habitats may lead to reduced survival and reproductive success because of decreased success in obtaining resources. In addition to the unknown spatial distribution of essential resources, the immigrants may be forced to adapt to a new ecological niche with new competitors.

Assuming the basic causes and limitations related to dispersal in animals apply equally to humans, we expect that geographic range expansions occur during periods of favorable conditions associated with population growth. We further conclude that living conditions and composition of the faunal and floral communities in regions adjacent to the source region are of critical importance for the timing and spatial patterning of human dispersals, because geomorphology, habitat, and climatic conditions often vary on small geographic scales. Moreover, conditions change over time, creating diachronic variability in the potential for expansion and contraction of human populations. Hence, each region features varying probabilities for a successful dispersal of human groups at different times. Projecting these factors on a global scale suggests that the spread of modern humans out of Africa was probably a complex process with much regional variability.

We argue here that many archaeological models underestimate the importance of occupation history and variations in natural conditions on a regional scale. In this paper we change the perspective and present diachronic data from three regions in Southwestern Asia, namely, in southwest Syria, southern Iran, and the UAE (fig. 1). We use our wide experience gathered during excavations of multiple stratified sites and comprehensive survey projects in these different parts of Southwestern Asia over the past decade to draw conclusions about the settlement dynamics in our study regions.

Case Studies

Southwestern Syria

We conducted fieldwork in southwestern Syria between 1999 and 2010 in the Tübingen- Damascus Excavation and Survey Project, which we denote using its German acronym TDASP (Tübingen-Damaskus Ausgrabungs- und Surveyprojekt). The project was conceived as a long-term, multidisciplinary research initiative to investigate the archaeology and paleoenvironments of Syria. The TDASP team decided to focus its resources on southwestern Syria in a region covering the transition from mountainous habitats of the Anti-Lebanon Mountains to the desert environments of the Syrian plateau (fig. 1). More precisely, the TDASP study region is located in the Qalamun region, near the villages of Ma'aloula, Jaba'deen, and Yabroud, located 50–70 km northwest of the old city of Damascus.

The work of the TDASP team in southwestern Syria builds on the solid foundation of Rust's (1933, 1950) work at Wadi Skifta in Yabroud, Suzuki and Kobori's (1970) and Bakdach's (2000) field surveys in the region, as well as excavations done by Ralf and Rose Solecki (1987–1988). We conducted systematic surveys of the Qalamun and documented 598 artifact-bearing localities from Lower, Middle, Upper, and Epipaleolithic periods among Holocene material distributed over all parts of the study region (Conard, Kandel, and Masri 2006). During the surveys we identified four new stratified Paleolithic sites where we conducted archaeological excavations: Baaz Rockshelter (1999–2004), Kaus Kozah Cave (2004–2006), Ain Dabbour Cave (2007–2008), and Wadi Mushkuna Rockshelter (2007–2010) as well as other sites that warranted further investigation. The combined record from our excavations and systematic surveys supplemented by the stratified assemblages excavated by Rust in Yabroud (Rust 1950) allows us to develop hypotheses about the occupation history of the region.

Our oldest stratified assemblages come from Wadi Mushkuna (fig. 2A) and represent a classic Levantine Middle Paleolithic (MP). We excavated a sequence of 20 archaeological horizons (AHs) from well-stratified deposits spanning a depth of about 4 m (Conard et al. 2010). Typo-technologically, the sequence in Wadi Mushkuna features a gradual evolution from a dominance of Levallois reduction methods toward an increasing importance of reduction from single platform cores in
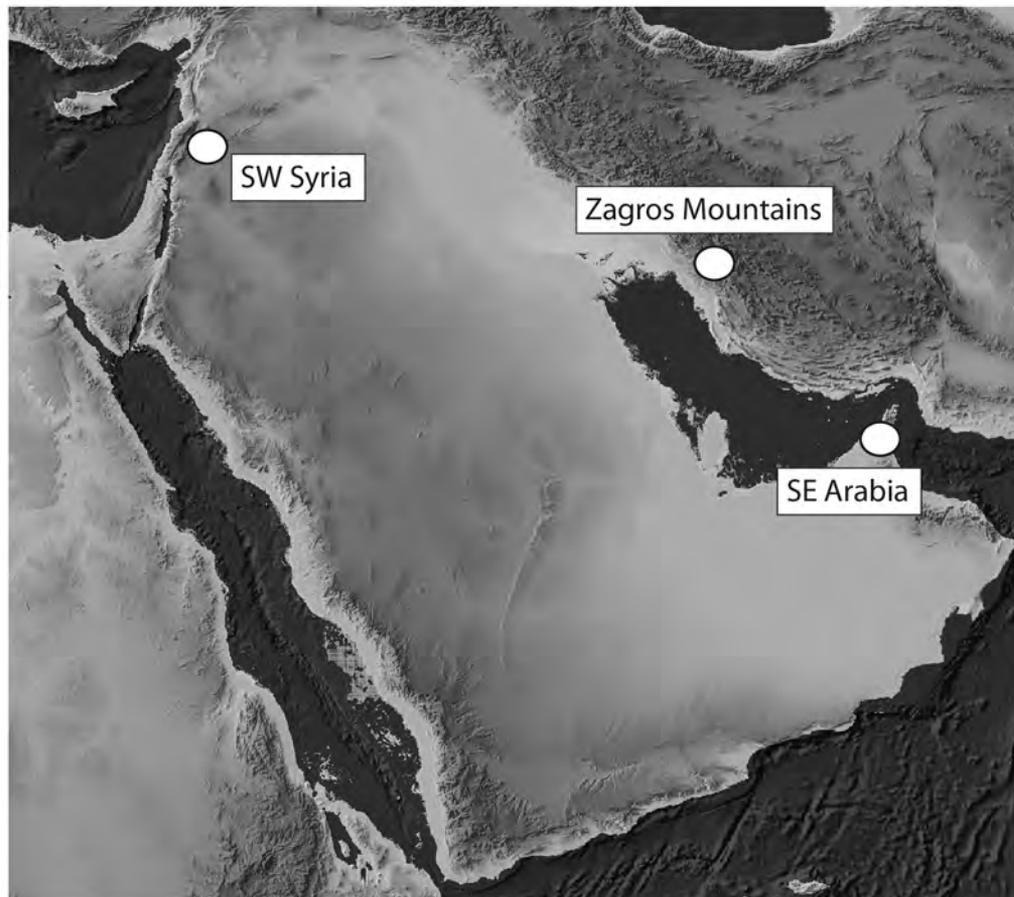
Figure 1. Map showing the location of the three regions considered in the text. A color version of this figure is available online.

the upper archaeological deposits (fig. 2*B*; table 1). Because of the beginning of the civil war in Syria, we had to stop our fieldwork at Wadi Mushkuna in 2010 and could not finish the dosimetry and sampling for thermoluminescence (TL) dating. Therefore, the sequence is undated, but we argue that the technological shift observed in the upper AHs fits well with characteristics typically assigned to the late MP. The lack of tool types often related to the MP to Upper Paleolithic (UP) transition—such as Emireh points (Garrod 1955), chamfered pieces (Newcomer 1970), or Umm el Tlel points (Boëda and Bonilauri 2006)—might indicate that this period is not well represented at Wadi Mushkuna, a pattern also observed in the sequences of the nearby Yabroud shelters (Hauck 2011; Rust 1950) and in the TDASP survey record.

Our data from Wadi Mushkuna provide evidence that the gradually changing lithic technological behavior contrasts with an abrupt change in settlement behavior (Bretzke, Kandel and Conard 2017). We consider artifact density (number of lithic artifacts per related volume of sediment) to be positively related to occupational intensity and negatively related to the degree of mobility (Hitchcock 1987). All things being equal, we expect that artifact density increases with increasing duration of stay because lithic reduction is a continuous part of on-site

activities. While saying this, we acknowledge that the density of lithic artifacts on a site may be affected by a variety of dynamics, such as taphonomic factors related to cultural, biological, and geological processes. Hence, the comparison of find densities is not a straightforward matter. However, given that these data come from one sequence deposited by similar processes, we argue that our density data provide robust signals for how the intensity of use changed through time.

Combining density data with tool frequency following Riel-Salvatore and Barton (2004), we conclude that intense occupations with a presumably lower degree of mobility characterize the lower AHs (XI–VIII), while assemblages from the top of the sequence (AHs V–II) feature less intense occupations during shorter stays potentially related to higher degrees of mobility (Bretzke, Kandel, and Conard 2017).

The earliest-dated UP assemblage in the TDASP record comes from AH VII at Baaz Rockshelter. Radiocarbon dates on charcoal indicate that the occupation of AH VII dates to 38,000–33,000 cal BP (Deckers et al. 2009). Lithic production in AH VII focused on laminar artifacts as indicated by the frequencies of bladelets and blades (table 2). Observed laminar technologies include blade and bladelet production from cores in addition to bladelet production from multiple burins, characteristics which

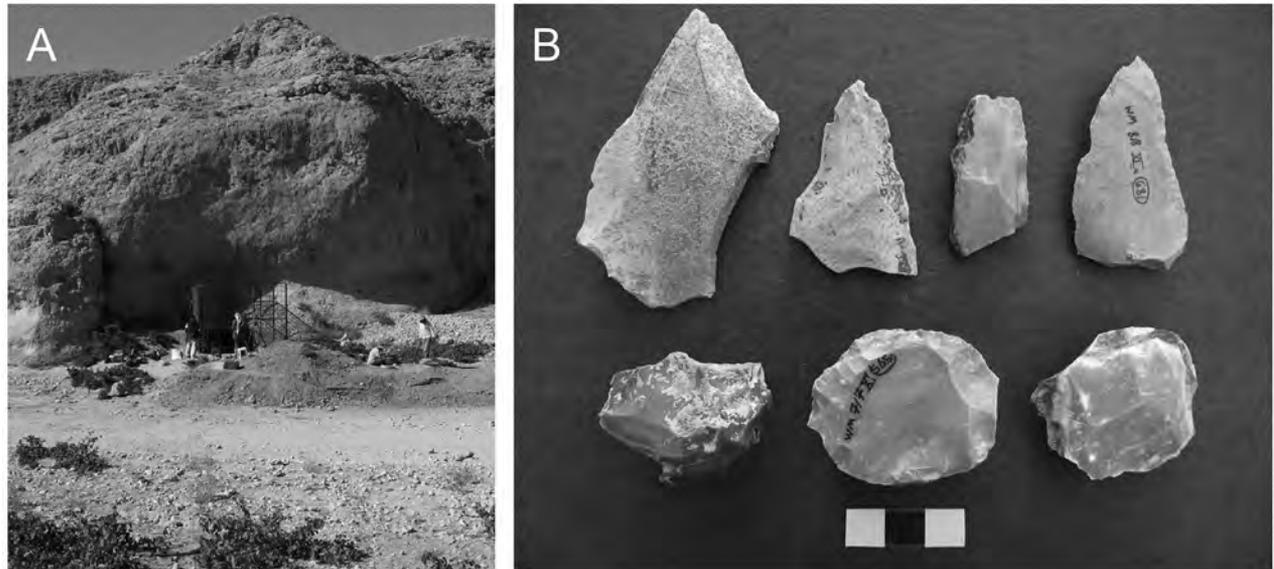Figure 2. Wadi Mushkuna Rockshelter, southwestern Syria. *A*, Overview of the site. *B*, Levallois flakes and tools. A color version of this figure is available online.

clearly distinguish this assemblage from lithic traditions of the MP. Younger UP assemblages from Baaz—such as AHs VI, V, and IV—feature strong typo-technological similarities with AH VII (table 2) and suggest continuity in the occupation history over a relatively long period of time given the dating of the occupation of AH V to approximately 26,000–24,000 cal BP (Deckers et al. 2009).

During eight seasons of fieldwork, the TDASP team conducted systematic surveys in an area of about 500 km² and recorded 598 localities. The record includes all major periods from the Lower Paleolithic to the Neolithic. We use the term "localities" to identify areas where artifacts were collected. At each locality, the survey team documented the presence or absence of every cultural entity and the respective artifact den-

sity. One surveyed locality may contain artifacts from different periods. At 181 localities the TDASP team identified UP artifacts. Based on these spatially explicit data, we conclude that the settlement dynamics of the Early UP in the TDASP study region are characterized by tethering of activities in small areas close to permanent water sources. Bretzke (2008) concludes that the distribution of UP finds in the TDASP study region reflect a UP activity area of about 50 km². Given the often-proposed average radius of 5 to 10 km for the range exploited around a main settlement (Kuhn 1992), the TDASP record suggests a relative small catchment area for the UP in the TDASP study region. This indicates a high degree of mobility due to an expected faster exploitation of organic resources in small areas (Bretzke, Drechsler, and Conard 2012).

Table 1. Wadi Mushkuna, southwestern Syria

AH	Type			Subtype							
	Levallois	Platform	Indet.	SP	DP	MP	RB	RU	RC	P	Indet.
I	...	2	...	1	1	...	...	...	...	...	...
II	1	3	3	2	1	...	1	...	...	...	3
III	4	...	5	...	...	...	1	...	2	1	5
IV	4	2	2	1	1	...	1	...	2	...	3
V	4	...	...	...	...	...	...	1	2	...	1
VI	1	...	...	...	...	...	...	...	1	...	...
VII	3	...	...	...	...	...	...	1	1	...	1
IX	1	...	2	...	...	...	...	...	1	...	2
X	...	...	1	...	...	...	...	...	...	...	1
XI	1	1	1	...	...	1	...	...	1	...	1
XIV	...	...	1	...	...	...	...	...	...	...	1
XX	...	...	2	...	...	...	...	...	...	...	2

Note. Core types and core subtypes: SP: single platform core; DP: double platform core; MP: multiple platform core; RB: recurrent bidirectional; RU: recurrent unidirectional; RC: recurrent centripetal; P: point; Indet: indeterminate.

Table 2. Lithic assemblages from the UP layers, Baaz Rockshelter, southwestern Syria

Assemblage	AH IV		AH V		AH VII	
	N	%	N	%	N	%
Debitage:						
Flake	215	52	834	48	147	57
Blade	82	20	359	21	25	10
Bladelet	114	28	543	31	87	34
Total	411	100	1736	100	259	100
Tool blanks:						
Flake	16	35	33	31	7	44
Blade	9	19	14	13	1	6
Bladelet	21	46	61	56	8	50
Total	46	100	108	100	16	100

In sum, our data from southwestern Syria provide evidence for technological continuity during the Late MP as well as during the Early UP, while the developmental trajectories from both periods cannot easily be related. Settlement behavior, on the other hand, is characterized by a relatively high degree of mobility for both Late MP and Early UP periods. Regarding the actual MP to UP transition, the record from southwestern Syria is not conclusive. In general, the following scenarios would be possible: (i) developmental continuity between MP and UP, (ii) abrupt replacement of populations carrying MP technology by populations carrying UP technologies without settlement gap, and (iii) reoccupation of the region by populations carrying UP technologies after settlement gap and abandoning of the region by populations carrying MP technologies. Based on the currently available record, we favor for our region the reoccupation scenario (iii). Models about the MP-UP transition in the Levant often emphasize a developmental continuity over this transition and do not consider the possibility of a pronounced regional discontinuity (Bar-Yosef 2002; Kuhn, Stiner, and Gulec 1999; Marks 2003). Both observations do not necessarily exclude each other. We agree here with Meignen (2012), who argued that cultural developments might occur in single regions and spread into neighboring regions, which leads to a mosaic pattern. An archaeological sequence can provide evidence for technological discontinuity from a regional perspective, while a supraregional view reveals that the chronologically separated assemblages from this sequence actually belong to the same developmental trajectory. With this in mind, we cannot exclude the possibility that the early UP as observed in our region developed out of a later MP in an adjacent region, a conclusion supported by the similarities in the settlement behavior.

We thus argue on the regional scale that our record from southwestern Syria reflects a scenario in which groups carrying UP lithic technologies reoccupied an empty region. On the supraregional scale, however, we agree that the Levant's MP and UP records often point to settlement continuity and consequently to a low probability for the technological shift observed at the MP-UP transition being related to a continental-scale expansion process of modern humans.

Southern Zagros Mountains

We have conducted Paleolithic fieldwork in the Southern Zagros Mountains in the context of the Tübingen Iranian Stone Age Research Project since 2006 (Conard and Ghasidian 2011; Conard et al. 2007, 2006; Ghasidian 2014; Ghasidian, Bretzke, and Conard 2017; Ghasidian et al. 2009; Heydari-Guran, Ghasidian, and Conard 2009). One geographic focus of TISARP is the Dasht-e Rostam-Basht region located in the northwestern part of the Fars Province. Systematic surveys led to the discovery of 121 Paleolithic sites, including open-air, cave, and rockshelter sites. The ongoing excavations at the cave site of Ghār-e Boof (fig. 3) in addition to many surface collections from the caves and shelters of the region provide an excellent basis for studying the region's occupation history during the late MP and early UP.

The Paleolithic sequence at Ghār-e Boof consists of nine AHs with evidence for MP occupations in AHs V, IVc, IVb, IVa, and UP occupations in AHs IV, IIIc, IIIb, IIIa, and III. While radiometric dating of the MP occupation is underway, radiocarbon dating of charcoal samples from AHs III and IV place the UP occupation phases of Ghār-e Boof Cave between 35 kyr cal BP and 41 kyr cal BP (Conard and Ghasidian 2011). Based on these age estimations, the UP at Ghār-e Boof currently represents one of the oldest UP assemblages in the Zagros Mountains (Becerra-Valdivia et al. 2015).

During our excavation in 2015 we recovered for the first time stratified finds from the MP. Typo-technological characteristics of the MP finds from AHs IVa, IVb, IVc, and V clearly point to the presence of a flake technology (fig. 4*B*). The role of Levallois methods currently remains unclear given the low find density (table 3). In contrast, the most striking characteristic of the UP assemblages from Ghār-e Boof (AHs IV–III) is a strong emphasis on the production of bladelets (table 3; fig. 4*A*) from single platform cores and the lack of evidence for

Figure 3. Ghār-e Boof, southern Zagros Mountains. *A*, Overview of the site. *B*, Overview of the excavation on November 2015. A color version of this figure is available online.

an intended flake production (Conard and Ghasidian 2011; Ghasidian 2014). Throughout the UP sequence from AH IV to AH III, bladelets are important blanks for tools (table 3). Although the MP assemblage is small and the chronology for the MP occupation needs to be established, few things can be said about the MP-UP transition in the Dasht-e Rostam region in the southern Zagros. The emphasis on the production of bladelets during the early UP observed in the surface and the stratified record of TISARP stands in stark contrast to the lithic tradition reflected in the MP finds from Ghār-e Boof and the survey. Given that the bladelet technologies occur very early, about 41 ka, and none of the adjacent regions provides evidence for a development of this distinct bladelet technology out of MP traditions, we argue that the record from the Dasht-e Rostam hints at a technological discontinuity between UP and MP in the southern Zagros Mountains. The low density of MP sites in the Dasht-e Rostam region in addition to the ephemeral character of the MP occupation at Ghār-e Boof may point to a low occupation density in the region during the later MP.

Based on these observations, we currently hypothesize that the early UP occupation in the southern Zagros Mountains was related to a displacement of thinly scattered groups carrying MP technology. Key for this replacement might be new hunting systems as indicated by the bladelet component in the

early UP assemblages. We thus argue that for the TISARP study region in the southern Zagros Mountains, the probability for the occurrence of supraregional expansion process at the MP-UP transition is relatively high.

Southeast Arabia

The University of Tübingen has conducted Paleolithic fieldwork in southeast Arabia in collaboration with the Sharjah Archaeology Authority since 2003. Our surveys of the region in addition to our excavations of the deeply stratified deposits at Jebel Faya provide for Arabia a rare possibility for a detailed diachronic analysis of the occupation history of the region (Armitage et al. 2011; Bretzke 2015; Bretzke, Conard, and Uerpmann 2014; Bretzke et al. 2013).

We focus our fieldwork in the interior plain of the Emirate of Sharjah, about 60 km inland from the coast of the Persian Gulf. Geographically this plain represents the northern end of the Rub' al-Khali, the largest sand sea in the world (Besler 1982). The plain is located between sand dune fields to the west and the al-Hadjar Mountains to the east. Drainage of surface and subsurface water from the al-Hadjar Mountains into the plain leads to a well-developed vegetation cover and creates favorable living conditions relative to adjacent areas, a pattern
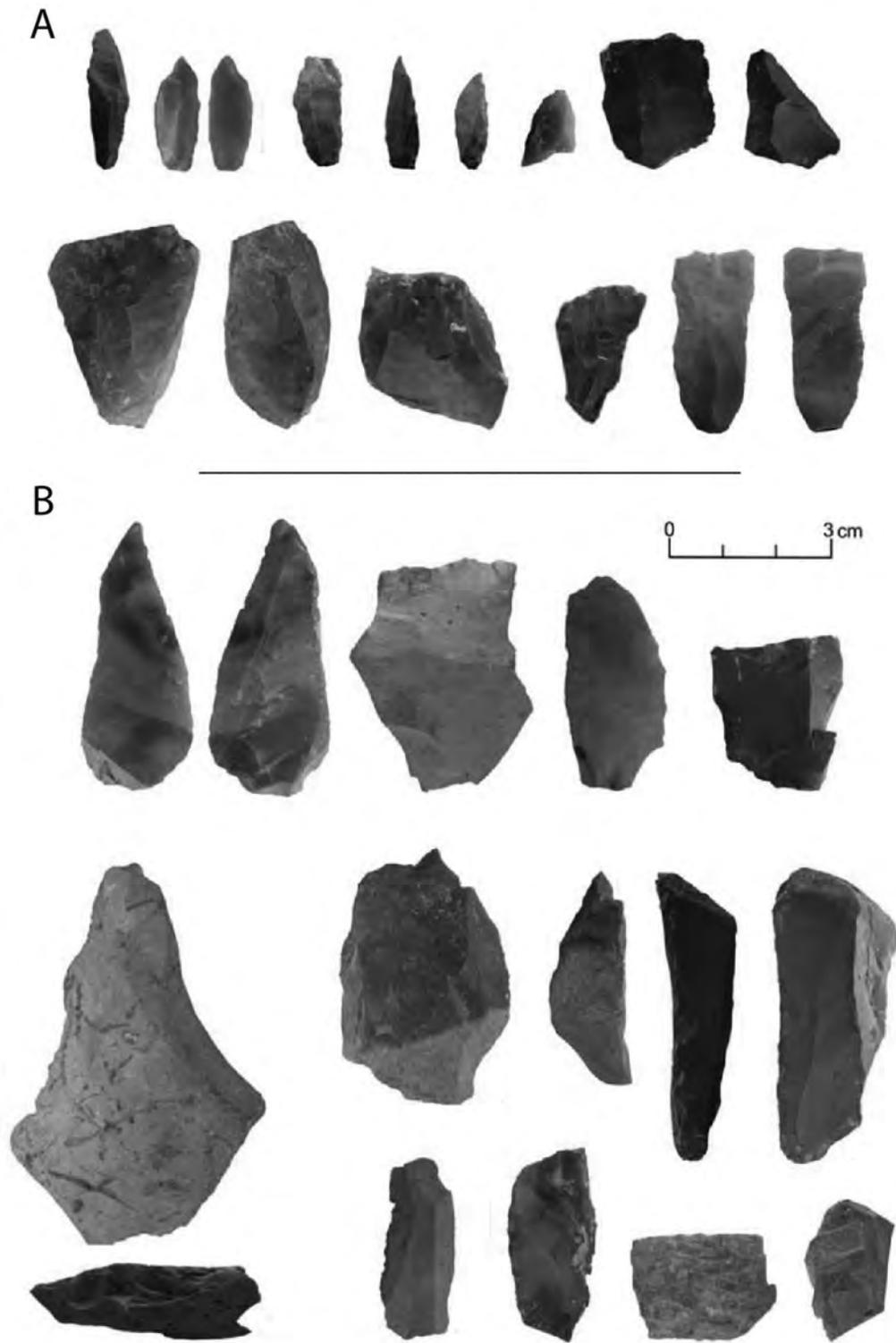
Figure 4. Ghār-e Boof. Examples of lithic artifacts excavated in 2015. *A*, UP artifacts from AHs IV, IIIc, IIIb, and IIIa. *B*, MP artifacts from AHs IVc and V. Please note the bladelets and bladelet cores in *A*. A color version of this figure is available online.

Table 3. Composition of lithic assemblages from our 2015 excavation, Ghār-e Boof, southern Zagros Mountains

Assemblage	AH III N	AH III %	AH IIIa N	AH IIIa %	AH IIIb N	AH IIIb %	AH IIIc N	AH IIIc %	AH IV N	AH IV %	AH Iva–c N	AH Iva–c %	AH V N	AH V %
Debitage:														
Flake	142	38	42	43	71	53	13	31	10	56	8	62	3	60
Blade	58	16	10	10	14	10	5	12	2	11	4	31	2	40
Bladelet	174	47	45	46	49	37	24	57	6	33	1	8	…	…
Total	374	100	97	100	134	100	42	100	18	100	13	100	5	100
Tool blanks:														
Flake	65	42	4	40	17	38	2	12	…	…	1	50	1	33
Blade	35	22	2	20	8	18	3	18	…	…	1	50	2	67
Bladelet	56	36	4	40	20	44	12	71	2	100	…	…	…	…
Total	156	100	10	100	45	100	17	100	2	100	2	100	3	100

that can be expected to develop regularly during periods of increased precipitation. While we recorded a number of areas with good potential for Paleolithic research, currently the most important area with regard to early modern humans is an anticline structure at the western edge of the inland plain with a length of about 20 km and mountains towering over the plain about 240 m in height. The roughly south-north-oriented structure is covered by Upper Cretaceous limestone bearing the Faya rock-shelter and the 4 m deep Late Pleistocene archaeological sequence from the site FAY-NE1 (fig. 5A).

The occupation history at Jebel Faya is well exhibited in two sequences excavated from deposits in front of the rock-shelter and under the current rock-shelter. The terrace sequence includes assemblages A to D, where assemblage A was dated by optically stimulated luminescence (OSL) to about 40 kyr BP and assemblage C to about 125 kyr BP (Armitage et al. 2011; Bretzke et al. 2013). The Faya shelter sequence, on the other hand, consists of seven AHs. Both sequences correlate through the stratigraphic connection of AHs IV, V, and VI with assemblages A, B, and C, respectively (Bretzke, Conard, and Uerpmann 2014).

Lithic technological characteristics throughout the archaeological sequences in Jebel Faya change significantly and suggest developmentally unrelated entities (fig. 5B; table 4). Our analysis of the archaeological record complemented by chronological data and data from paleoenvironmental research at the site clearly indicates that the Late Pleistocene occupation history was characterized by pulses of occupations intervened by long periods featuring no evidence for human inhabitation (Bretzke 2015). Paleoenvironmental data from Jebel Faya show that human habitation is related to relatively favorable living conditions developing during periods of increased precipitation, whereas layers representing dry conditions lack evidence for human occupation of the site (Bretzke et al. 2013).

To examine the Jebel Faya sequence for changes in land-use behavior and mobility, we calculated the ratio of retouch frequency and artifact density per cubic meter following Riel-Salvatore and Barton (2004). The results show shifts throughout the sequence and provide evidence for differences in land use and mobility (table 4). Given that habitats at Faya and in the surrounding areas are relatively stable and shift mainly between wet and dry variants of the same faunal and floral composition, we might hypothesize from the variations in land use that the different human groups occupying Jebel Faya during the Late Pleistocene are related to distinct traditions in spatial behavior. Based on our record from Jebel Faya, we argue that the presence of human groups in the northeastern Rub' al-Khali desert is strongly driven by climate and climatic change and that Jebel Faya was repeatedly reoccupied after periods of nonoccupation. We conclude that the climatically driven pulses of occupation observed in our record in addition to long occupation gaps provide arguments supporting a high probability for the occurrence of multiple supraregional dispersals of modern humans in our study region in southeast Arabia during the Late Pleistocene.

Discussion

Our results for southeast Arabia suggest climatically driven pulses of modern human occupation during the Late Pleistocene. The potential source regions for those groups settling at Faya throughout the Late Pleistocene remain unknown. Given widespread favorable conditions during MIS 5e in Arabia (Parker 2009), Bretzke (2015) suggests that similarities in stone-tool behavior inferred from surface assemblages recorded in Yemen (Crassard 2009), southern and central Saudi Arabia (Crassard and Hilbert 2013; Crassard et al. 2013), and southern Oman (Rose 2007) could point to connectivity and exchange among human groups occupying the Arabian Peninsula. We thus argue that the 125 ka occupation at Faya was related to a spatially broader phenomenon, the expansion of a human population over the entire Arabian Peninsula at the onset of the favorable conditions of MIS 5e.

Because of the lack of fossil evidence, the taxonomic status of the populations occupying the Arabian Peninsula during this period remains unclear. Two scenarios are plausible: (i) Arabia was not inhabited by humans at the end of hyperarid MIS 6, and the MIS 5e populations in Arabia are related to an early out-of-Africa expansion of modern humans; or (ii) relict populations of premodern humans survived the arid MIS 6 in
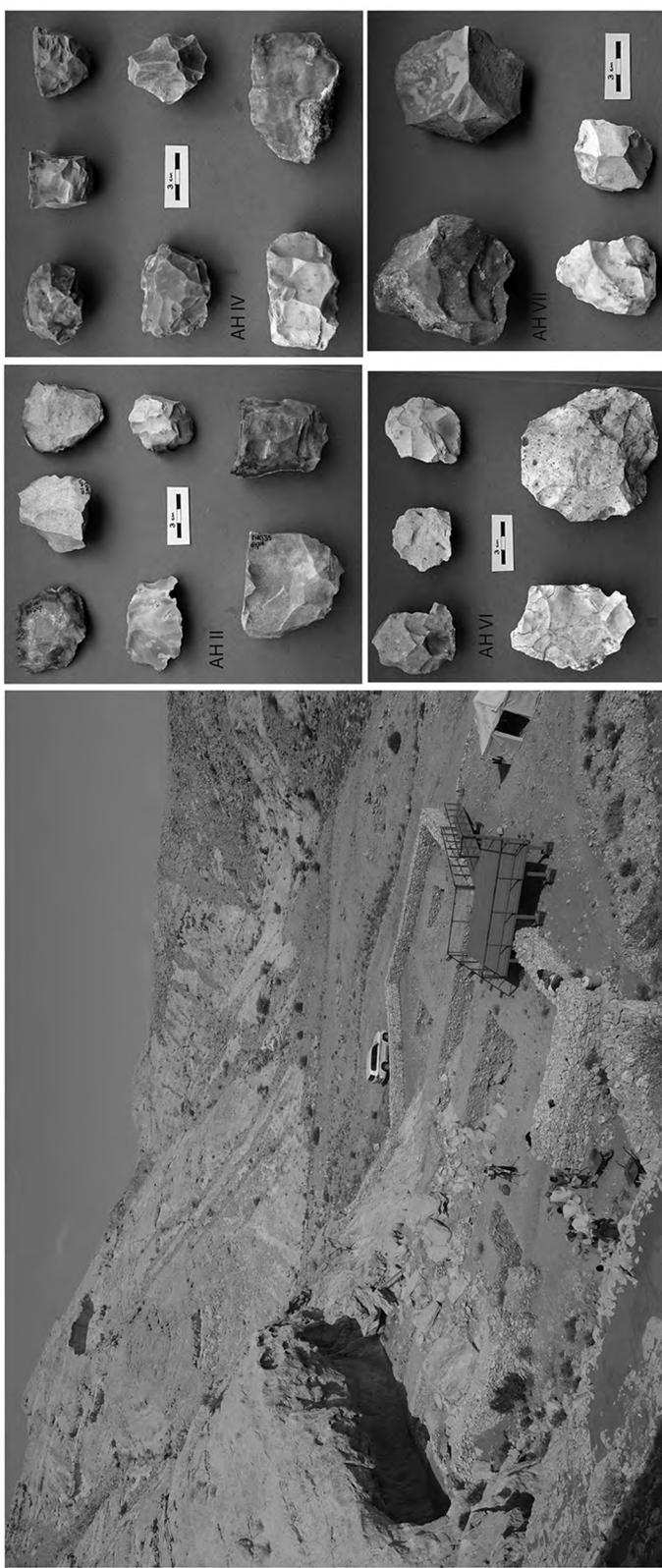
Figure 5. Jebel Faya, UAE. *A*, Site overview. *B*, Examples of cores from the Jebel Faya Shelter sequence's AH II, IV, VI, and VII. A color version of this figure is available online.

Table 4. Jebel Faya, southeast Arabia, United Arab Emirates

Technology and behavior	AH II		AH IV		AH VI		AH VII	
	N	%	N	%	N	%	N	%
Cores scar pattern:								
Parallel	3	14	29	28	1	8	5	36
Orthogonal	2	9	25	24	...	...	...	...
Crossed	...	...	11	10	2	15	1	7
Bidirectional	14	64	15	14	...	...	1	7
Convergent	...	...	3	3	1	8	1	7
Centripetal	...	...	4	4	7	54	1	7
Discoidal	...	...	...	...	...	...	2	14
Multiple platforms	3	14	18	17	2	15	3	21
Total	22	100	105	100	13	100	14	100
Settlement behavior:								
Tool frequency	56	7	114	10	32	8	19	7
Artifact density	225.8		149.5		169.6		167.2	

Note. Technological and occupation data from the Faya Shelter sequence. AHs I, III, and V are not included here because the lithic assemblages are too small to provide meaningful data.

refugia, such as the highlands in southwest Arabia or southern Iran, and expanded under the more favorable conditions during MIS 5e. Support for (i) comes from fossils of modern humans dated about 100–130 ka found in the central Levant in the caves of Skuhl and Qafzeh (Grün et al. 2005; Trinkaus 1993). These finds indicate an out-of-Africa expansion that could have also involved the Arabian Peninsula. Similarities of typo-technological characteristics of Jebel Faya's assemblage C with synchronous East African assemblages (Armitage et al. 2011) are additional aspects cited to support hypothesis (i). However, the scarcity of well-dated pre-MIS 5e evidence from Arabia and Iran makes an assessment of the alternative hypothesis (ii) difficult. Given the currently available record, we favor hypothesis (i), which consequently led us to side with Armitage et al. (2011) and hypothesize that the MIS 5e record from Faya indicates an occupation of southeast Arabia by modern human groups related to an out-of-Africa expansion.

Given that no assemblages with typo-technological characteristics similar to Jebel Faya's assemblage C and AH VI, dated to 125 ka, have been recorded in later parts of the Late Pleistocene in Arabia, the question arises, what happened to these populations? It seems likely that they were pushed out of Arabia during the following period of desiccation and reached territories northeast of the Persian Gulf and further dispersed from there. Unfortunately, the MP of southern Iran is not very well understood. Known assemblages concentrate in the northwestern part of the country and in the northern and central parts of the Zagros Mountain range. Our own work in the southern Zagros currently sheds no light on the early Late Pleistocene occupation history beyond the notion that the MP occupation was less dense than the UP.

Site Qaleh Bosi from the southwest edge of the Iranian Central Plateau contains lithic assemblages that feature typo-technological similarities with Jebel Faya's assemblage C, including bifacial tools (Biglari et al. 2009). Although bifacial technology is currently unknown from the region, it remains

very speculative whether the Qaleh Bosi site represents a population influx linked to an eastward dispersal of Arabian groups given the singularity of the site and the overall small number of sites in the vast territory of Iran and Arabia.

Other assemblages from the Iranian Central Plateau feature a dominant use of Levallois techniques (Heydari-Guran, Ghasidian, and Conard 2015; Nasab, Clark, and Torkamandi 2013). This stands in contrast to assemblages assigned to the Zagros Mousterian, where Levallois often plays a minor role and tool assemblages are dominated by heavily retouched tools with convergent edges (Dibble and Holdaway 1993). Given the present state of research on the MP of Iran, the small number of sites, and the lack of detailed chronological control over the different typo-technological characteristics, it remains unclear what caused the observed diversity. The role of the Zagros Mountain range, the Iranian Central Plateau, as well as the deserts to the north and the east remain interesting regions for future research but currently provide no arguments regarding the timing and spatial patterns of the early human expansion during MIS 5.

The situation is different with regard to potential expansion processes during MIS 3. Our data from Dasht-e Rostam indicate a significant shift in the lithic technology from flake production to highly sophisticated bladelet production. This change is accompanied by changes in settlement behavior, with a much denser occupation during the early UP compared with the MP. Given the dating of the deepest UP layer at Ghār-e Boof to about 41 kyr cal BP and the lack of evidence for a significant gap in the sediment record, we can conclude that the replacement of the MP lithic traditions by UP lithic traditions in our study region was a relatively rapid process that occurred shortly before 41 kyr BP. At first glance, this observation provides support for models arguing for an expansion of modern humans out of Africa between 60 and 40 kyr BP (Mellars 2006). However, our record from southeast Arabia provides data that contradict this model. Stone-tool behaviors reflected in those

assemblages dated to about 40 ka from our study regions in Iran and UAE, with a sophisticated bladelet production in the Dasht-e Rostam (Conard and Ghasidian 2011), and opportunistic flake production in southeast Arabia (Bretzke, Conard, and Uerpmann 2014) cannot easily be linked. While we cannot rule out the possibility that the replacement of MP technology by UP technology in the Dasht-e Rostam was related to the arrival of an African/Arabian population, we argue that the currently available record more likely reflects a scenario not covered by traditional west-east dispersal models. At this stage we have no solution to the question of where to locate an alternative source population, but we side here with researchers arguing that there is no reason why east-west dispersals could not have occurred (Dennell and Roebroeks 2005).

The taxonomy of the MP and UP hominin groups in the southern Zagros is still unknown, but we assume that the bladelet industries from our record are produced by modern humans. Recent discoveries of anatomically modern humans in Eastern Asia dating to before 40 ka (Bae et al. 2014; Demeter et al. 2012; Liu et al. 2010, 2015; Michel et al. 2016) indicate that early modern humans already occupied regions east to the Zagros at 40 ka, making an east-west dispersal probably along the northern route through Central Asia a possible scenario.

One critical region for our understanding of expansions of early modern humans into Central and Eastern Asia so far not considered is the Caucasus region. Along the potential northern route for modern human expansions into Asia, the Caucasus regions must have played a significant role. From a geographic perspective, the Greater Caucasus, with its many peaks above 4,500 m elevation, represents a significant barrier for expansion from the south. Differences between assemblages north and south of the divide from the early MP (ca. 250–70 ka) clearly demonstrate this point. MIS 5 assemblages such as layers 7–5 from Matuzka Cave (Baryshnikov and Hoffecker 1994) in the northwestern Caucasus, for example, are characterized by the absence of Mousterian points and the presence of bifacial tools (Golovanova and Doronichev 2003). Djruchula Cave in the southern Caucasus, on the other hand, contains two archaeological layers with assemblages typo-technologically characterized by a high proportion of elongated retouched points of different size and retouched blades produced by Levallois techniques (Meignen and Tushabramishvili 2006). TL ages provided by Mercier et al. (2010) indicate two chronologically well-separated occupation phases at Djruchula Cave, the older one between 285 and 176 ka and the younger one between 153 and 123 ka. Despite this chronological gap, the typo-technological characteristics between the two layers are very similar (Meignen and Tushabramishvili 2010).

A number of sites with similar assemblage characteristic are known from South Caucasus and grouped as the Djruchula-Koudaro complex (Golovanova and Doronichev 2003; Liubin 1977). The chronology of the Djruchula-Koudaro complex is not well developed, given the scarcity of well-dated sites from this period. However, data presented by Pinhasi et al. (2008) from Hovk-1, about 100 km northeast of Yerevan in Armenia,

may provide evidence for widespread distribution in the South Caucasus and continuity of Djruchula-Koudaro complex's typo-technological characteristics into MIS 5. Layer 8 at Hovk-1 was dated by OSL technique to 104 ± 9.8 ka (Pinhasi et al. 2008). Gasparyan et al. (2014) argue that their techno-typological analysis of layer 8 highlights similarities with the Djruchula-Kudaro group through the high frequency of elongated Levallois points. Accepting the presence of the Djruchula-Kudaro group in the southern Caucasus in MIS 5, provides arguments in support of the Great Caucasus being indeed a barrier for human expansions from the south during MIS 5, given its marked difference from the assemblages in the northwest Caucasus.

The taxonomic status of populations that produced the different assemblages remains speculative because of the very limited record. Golovanova and Doronichev (2017) argue that the two incisors found in layers 6 and 5b at Matuzka Cave represent Neanderthals dated to MIS 5c and 5a respectively. Human fossils have also been found in Djruchula Cave. Here, one first-upper-left molar of an adult is also cited as a Neanderthal fossil (Moncel et al. 2015). The origin of the hominin populations occupying the southern Caucasus during MIS 8–5 is debated among researchers. Meignen and Tushabramishvili (2006) point to the clear technological affinities of the Djruchula Cave assemblages with the Early Levantine MP as known from assemblages such as Hayonim lower E and F, Tabun D, Hummal 1a, and Abou Sif falling in the time frame 270–160 ka. This observation might suggest a connection between the two regions. Moncel et al (2015:99) argue to the contrary and conclude that "in the present state of knowledge, different factors suggest that the Djruchula-Koudaro complex of sites located in the Southern Caucasus may result from a combination of influences from the Northern Caucasus and from a local Acheulean." Regardless of interpreting the pre-MIS 4 archaeological record as reflecting population replacement or settlement continuity, the current paleoanthropological record from the region provides no arguments in favor of scenarios where populations of modern humans occupy the Caucasus region as part of an early expansion along the northern route during MIS 5.

Regarding the late MP in the Caucasus (ca. 70–40 ka), differences between northern and southern Caucasus remain observable. Mezmaiskaya Cave, in the northwestern Caucasus, about 70 km north of Sochi in Russia, provides evidence for Neanderthal occupations between 70 and 60 ka (Skinner et al. 2005) and 45–43 kyr BP (Pinhasi et al. 2011). Neanderthal fossils were found in layers two and three. The specimen from layer two was directly dated to 44,600–42,960 cal BP (Pinhasi et al. 2011). The partial skeleton from layer 3 (Golovanova et al. 1999) might date to the time frame between 70 and 60 ka given electron spin resonance (ESR) results for this layer (Skinner et al. 2005). The lithic assemblage from the older occupation features similarities with assemblages grouped as Eastern Micoquian, which are characterized by the presence of bifacial technology, the lack of Levallois technique, low frequencies of laminar blanks, and the absence of true handaxes (Golovanova and

Doronichev 2017). In contrast, the southern Caucasus provides not much evidence for the Micoquian (Golovanova and Doronichev 2003). The late MP assemblages from Ortvale Klde in Georgia, for example, feature a dominance of the recurrent unidirectional Levallois technique, a high percentage of convergent scraper, and a high frequency of basal thinning. Assemblages from Lusakert Cave in Armenia also indicate a dominance of Levallois technique and the presence of truncated facetted pieces (Gasparyan et al. 2014). Characteristics observed in late MP assemblages from the southern Caucasus appear to mirror patterns identified among sites in the Zagros Mountain range (Adler and Tushabramishvili 2004). Adler and Tushabramishvili (2004:124) point out that "lithic analyses demonstrate that Neanderthals in the southern Caucasus shared more technological affinities with their neighbors to the south than they did with those located to the north where Micoquian and para-Micoquian assemblages are common." We can thus conclude that the Greater Caucasus remains a barrier for expansions during the late MP. Differences in the composition of faunal remains provide further support for this conclusion (Golovanova and Doronichev 2003). The fossil evidence from sites such as Bronze Cave (Pinhasi et al. 2012), Ortvale Klde Cave (Moncel et al. 2015), or Sakajia Cave (Pinhasi et al. 2012) in Georgia indicate that Neanderthals occupied the southern Caucasus during the late MP, providing no evidence for an incoming modern human population between ca. 70 and 40 ka.

Probably the most significant change in the Paleolithic record of the Caucasus region occurred after 40,000 years ago. The late MP assemblages were replaced all over the region, including areas north and south of the Greater Caucasus, by early UP assemblages featuring a developed blade and bladelet technology. Evidence comes from sites such as Mezmaiskaya Cave (Golovanova et al. 1999), Ortvale Klde (Adler et al. 2008), Bondi Cave (Tushabramishvili et al. 2012), Sakajia Cave (Pinhasi et al. 2012), or Hovk-1 (Pinhasi et al. 2008). The chronology of the occurrence of the UP assemblages slightly differs among the regions. A signal in common, however, is a rather fast replacement within a narrow time frame roughly between 40 and 37 kyr cal BP.

Given the Late Pleistocene archaeological and fossil records of the Caucasus region, the significant change related to the MP to UP transition currently provides the best evidence for an incoming population of modern humans along the northern route to eastern Asia. In contrast, the currently available record provides no strong evidence that earlier expansions of modern humans reached the Caucasus. The probable continuous presence of Neanderthals in this region might have prevented the influx of modern humans before roughly 40 kyr BP.

Although we emphasize changing environmental and climatic conditions as important driving forces for variations in spatiotemporal patterns in the distribution of human groups, we also acknowledge the importance of the socioeconomic background of the human populations studied. Mapping paleoenvironmental conditions alone does not provide a valid basis for developing models for human expansion processes. Moreover, the probability for local extinctions or survival during periods of unfavorable conditions is a topic not very well understood and often not well represented in dispersal models. One open question in this context is how climatically dry conditions affect occupation density in arid regions. It is often argued that decreased precipitation leads to hostile conditions. Detailed knowledge about the geography of a region is necessary to prove this conclusion. Local fresh water springs, for example, can keep a region's potential for human occupation high even under climatically dry conditions. Another factor in this context is human behavioral flexibility. It can change through time (Kandel et al. 2015) and potentially opens new options for adaptations to increasingly arid environments and survival under dry conditions. Understanding population responses to climatic extremes would be an important factor in the assessment of regions with regard to geographic range expansion and contractions of human populations.

Our case studies demonstrate that different regions provide different signals for human immigration and dispersal through time. The results presented here reveal that simple unidirectional models inadequately represent processes of human dispersals and underestimate factors such as local geographic conditions, behavioral flexibility, and multidirectionality in the dispersal process. The northern and the southern routes into Central and Eastern Asia might have been used very differently throughout the Late Pleistocene. To refine our expansion models we require more regional data along both pathways.

Conclusion

The three study regions presented in this paper are located at important positions along the potential northern and southern expansion routes of modern humans out of Africa and into Central and Eastern Asia. Their archaeological records provide evidence for distinct occupation histories, including pulses of occupation with long occupational gaps in southeast Arabia, a mosaic pattern of settlement continuity and discontinuity in southwest Syria, and a pronounced discontinuity in the southern Zagros. Based on our survey and excavation records from these regions, we demonstrate that the potential for dispersals varies between the regions and through time, suggesting a high degree of complexity in the process of modern human dispersals. This conclusion contrasts with models of modern human dispersals that often delineate simple unidirectional connections between regions or even continents frequently denoted as arrows on maps. To gain insight into the chronology and the spatial patterns of the dispersal process and to develop meaningful models, we argue that we instead need to address the complexity observed when focusing on the regional scale.

Acknowledgments

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Environments and Cultural Change in the Indian Subcontinent

Implications for the Dispersal of *Homo sapiens* in the Late Pleistocene

by James Blinkhorn and Michael D. Petraglia

The Indian subcontinent lies on a key east-west corridor for hominin expansions across Asia, which has led to it playing a prominent role in debate surrounding the dispersal of modern humans. The current geography and ecology of the region consists of a diverse array of habitats. An examination of changes in monsoonal intensity indicates that geographic reconfiguration of ecological diversity occurred, but at a regional level, South Asia is shown to provide suitable environments for hominin occupations throughout the Late Pleistocene. Unfortunately, the fossil record of South Asia remains poor, preventing decisive resolution of modern human dispersal debates. However, in the past decade new interdisciplinary approaches to the archaeological record have overhauled the framework for understanding behavioral change during the Late Pleistocene. While the nature of the Late Acheulean to Middle Paleolithic transition remains to be resolved, it is now clear that it appears significantly later than in other Old World regions and may coincide with the expansion of modern humans across Asia. Mounting evidence supports a gradual rather than abrupt transition from Middle to Late Paleolithic technologies, which does not easily reconcile with arguments for the introduction of microlithic tool kits by the earliest expansions of modern humans.

The Late Pleistocene record of Asia is marked by significant changes in human demography and behavior, including, most notably, the expansion of *Homo sapiens* from Africa (Athreya 2015; Barker et al. 2007; Demeter et al. 2012; Grun et al. 2005; Kennedy and Deraniyagala 1989; Liu et al. 2015; Mijares et al. 2010) and their interbreeding with archaic populations (Green et al. 2010; Kuhlwilm et al. 2016; Nielsen et al. 2017; Prüfer et al. 2014; Rasmussen et al. 2011; Reich et al. 2010). The Indian subcontinent is a critical region to explore human dispersals because of its geographic position on major east-west routes of human migration across Asia (e.g., Boivin et al. 2013; Petraglia et al. 2010; Reyes-Centeno et al. 2014). Yet the complexities of the archaeological record of the Indian subcontinent have historically been overlooked in grand, sweeping narratives of human expansion (e.g., Oppenheimer 2012; Stringer 2000).

For much of the twentieth century, incremental advancement of technology in the South Asian Paleolithic was accepted as part of the gradual, regional evolution of human populations (e.g., Misra 1989). In the past several decades, however, a growing body of biomolecular evidence has clearly indicated that all living populations shared a recent and common African ancestry, focusing debate on how and when modern humans first left Africa (Cann, Stoneking, and Wilson 1987; Harpending et al. 1993; Stoneking 1989). In light of a stark change in population, a hunt was triggered to identify a similarly sharp change in the behavioral record of the Indian subcontinent echoing the Upper Paleolithic "revolution" of Western Europe (Misra in Agrawal and Ghosh 1973; James and Petraglia 2005). Contemporary analyses support an African origin of our species, but it is now clear that dispersing populations of modern humans interbred with local archaic populations across Eurasia (see Nielsen et al. 2017). Recent research indicates that South Asian populations preserve a relatively high proportion of Denisovan DNA compared with other Eurasian populations, which has implications for understanding the number, timing, and geography of interbreeding episodes (Sankararaman et al. 2016). This more complex demographic scenario is accompanied by wider awareness of the diverse factors that influence cultural evolution and technological innovation (e.g., Collard, Buchanan, and O'Brien 2013; Grove 2015; Vaesen et al. 2016).

Major changes in our understanding of the Late Pleistocene hominin occupation of the Indian subcontinent have resulted

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from interdisciplinary research projects implemented over the last decade and particularly the application of chronometric dating methods (see below). Better dating controls have led to new explanations for when major changes occurred in technological and cultural developments. In particular, current debate centers on two key issues: (1) whether technological continuities occur between Late Acheulean and Middle Paleolithic industries (Mishra, Chauhan, and Singhvi 2013) or between Middle and Late Paleolithic industries (Petraglia et al. 2009, 2012), and (2) whether modern humans first arrived in South Asia using Middle Paleolithic technologies (Blinkhorn et al. 2013; Clarkson, Jones, and Harris 2012; Petraglia et al. 2007) or Late Paleolithic technologies (Mellars 2006; Mellars et al. 2013; Mishra, Chauhan, and Singhvi 2013). Here, we review the current body of evidence for Late Pleistocene occupation of the Indian subcontinent and reexamine what impli-

cations these discoveries have for understanding technological change, human expansions, and hominin admixture.

Geographic Context

The Indian subcontinent broadly corresponds with the political region of South Asia (Bangladesh, Bhutan, India, Nepal, Pakistan, and Sri Lanka). Continental borders with surrounding regions are characterized by high-relief mountain chains and plateaus, such as the Hindu Kush, the Himalaya, and the Patkai ranges (fig. 1), which are the orogenic product of the collision of the Indian and Eurasian tectonic plates (van Hinsbergen et al. 2012). It is within these extreme high-relief borders to the region that the source for the three largest river systems of the subcontinent—the Indus, the Ganges, and the Brahmaputra—are to be found. Within the subcontinent, a number of smaller
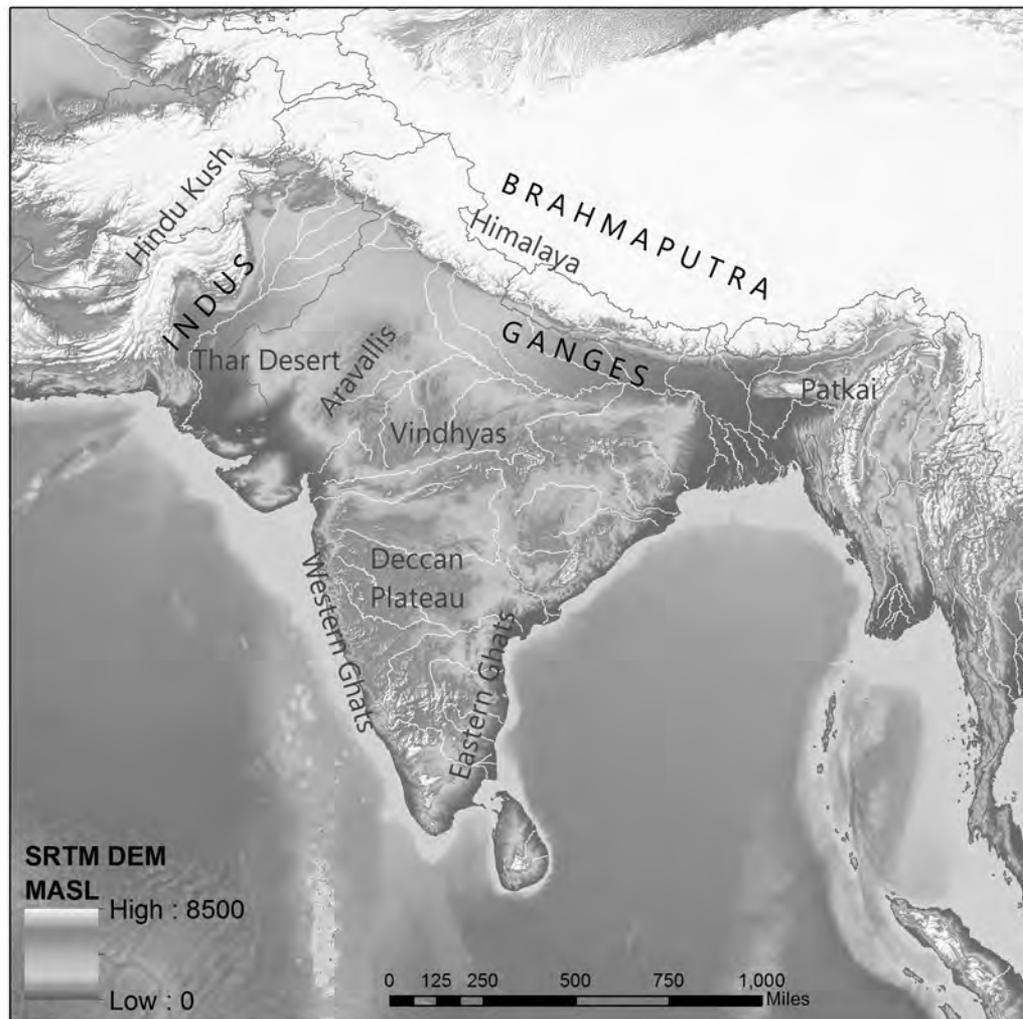

Figure 1. Digital elevation model of the Indian subcontinent (US Geological Survey 2006). The subcontinent's broad, low-relief fluvial network stands in stark contrast to the extreme topography found to the west, north, and east. A color version of this figure is available online.

mountain ranges and elevated plateaus are also present, including the Aravalli and Vindhyan ranges, the Western and Eastern Ghats, and the Deccan Plateau. These provide the source for other major fluvial systems, such as the Narmada, that drain westward from the Vindhyas and the Godavari, Krishna, and Kaveri rivers that drain eastward across the Deccan Plateau and Eastern Ghats.

The stepwise uplift of the Tibetan Plateau and surrounding mountain ranges has also played a defining role in the evolution of the dominant environmental feature of the Indian subcontinent: the monsoon (Molnar, England, and Martinod 1993; Zhisheng 2001). The monsoon system is driven by a cross equatorial atmospheric pressure gradient resulting from differential heating of the Asian landmass, principally the Tibetan Plateau, and the Mascarene high-pressure zone in the southern Indian Ocean (Clemens et al. 1991; Gadgil 2003; Leuschner and Sirocko 2003). Strong southwesterly winds occur during the summer months, delivering the majority of the subcontinent's precipitation following evaporation from the Arabian Sea, whereas weaker and regionally restricted northeasterly winds deliver more limited precipitation during the winter months (Clemens et al. 1991; Gadgil 2003; Leuschner and Sirocko 2003). Recent stepwise tectonic uplift ~150 ka was localized in the northeast Tibetan Plateau and is unlikely to have significantly affected the South Asian monsoon (Li et al. 2014). However, the increased aridification of the Asian interior that resulted from this may have altered the importance of the habitable landscapes in South Asia for hominins.

Although the effects of the monsoons are felt across the Indian subcontinent, the distribution of precipitation is distinctly regional and highly seasonal. Yet beyond relief, the geological structure of the Indian subcontinent plays another important role in patterns of habitability in the region. The analysis of the structure of geological basins within the Indian subcontinent led Korisettar (2007) to the conclusion that the Purana basins exerted a strong influence on hominin dispersals and occupation history. Although direct precipitation within the Purana basins is lower than other regions of the subcontinent, perennial supplies of freshwater are available because of spring activity from aquifers that deliver water resources from regions that receive much higher monsoonal precipitation. As a result of reliable water resources and abundant raw materials for stone tool manufacture, these geological basins are thought to have acted as refugia not only for hominin populations but also for varied flora and fauna (Korisettar 2007).

The importance of such Purana basins for providing refugia is well exemplified by the recent study of fauna from the Billasurgum caves, located within the Cuddapah Basin. Here, excavations revealed the first stratified sequence to document patterns of faunal occupation spanning the late Middle Pleistocene to Late Pleistocene (Roberts et al. 2014). This study illustrated the long-term continuity of large-bodied fauna within South Asia with only a single taxon of twenty-four identified as having gone extinct across the subcontinent (Roberts et al. 2014). Patterns of environmental change throughout the Late Pleisto-

cene are likely to have resulted in the significant redistribution of South Asia's habitats. However, the broad ecological mosaic of the region appears to have buffered such changes, helping to prevent widespread megafaunal extinctions as observed elsewhere in the world (e.g., Koch and Barnosky 2006).

Environmental Context

The modern environments of the Indian subcontinent are diverse and sustain over a sixth of the world's current human population (United Nations Department of Economic and Social Affairs and Population Division 2015) in a mosaic of deserts and tropical rainforests, alpine tundra and savannahs, and subtropical woodland and mangroves, and riparian corridors (Mani 2012; fig. 2). Given the region's latitude, South Asia is subject to warm temperatures with limited seasonal change. This stands in stark contrast to regions immediately to the north and west, where high-amplitude temperature change can be observed both daily and seasonally. Fluctuating humidity, controlled primarily by monsoonal intensity, provides the more significant climatic factor that may have influenced habitat distribution and hominin demography across South Asia during the Late Pleistocene.

Variability within Pleistocene monsoonal circulation patterns must be considered in the context of interhemispherical oceanic and atmospheric interactions (Wang et al. 2005). Increases in solar insolation, predominately due to 19,000–23,000-year precessional cycles, result in the northward movement of the Inter-Tropical Convergence Zone (ITCZ) because of raised sea surface temperatures at low latitudes (Yi et al. 2012). The northward movement of the ITCZ results in increased monsoonal circulation capable of delivering a greater level of precipitation. Maximum global ice volumes, which are dominated by ~100,000-year cycles, may modulate monsoonal circulation by reducing sea surface temperatures and sea levels, altering the availability of water vapor for precipitation (Guo et al. 2002; 2004). Global ice volume variability and differences between hemispheres may also affect the heat differential and moisture availability between the ocean and land that drives monsoonal circulation because of an increased continental surface (Wang 1999). Studies of monsoonal intensity over the past million years indicate that monsoonal minima rarely coincide with glacial maxima due to differences in patterns in glaciation at the poles (Caley et al. 2013; Liu et al. 2011; Zhisheng et al. 2011). As a result, an examination of patterns of climatic change over the Late Pleistocene in South Asia must combine both high- and low-latitude archives of paleoenvironmental variability.

In figure 3, we combine data from Bittoo Cave, northwest India (Kathayat et al. 2016), a Bay of Bengal marine core (Site 758; Bolton et al. 2013), and two Arabian Sea marine cores (MD04-2861, Caley et al. 2011; Owen Ridge, Clemens and Prell 2003), as local proxies for summer monsoon intensity, with Arctic (SPECMAP, Imbrie et al. 1984) and Antarctic (Vostok, Petit et al. 1999) oxygen isotope records to present both the regional and global context of climate change over the past 350 ka.
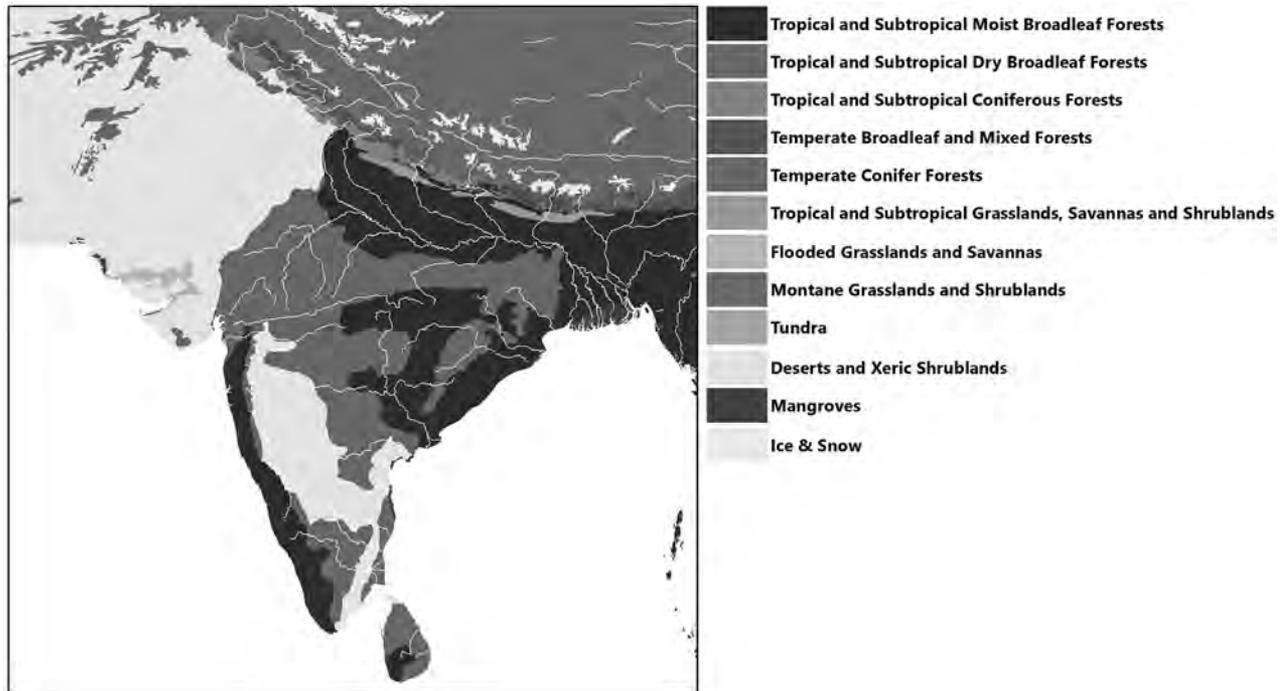
Figure 2. Map of modern ecology within the Indian subcontinent (following Olson et al. 2001) illustrating a mosaic of dry shrubland, tropical grassland, and forest habitats in contrast to the exclusively arid habitats to the west, montane grasslands to the north, and tropical forests to the east. A color version of this figure is available online.

Although in this paper we review behavioral evidence for the past 140 ka, the paleoenvironmental records illustrated in figure 3 indicate a number of differences over longer time frames that may be relevant to broader questions regarding Asian hominin demography throughout the Pleistocene. Most critically, peaks of monsoonal intensity can be repeatedly observed during glacial phases that match those present in interglacial phases. Marine isotope stages (MIS) often provide a useful means for organizing discussion of changing human behavior through time and indeed do so at an appropriate scale for the resolution of the South Asia archaeological record and so are used below. However, as the resolution of the archaeological data improves, it is anticipated that reference to global events, such as Heinrich events, or regional variability in monsoon intensity will become critical. Below we describe the key trends in monsoonal intensity for the Late Pleistocene identified in proxy data sets presented in figure 3.

At the end of MIS 6 (~140–150 ka), proxies of monsoonal intensity indicate a period in which peaks of monsoon activity match the scale observed during interglacial conditions, which is particularly evident in the Site 758 Bay of Bengal records. However, a sharp decline in monsoonal intensity follows this period that approaches the scale of other Middle Pleistocene monsoonal minima, evident in the records at Bittoo and MD04-2861. The advent of interglacial conditions in MIS 5 (71–130 ka) sees the return of more intense monsoonal conditions. However, the four regional data sets indicate peak monsoonal intensity occurring during different phases: during MIS 5e (115–

130 ka) in Owen Ridge, during MIS 5c (93–106 ka) in MD04-2861 and Bittoo, and during MIS5a (71–84 ka) in Site 758. All regional data sets presented in figure 3 indicate a sharp decline of monsoonal intensity correlated with MIS 4 (59–71 ka), with one Arabian Sea record suggesting lower monsoonal intensity than the last glacial maximum (LGM), and rivalling the penultimate glacial maximum ~150 ka. The return of stronger monsoonal conditions is observable from the start of MIS 3 (28–59 ka) across all proxy records and in each case records peaks of monsoonal intensity that are close to or exceed peaks observed during MIS 5, particularly between ~40 and 59 ka. Records from Bittoo and MD04-2861 suggest that higher amplitude and frequency of oscillations in monsoonal intensity occur during this period, with all records displaying a gradual decline in monsoonal activity toward the end of MIS 3. With minima in monsoonal intensity observed in all records ~21 ka, there is little evidence to suggest the monsoonal minimum significantly predates the LGM.

The availability and distribution of sufficient freshwater resources, largely relating to the intensity and geography of monsoonal precipitation, probably played a critical role in determining the spatial configuration of South Asia's diverse habitats and the viability of human occupation of the subcontinent. Figure 4 presents modeled distribution of precipitation for MIS 5e and the LGM (Braconnot et al. 2007; Otto-Bleisner et al. 2006). These offer useful analogies for the scale of variability of precipitation and its distribution between monsoonal minima and maxima identified above and in figure 3. Extreme
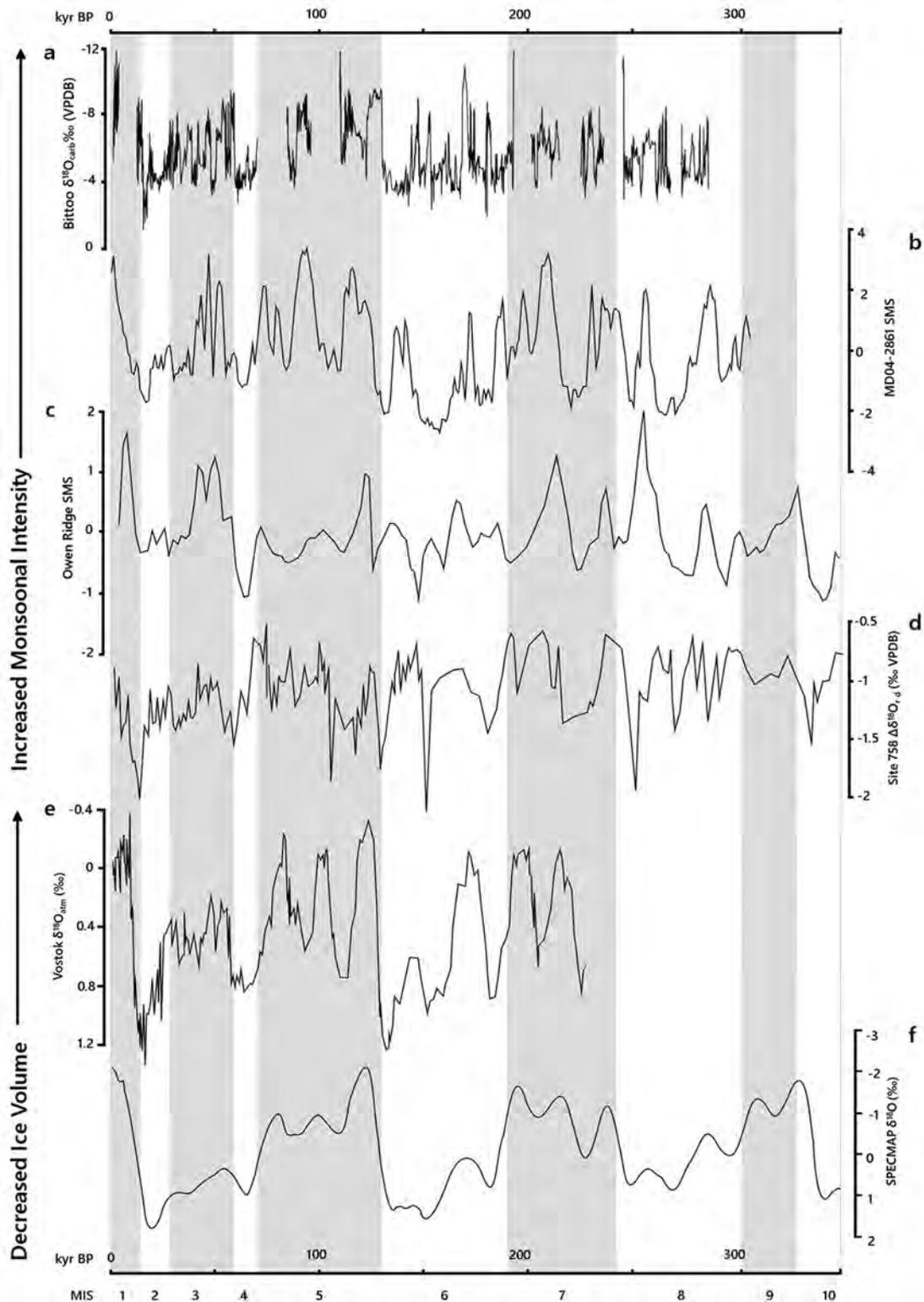
Figure 3. Four archives of environmental change in the Indian subcontinent, including oxygen isotope records from Bittoo Cave (*a*), two alternate summer monsoon stacks from the Arabian Sea (*b*, MD04-2861; *c*, Owen Ridge), and oxygen isotope records from Site 758, Bay of Bengal (*d*), plotted with high-latitude southern (*e*, Vostok) and northern (*f*, SPECMAP) oxygen isotope records spanning the past 350,000 years (modified from Bolton et al. 2013; Caley et al. 2011; Clemens and Prell 2003; Imbrie et al. 1984; Kathayat et al. 2016; Petit et al. 1999). Climatic archives from the Indian subcontinent illustrate different patterns of monsoonal intensity than are typically inferred from high-latitude records, which often provide the framework for discussing later Pleistocene environmental change globally and particularly the high monsoonal intensity observed during MIS 3.
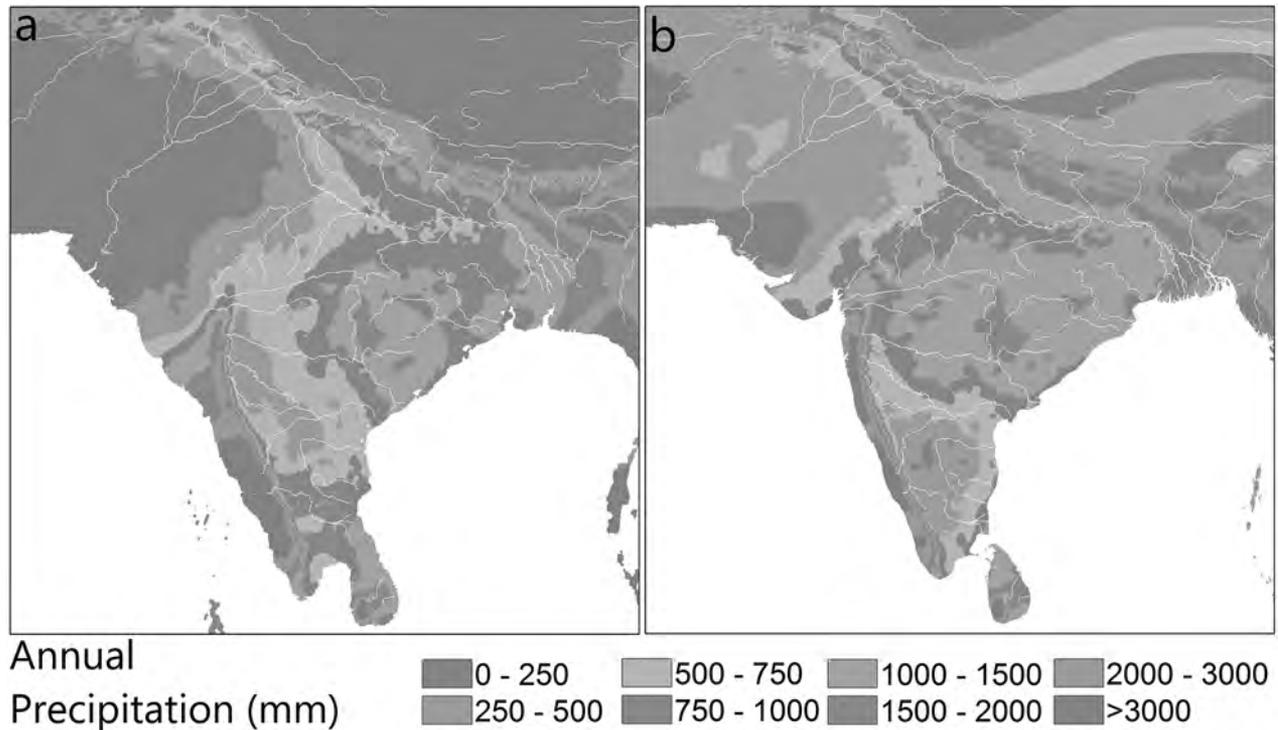
Figure 4. Precipitation models for the Indian subcontinent for the last glacial maximum (*a*, following Braconnot et al. 2007) and marine isotope stage 5e (*b*, following Otto-Bleissner et al. 2006), offering insight into the scale of change in precipitation between monsoonal minima and maxima, respectively. Notably, much of the subcontinent enjoys humidity within an ideal range for human inhabitation at both monsoonal minima and maxima. A color version of this figure is available online.

aridity (<200 mm annual precipitation) probably prevented occupation of the Thar Desert during suppressed monsoonal regimes. Although less prohibitive to human occupation, extreme levels of humidity (>2,000 mm annual precipitation) can be observed in the rain forests in northeastern regions of the Indian subcontinent, which may have demanded distinct biological and cultural strategies for humans to successfully adapt to these habitats (Roberts, Boivin, and Petraglia 2015). With these exceptions aside, the majority of the Indian subcontinent offers habitats that are not prohibitive to hominin habitation and indeed are likely to have offered ideal habitats for long-term occupation and expansion (see Finlayson 2013).

The Hominin Fossil Record

Limited change has occurred to the fossil record of hominins in South Asia over the past decade. The only reliable evidence for pre–*Homo sapiens* anatomy from the Indian subcontinent remains the Hathnora specimen, a calvarium recovered from gravel deposits in the Narmada Valley (Sonakia and Kennedy 1985). While appearing distinctly archaic given the thickness of cranial bone, the specimen presents derived traits, such as a globular cranium, as well as a cranial capacity matching contemporaneous populations (Athreya 2015; Rightmire 2015). Attributing this specimen to any existing taxa appears prob-

lematic, particularly as the specimen presents a mosaic morphology rather than distinctly African, West Eurasian, or East Eurasian traits (Athreya 2015). Although dating the specimen is problematic, the most secure age estimate is ~236 ka, with ongoing surveys in the region aiming to bolster the fossil record and better understand the sedimentary context from which the Hathnora specimen was recovered (Cameron, Patnaik, and Sahni 2004; Kennedy 2000; Patnaik et al. 2009). Recent evidence for pre-*sapiens* populations (Sankhyan 2013) has been critiqued for the lack of diagnostic elements to firmly attribute the specimens as being hominin compounded by the absence of clear stratigraphic provenance or chronometric dating (Chauhan, Ozarkar, and Kulkarni 2015).

Similarly, little has changed in the fossil record for the appearance of *Homo sapiens* in the Indian subcontinent, with the earliest well-dated specimens significantly postdating the arrival of modern humans across the Old World. A skull that is suggested to retain archaic features comparable to Asian *Homo erectus* has recently been reported from sediments dating between 30 and 50 ka in the Orsang Valley, western India, but direct dating of the specimen to the mid-Holocene complicates interpretation (Chamyal et al. 2011). The earliest definitive specimens of *H. sapiens* remain those from the cave sites of Fa Hien and Batadomba-Lena (see below) in Sri Lanka, appearing from ~36 to 28 ka onward (Deraniyagala 1992; Kennedy and Deraniyagala 1989; Perera et al. 2011). Within the

past decade, four burned cranial vault fragments and a single tooth were recovered from a horizon dating to 12–20 ka at Jwalapuram 9, which are the oldest *H. sapiens* specimens from mainland South Asia at present (Clarkson et al. 2009). Other sites within and adjacent to South Asia, such as Bhimbetka (India), present modern human specimens with some archaic features (Athreya 2015). Interpreting the meaning of this morphological diversity is complicated by the absence of reliable ages or certain associations with cultural deposits (Athreya 2015).

The Archaeological Record

The Indian subcontinent has a long history of Paleolithic research leading to the identification of numerous Late Pleistocene archaeological sites (Misra 2001; Pal 2002; Raju and Venkatasubbaiah 2002). Here, we will use the terms Late Acheulean, Middle Paleolithic, and Late Paleolithic to describe the three main Middle and Late Pleistocene Paleolithic industries following James and Petraglia (2005). This broadly relates to the production of bifaces and limited flake tools (Late Acheulean), the use of hierarchically prepared cores to produce predetermined blanks for more diverse flake tools (Middle Paleolithic), and microlithic/microblade-based industries showing some variation, such as the presence of prepared cores (Late Paleolithic). In the past, significant continuity has been identified between these technological phases. However, the general lack of dated sites with controlled understanding of assemblage formation processes may have served to blur the boundaries between industries. Poor chronometric controls and limited associations between fossil specimens and material culture have hampered critical assessment of behavioral changes associated with the arrival of *Homo sapiens* in South Asia.

Significant advances have been made in understanding the chronology of the Late Pleistocene archaeological record of South Asia in the past decade. The overall number of sites dated before the review presented by James and Petraglia (2005) was not insubstantial. However, the majority of these were Late Paleolithic sites dated by traditional radiocarbon methods, which is limited to the past ~45 thousand years. As a result, discussion of the tempo of behavioral changes, such as from the Middle to Late Paleolithic, has been problematic. The application of luminescence methods within the past decade has been critical for shedding light on the chronology of Middle Paleolithic occupations of the Indian subcontinent as well as establishing the lower age bounds of Late Acheulean occupations. Figure 5 presents a compilation of chronometric age estimates associated with Late Paleolithic, Middle Paleolithic, and Late Acheulean artefact assemblages dating between 20 and 140 ka across South Asia. Below, we focus our review predominantly on the results of the most recent programs of controlled excavations that have applied contemporary dating methods to present the most secure chronometric framework for cultural change in South Asia. However, it is worth noting

few major discrepancies occur between this group and the wider corpus of dated sites presented in figure 5.

The Final Late Acheulean (Up to 100 ka)

Owing to new chronometric dating, it is now evident that the Late Acheulean of the Indian subcontinent includes some of the youngest occurrences of these industries worldwide. Recent research in the Middle Son Valley, north-central India, has constrained the youngest Late Acheulean assemblages. Excavations at the site of Bamburi 1 revealed a 4 m deep section including poorly sorted gravels and cobbles relating to the lower member of the Sihawal Formation and pedogenised sandy silts from the upper member of the Sihawal formation (Haslam et al. 2011). The interface of these two sediment units is constrained by three statistically indistinguishable optically stimulated luminescence (OSL) dates of 131 ± 9 ka (BAM3/2, Lower Member), 125 ± 13 ka (BAM1/2), and 131 ± 10 ka (BAM1/1, Upper Member; Haslam et al. 2011). The topmost deposits of the Lower Member yielded fresh examples of multiplatform and bifacially worked cores alongside a refined biface and are attributed to the Late Acheulean. Two dates from the Patpara Formation, which disconformably overlies the Sihawal Formation, of 137 ± 10 ka (PAT4/1) and 140 ± 11 ka (PAT3/2) are also associated with fresh Late Acheulean artefacts (Haslam et al. 2011). These dates correspond well with previous dating in the region, providing minimum ages for the Sihawal Formation to $>90 \pm 20$ ka (B-1), >100 ka (N-1), and $>103.8 \pm 19.8$ ka (Alpha 899; Pal et al. 2005; Williams and Clarke 1995; Williams et al. 2006). Critically, this research helps constrain the end of the Late Acheulean with maximum ages, whereas earlier studies on the youngest Late Acheulean in western and central India have only provided minimum ages (Ajithprasad 2005; Bednarik et al. 2005; Juyal et al. 2000).

Middle Paleolithic (96–34 ka)

Until recently, the time frame for the Middle Paleolithic was very poorly defined, based primarily on a small number of radiocarbon and uranium series dates that returned minimum ages. Preliminary studies at 16R Dune, in the Thar Desert in western India, indicated the presence of Middle Paleolithic technologies within contexts dating to ~109 ka (TL24) and ~130 ka (TL19; Misra and Rajaguru 1989; Raghaven, Rajaguru, and Misra 1989; Singhvi et al. 2010). However, subsequent technological analysis by Gaillard (1993) failed to identify any artefacts among these assemblages that could securely be attributed to either Middle Paleolithic or Late Acheulean technologies.

Excavations at the site of Katoati, on the eastern margin of the Thar Desert, have identified a number of Middle Paleolithic assemblages (Blinkhorn et al. 2013), which currently include the oldest excavated and dated examples of this industry in South Asia. The archaeological horizons comprise deposits from the edge of a braided channel overlain by a cap of sand
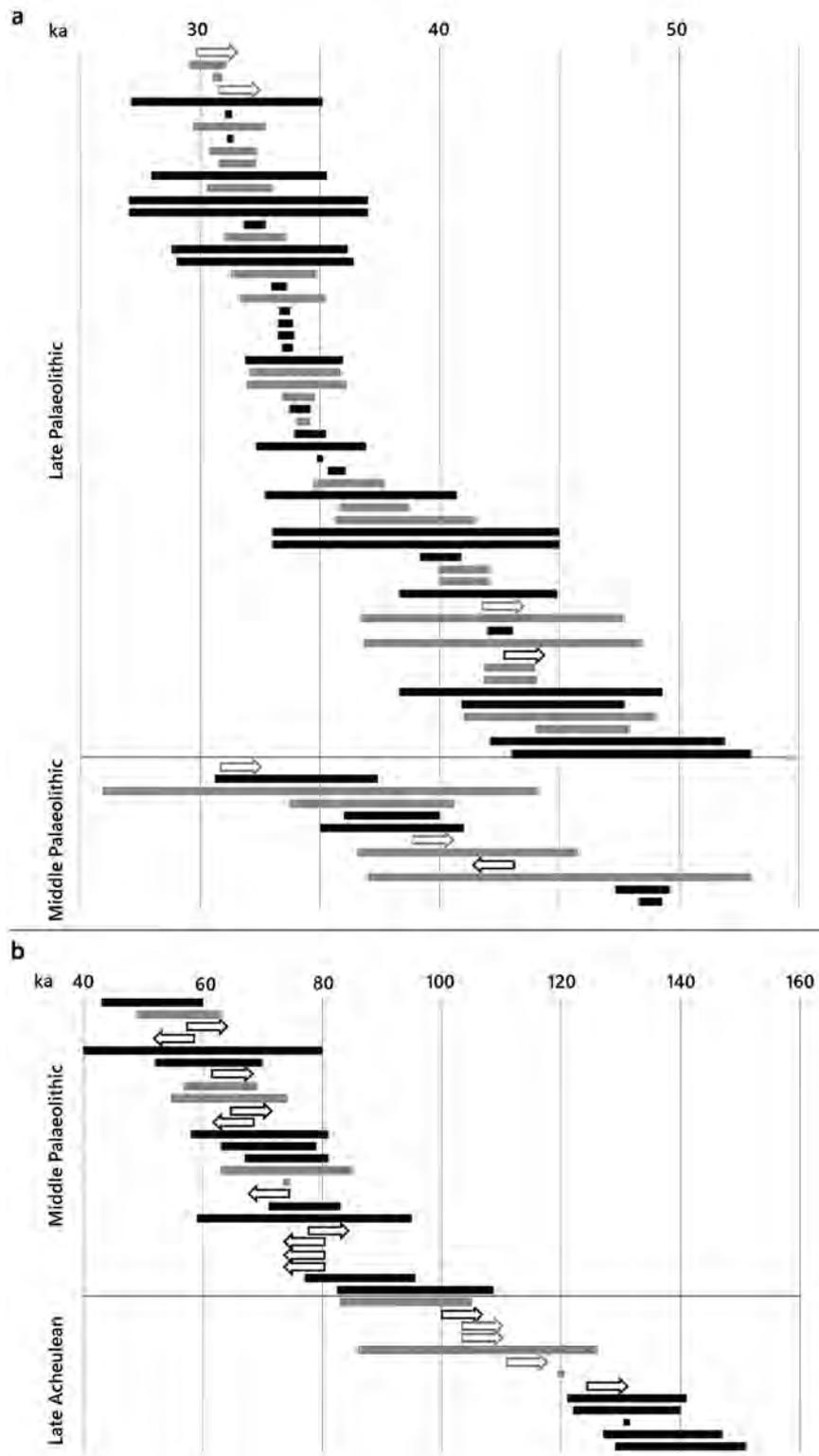
Figure 5. Age ranges for Late Pleistocene Paleolithic sites in South Asia where the central age estimate dates between 30 and 50 ka (*a*) and 50 and 140 ka (*b*). Arrows indicate minimum and maximum age estimates. Bars or arrows in black represent dated assemblages reported since 2007; bars or arrows in gray represent dated assemblages reported before 2007. Recent dating supports considerable chronological overlap between Middle and Late Paleolithic assemblages. The number of dated Middle Paleolithic assemblages has increased significantly in the past decade with the limited evidence for chronological overlap with Late Acheulean assemblages not supported by the most recent dating.

dune deposits. Large proportions of the main assemblages—dating to 95.6 ± 13.1 ka (LD-1149), 96–77 ka, 77 ka (LD-1090), and ~60 ka—are composed of highly cortical simple cores and flakes. This probably represents a focus on primary reduction activities, exploiting the availability of cobbles made up of diverse materials associated with uplifted deposits from the Jayal Gravel ridge (Blinkhorn et al. 2017). Based on raw material types, only a single artefact can be identified as exotic to the site. Evidence for more formalized reduction strategies are evident in both the core and debitage assemblages, suggesting a focus on radial preparation of cores to remove large, broad flakes (Blinkhorn 2012). Similarly, a focus on point production is evident with the presence of prepared point cores analogous to Nubian core methods, Levallois and pseudo-Levallois points, and retouching of flakes to produce convergent margins or basal modification (including shoulders, basal thinning, and a tang) to assist hafting of pointed flakes (Blinkhorn, Achyuthan, and Ajithprasad 2015).

Turning to southern India, sites from the Jurreru Valley also document patterns of Middle Paleolithic technological behavior during MIS 5. The site of Jwalapuram Locality 22 contains a large number of lithic artefacts recovered from a paleosol constrained by overlying deposits of YTT (74 ka) and an underlying OSL date of ~85 ka (J22/5; Haslam et al. 2012). At Jwalapuram Locality 3, artefacts are found within a ~25 cm thick pebbly horizon constrained by an underlying OSL age of 77 ± 6 ka (JLP-380) and an overlying deposit of primary YTT ash (Petraglia et al. 2007). Middle Paleolithic technologies at these sites include recurrent Levallois and discoidal core reduction methods alongside less formal single and multiplatform cores, a range of point forms (including Levallois points and single instances of unifacial, bifacial, and tanged points), retouched tools (predominately notches and scrapers), and notable proportions of blades, burins, and microblades (Clarkson, Jones, and Harris 2012). Paleoenvironmental work across the Jurreru Valley has indicated significant variability at a landscape scale that was preserved by a blanket of primary YTT ashfall. Isotopic and phytolith evidence indicates mixed C_3 and C_4 foliage with varying proportions depending on topographic position within the landscape and association with identifiable depositional centers (Blinkhorn et al. 2012).

Evidence for Middle Paleolithic assemblages in Sri Lanka predates sand dunes deposited between 74 and 64 ka at Site 50 and appears in gravel deposits at Site 49, suggested to have been deposited in the early Upper Pleistocene (Deraniyagala 1992; Singhvi, Deraniyagala, and Sengupta1986). This finding is consistent with the appearance of Middle Paleolithic technology elsewhere in South Asia during MIS 5, but current descriptions of the technology do not enable comparative studies.

Besides Katoati, a number of sites in the Thar Desert preserve evidence of the Middle Paleolithic that postdate MIS 5. A new synthesis of the archaeological and chronometric evidence from 16R Dune suggests that a Middle Paleolithic occupation of the site is constrained by OSL dates of 80 ka (TL13) and 40 ka (TL11; Blinkhorn 2013). The artefact-bearing horizon is found overlying the top of a number of carbonate layers, which form as postdepositional features over millennial time scales that are also bracketed by the OSL dates. As a result, it is suggested that this Middle Paleolithic occupation may be more closely associated with the younger end of this time bracket (Blinkhorn 2013). In addition to these excavations, artefact collections from Shergarh Tri Junction in the Thar Desert are attributed *post quem* dates of 60 ka and 43 ka (Blinkhorn 2014). Among the smaller collection dating to <43 ka are numerous cores with bidirectional blade removals from both Levallois and non-Levallois cores.

A number of sites from the Jurerru Valley have yielded Middle Paleolithic assemblages postdating the eruption of Toba. Luminescence age estimates for artefact assemblages from JWP3/3b, 20, 21, and 23 span 55–34 ka and indicate some continuity of technological behavior but with certain aspects of earlier practices subject to greater emphasis (Petraglia et al. 2012). Most notable is the more limited role of prepared-core (Levallois; discoidal) methods and greater focus on single platform cores (Clarkson, Jones, and Harris 2012). Meanwhile, continuity in the proportions of retouched tool types such as scrapers, notches and burins, and blades and microblades is observed (Clarkson, Jones, and Harris 2012). In contrast to this continuity in the presence of certain behaviors, it is within the context of these Late Middle Paleolithic assemblages that bipolar technologies first appear.

A Middle Paleolithic site with a clear component of blade production embedded in prepared-core technologies is Patne (James 2011). In spite of a stratigraphic disconformity between Middle and Late Paleolithic horizons at the site and the presence of only a single radiocarbon age estimate obtained in the 1980s, Patne remains a key feature of debate for Late Pleistocene behavioral change as a rare example of a single sedimentary sequence preserving evidence for the use of both industries.

Late Paleolithic (~45 ka Onward)

Despite evidence for the Late Pleistocene antiquity of microlithic industries in Sri Lanka (i.e., Batadomba-Lena, Fa Hien, Kitugala Beli-Lena; Deraniyagala 1992) and in India (i.e., Patne; Sali 1985,1989), the early age of these technologies has only recently been widely accepted, as previous analysts considered these small-tool assemblages to be Holocene in age (Misra 1989). Realization of their antiquity is a consequence of increasing numbers of older chronometric ages from new excavations and detailed attribute-based lithic analyses that show developmental trends through time.

Excavations at Mehtakheri, in the Narmada Valley, currently present the oldest lithic assemblage argued to represent the shift to Late Paleolithic technologies and dating to ~45 ka (Mishra, Chauhan, and Singhvi 2013). Abraded (and undescribed) Middle Paleolithic artefacts are known from lower deposits dating to MIS 4. An assemblage of 849 artefacts is derived from Unit 2 at the site and is dated by a number of OSL age estimates and an

infinite ^{14}C date, with the basal OSL date of 44.3 ± 4.3 ka (MHK-09-10). Among these artefacts, two different reduction sequences are evident, one focusing on larger flake production from unidirectional or radial quartzite cores and the other centered on blade production from chalcedony and chert cores. The excavators identify the prominence of 10 microblade cores (mostly 20–30 mm), 50 complete blades, 100 broken blades, and two backed blades within the assemblage as key evidence to attribute the assemblage to the Late Paleolithic (Mishra, Chauhan, and Singhvi 2013). However, both the low density of diagnostic artefacts and limited published information regarding the dates, specifically the absence of dose rate distributions or report of aliquot sizes, complicate interpretations (see Groucutt et al. 2015b).

Recent surveys and excavations in West Bengal have identified the earliest Paleolithic sites in the eastern regions of South Asia within and eroding from pediment colluvium at the sites of Kana and Mahadeberra (Basak and Srivastava 2014). At Kana an assemblage attributed to the Late Paleolithic comprises seven blade cores (up to 60 mm in length) and 29 microblade cores (between 20 and 40 mm in length) along with microblade debitage and large flakes from 40 mm and upward of 60 mm and is dated by OSL to 42 ± 4 ka (Kana-1.4 m). The larger buried Late Paleolithic assemblage at Mahadebbera ($n = 111$) dates between 25 ± 3 ka (Maha-0.69 m) and 34 ± 3 ka (Maha-2.03 m) and predominately focuses on microblade reduction and the production of retouched lunates, points, triangles, and backed blades.

An examination of the origins of Late Paleolithic technologies must, however, go beyond identification of the earliest microblade industries given the presence of blades and microblades in some late Middle Paleolithic assemblages. This is particularly pertinent in light of models for a gradual Middle to Late Paleolithic transition and questions over where to place the elongate-flake-focused assemblage from Riwat (Site 55) dating to ~45 ka (Dennell et al. 1992). Rather, there is a need to illuminate change across the breadth of technological behavior through time. Such detailed studies are available from Sri Lanka, the Jurreru Valley, and Patne.

In Sri Lanka, a number of new studies have been conducted within the past decade concerning the three key sites of Batadomba-Lena, Fa Hien, and Kitugala Beli-Lena. Roberts and colleagues (Roberts, Boivin, and Petraglia 2015) have undertaken a fresh assessment of the dating of these sites, conducting Bayesian modeling to help constrain the upper age ranges for occupation of the site. At Fa Hien, bulk sampling for radiocarbon dating in the oldest horizons results in an age bracket of 38.5–35 ka. Yielding human fossils as well as geometric microliths, beads, and bone tools, these horizons provide a critical benchmark for both the certain appearance of *H. sapiens* in the Indian subcontinent as well as a range of other "modern" behaviors. A conservative age estimate is presented by Roberts and colleagues (Roberts, Boivin, and Petraglia 2015) for the oldest horizons at Batadomba-Lena, a Bayesian modeling framework, offers a wide age bracket of 35–28 ka. At Kitugala Beli-Lena, an age bracket of 31–26 ka is presented for the appearance of microlithic technologies (Roberts, Boivin, and Petraglia 2015). From the LGM onward, dating of these sites becomes significantly more refined, with long-term occupations at Batadomba-Lena and Kitugala Beli-Lena extending into the Holocene.

Lewis and colleagues (Lewis, Perera, and Petraglia 2014) have undertaken a technological assessment of a sample of lithic assemblages from the oldest Late Paleolithic horizons at Batadomba-Lena. Previous researchers have commented on the scarcity of retouched microlithic artefacts within these horizons, noting the large volumes of flakes and flaking debris. Lewis and colleagues (Lewis, Perera, and Petraglia 2014) have demonstrated that the inhabitants of the site were using flake blanks for retouching into typologically distinguishable microlithic forms. This marks a notable difference from contemporaneous sites in India where microblade reduction strategies provide blanks for retouched microlithic artefacts.

The excavations at Jwalapuram 9, a rock-shelter in the Jurreru Valley, have played a key role within the last decade for firmly establishing the Late Pleistocene antiquity of microlithic assemblages in mainland South Asia (Clarkson et al. 2009; Clarkson, Jones, and Harris 2012; Petraglia et al. 2009). The earliest Late Paleolithic horizon at Jwalapuram 9 (>29.4 ± 0.19 ka BP [shell aragonite, bivalve; OxA-14829]; >34.3–33.4 ka Cal BP) indicates the presence of a comparable proportion of notches and scrapers to the youngest Middle Paleolithic sites in the Jurreru Valley but a much larger proportion of microblades than previously present. A gradual decline in the proportion of scrapers and notches is evident in younger Late Paleolithic levels, in which microblade cores and backed artefacts become prominent features of lithic technology (Clarkson, Jones, and Harris 2012). Varying proportions of single and multiplatform cores, blades, burins, and bipolar flakes are also present, typically at lower proportion than in young Middle Paleolithic horizons (Clarkson, Jones, and Harris 2012). Alongside the rich record of lithic technology and long-term occupation history from >34 ka into the Holocene, the rich material culture at the site beyond lithic technology includes the production of nonlithic tools, stone beads, and human remains (Clarkson et al. 2009).

At Patne, a younger Late ("Upper") Paleolithic horizon (IIIA) was dated to 24.27 ± 0.195 ka BP (ostrich eggshell; GRN7200) through ^{14}C dating of an engraved fragment of ostrich eggshell underlying two further young Late Paleolithic levels and overlying five early Late Paleolithic and a single Middle Paleolithic horizon (Sali 1989). Sali (1985, 1989) identified a gradual decline in average size from ~45 mm to 30 mm and a broad decrease in prevalence through time of burins, borers, scrapers, and retouched points. Prepared cores are present alongside blade cores only in the Middle Paleolithic and the two oldest Late Paleolithic horizons, whereas less formal flake cores are only present in the overlying four Late Paleolithic horizons. Retouched blades, including burinated and backed blades, first appear in the Late Paleolithic, whereas classic microlithic forms only appear in the younger Late Paleolithic

horizons. Statistical analyses as part of an attribute-based study of a sample of these assemblages further corroborates these results (James 2011). Pairwise analyses between adjacent horizons within the stratigraphic sequence failed to identify significant differences in lithic technology, supporting gradual change between horizons. Only at a groupwise level were significant differences identified: between the Middle Paleolithic horizon and the youngest Late Paleolithic level.

In addition to these well-studied sites, the western area of the subcontinent offers further evidence for Late Paleolithic occupations. The earliest microlithic artefacts identified in the region date to 21 ± 3 ka (LD-1099) near Katoati (Blinkhorn 2012; Blinkhorn, Achyuthan, and Petraglia 2015). Assemblages at Buddha Pushkar, which appear to date to less than 27 ± 2.6 ka (PSH 92/3; Singhvi et al. 1994), offer further evidence for a gradual decrease in the size of blade and microblades through time (Allchin, Goudie, and Hegde 1978). Further evidence for the continued presence of a range of prepared-core technologies and retouched tool types known from regional Middle Paleolithic industries within Late Paleolithic assemblages is observed at Buddha Pushkar. The large number of Late Paleolithic assemblages dating to >20 ka (fig. 5) typically contain artefact inventories that considerably overlap with those reported above (James 2011). However, integrating them further into contemporary analyses is problematic because of frequent mixing of surface and buried artefacts, unsystematic sampling methods, and variable use of terminology over the extended time frame in which these sites have been originally recorded.

Discussion

The Late Acheulean to Middle Paleolithic Transition

Evidence from the Middle Son Valley dating between ~140 and 125 ka suggests that Late Acheulean populations survived any climatic downturns toward the end of MIS 6 (fig. 3). Sites found elsewhere in central and western India may indicate that Late Acheulean populations were still present during MIS 5, up to ~100 ka. However, such an assertion rests on minimum age ranges and requires further examination to support fully. The earliest currently known Middle Paleolithic horizon at Katoati, dating to ~96 ka, follows this latter time frame closely, but by the end of MIS 5 (and close to the error range of the lowest-dated level at Katoati), Middle Paleolithic occupations are known from numerous sites across South Asia. From this early appearance, Middle Paleolithic technologies combine prepared-core technologies (including varied Levallois schemes of reduction) with a diversified retouched flake tool kit, including unifacial and bifacial points and multiple forms of basal modifications (e.g., tangs, shoulders). This major change in South Asian technological behavior, from Late Acheulean to Middle Paleolithic technologies, appears to occur during MIS 5, significantly later than in other Old World regions (Adler et al. 2014; Kuhn 2013; Malinsky-Buller 2016; Porat et al. 2010; Tryon and McBrearty 2002; van Peer et al. 2003; White and Ashton 2004). Currently, the scarcity of archaeological assemblages with clear chronological control within MIS 5 makes any assessment of change during this phase difficult and an important target for future research.

In the absence of chronometric dating and often through the analysis of surface sites, many researchers have suggested substantial continuity from Late Acheulean to Middle Paleolithic industries. The apparent refinement of bifacial technologies throughout Late Acheulean assemblages and the continued appearance of diminutive bifaces within Middle Paleolithic assemblages, including at 16R Dune between 40 and 80 ka, has been suggested to illustrate transition between these two industries (e.g., Ajithprasad 2005). Continued use of bifacial technologies within Middle Paleolithic (and other) industries is, however, widespread in the Old World (e.g., Ruebens 2014; Tryon and Faith 2013). As a result, this continuity alone offers only limited insight into the nature of technological change, and a broader evaluation of how bifacial flaking approaches were used in different assemblages is clearly warranted. More recently, Mishra and colleagues (Mishra, Chauhan, and Singhvi 2013) assert continuity between Late Acheulean and Middle Paleolithic industries in South Asia on the absence of projectile or blade technologies in the latter. However, the presence of blade technologies among Middle Paleolithic industries is well established in South Asia (e.g., Misra 1982) and recently affirmed through dated studies (e.g., Blinkhorn 2014; Clarkson, Jones, and Harris 2012; Sali et al. 1989). Similarly, evaluation of Middle Paleolithic point technologies indicates that their use as projectiles cannot simply be ruled out (Costa 2012), especially considering the diverse forms of point technology within Middle Paleolithic sites (Blinkhorn, Achyuthan, and Ajithprasad 2015).

A more nuanced assessment of technological changes from Late Acheulean to Middle Paleolithic technologies has been undertaken by Shipton and colleagues (2013). In the Middle Son Valley, the dated Late Acheulean assemblage from Patpara and an undated Middle Paleolithic assemblage in the immediately overlying sediment unit were compared. In the final stages of Late Acheulean biface reduction, Shipton and colleagues (2013) identify their use as cores at the end of their use life with the raising of the plane of intersection between the two bifacial surfaces in order to strike invasive flakes from one surface. This hierarchical organization of flaking surfaces is argued to mark a clear step toward a critical concept underlying Levallois core technology, a major hallmark of the Middle Paleolithic. Within overlying Middle Paleolithic assemblages, greater levels of hierarchical organization of behavior and a recursive approach to blank production are widely apparent in the dominance of recurrent Levallois reduction strategies (Shipton et al. 2013). An alternate aspect of Levallois reduction is argued to be apparent in biface production in Late Acheulean levels at Bhimbetka, potentially dating to ~100 ka (Shipton 2016). Here, the ability to successfully strike large, end-struck flakes through the control of a shallow, symmetrical flaking surface for use as biface blanks is compared with the preparation and striking of Levallois flaking faces. Shipton (2016) postulates that this could indicate alternate routes for local innovation of key Middle

Paleolithic technologies in different locations within South Asia. However, the examples from the Bhimbetka and the Middle Son Valley occur at the beginning and end of reduction sequences, respectively, and may form part of a wider technological approach. Critically, these studies illustrate that aspects of more complex, hierarchical, and recursive technological behavior were emerging in the youngest Late Acheulean industries within South Asia. As a result, a local transition from Late Acheulean to Middle Paleolithic clearly remains possible but demands more detailed evidence from MIS 5 to evaluate further.

The Middle to Late Paleolithic Transition

Debates surrounding the effect of the eruption of Toba 74 ka, the climatic effect of MIS 4 (as apparent in highly suppressed monsoonal intensity in fig. 3), and the dispersal of modern humans have led some researchers to question whether there is continuity between Middle Paleolithic industries from MIS 5 to MIS 3 (Ambrose 1998; Mellars et al. 2013). Research both in the Jurreru Valley and Thar Desert offer no indication of any stepwise change in technology within Middle Paleolithic industries but rather a gradual change in behavior. This is most apparent in the diversification of Middle Paleolithic core reduction practices from the onset of MIS 3, including the appearance of blade and bipolar technologies as targeted reduction strategies and a decrease in artefact size. It therefore appears that South Asian Middle Paleolithic technologies are not static but share the piecemeal appearance of new features that are also observed elsewhere.

The identification of significant change in lithic technology associated with the Late Pleistocene is focused most heavily on microlithic technology, reliance on blade production, and the use of backing as a retouch strategy. Although argued to mark a clear break from earlier technologies (Mishra, Chauhan, and Singhvi 2013), this is not borne out by evidence from Patne or the Jurreru Valley. These sites indicate bipolar techniques first appear embedded in Middle Paleolithic reduction strategies, decreasing blade sizes appear to transcend the Middle to Late Paleolithic transition, and backing only becomes apparent once blade reduction has become the dominant core technique. Further continuities from the Middle Paleolithic can be observed in the retouch tool kits associated with early Late Paleolithic assemblages and the continued use of alternate flake reduction strategies. This is apparent in isolated assemblages such as Mehtakheri and Kana as well as better-resolved sequences at Patne and the Jurreru Valley. Indeed, casting the appearance of Late Paleolithic technology as a revolutionary change has served to downplay the importance of variability *within* Late Paleolithic assemblages, which recent studies are starting to shed light on (e.g., Lewis 2015; Lewis, Perera, and Petraglia 2014).

Beyond lithic technology, however, a stark difference between Middle and Late Paleolithic is apparent in the diversity of material culture found in the latter phase. The appearance of nonlithic tools, such as antler and bone points; the production of beads and engravings on both stone and other materials, including ostrich eggshell; the use of ochre; and the presence of burials remain solely associated with Late Paleolithic assemblages. In the past, such forms of material culture were argued to be the result of uniquely modern human patterns of cognition (e.g., Klein 1995; Misra 2001). However, the appearance of such behavior among modern human populations occurred in a piecemeal fashion (e.g., James and Petraglia 2005; McBrearty and Brooks 2000), and there is now clear evidence that other human populations, such as Neanderthals, might have engaged in similar behavior (e.g., Finlayson et al. 2012). As a result, this change in material culture in South Asia may not simply relate to the arrival of a new population, and there are more complex factors potentially driving their emergence (e.g., Petraglia et al. 2009).

Currently, the earliest evidence for Late Paleolithic industries in South Asia occurs ~45 ka, whereas the youngest securely dated Middle Paleolithic industries continue until 34 ka (fig. 5). In addition to this significant temporal overlap between technologies, substantial spatial heterogeneity can be observed in the transition from Middle to Late Paleolithic industries across South Asia (fig. 6). No single epicenter from which Late Paleolithic technologies radiate can readily be identified. This complex pattern of behavior appears to occur in the context of strong but fluctuating monsoonal activity during mid-MIS 3 (fig. 3). By the end of MIS 3, Middle Paleolithic technologies appear to have mostly been replaced across South Asia.

Explaining Cultural Developments in the Indian Subcontinent

This review of contemporary evidence for technological change during the Late Pleistocene in South Asia indicates that (1) although a gradual evolution from Late Acheulean to Middle Paleolithic technologies is plausible, it is not currently well supported by the archaeological record, and (2) the transition from Middle to Late Paleolithic lithic industries is spatially and temporally varied and best characterized by gradual change with piecemeal additions of new technological approaches rather than a revolution in behavior. Unlike in the twentieth century, such apparent continuity cannot be resolved by suggesting long-term population continuity in the face of overwhelming evidence for the dispersal of modern humans. Meanwhile, no single behavior or checklist of behavioral traits appears both universal and unique among modern humans, making it difficult to securely identify the arrival of modern humans in South Asia. Explaining the patterns identified in the Late Pleistocene cultural record must accommodate both how gradual change in behavior may have occurred in the region and the dispersal of modern humans into South Asia.

Petraglia and colleagues (2009) argued that the combination of significant increases in population size in circumscribed regions, as apparent in the Jurreru Valley, and deteriorating climatic conditions during MIS 3 provided circumstances in which innovations led to the gradual replacement of Middle Paleolithic by Late Paleolithic technologies. Over the past decade there has been considerable interest in the influence of demography on innovation in Paleolithic societies. A number of recent studies
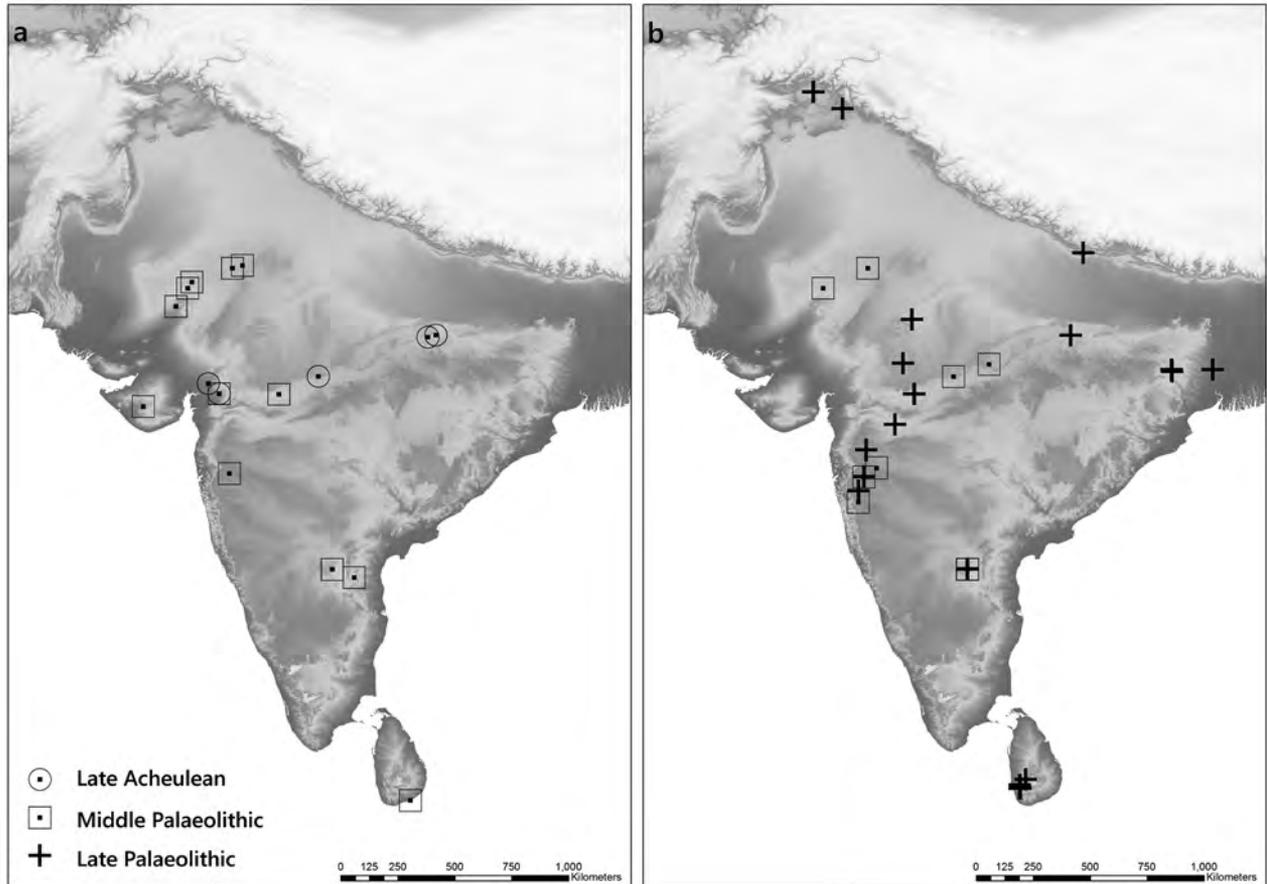
Figure 6. Map illustrating the changing quantity and distribution of dated Late Pleistocene sites in the Indian subcontinent from 50 to 140 ka (*a*) and 30 to 50 ka (*b*). A color version of this figure is available online.

now indicate that, rather than gross population size, it is population density and mobility strategies and their use to mitigate environmental/subsistence risk that may preserve and promote adaptive innovations (Collard, Buchanan, and O'Brien 2013; Grove 2015; Vaesen et al. 2016). The spatially, temporally, and technologically heterogeneous transition from Middle to Late Paleolithic technologies in South Asia could therefore result from discrete populations reaching critical thresholds of subsistence risk in different ecological settings.

Similar arguments have been made elsewhere, suggesting that the emergence of Middle Paleolithic technologies from Late Acheulean traditions resulted from the interplay between environmental and demographic factors (e.g., Adler et al. 2014). An increase in the amplitude and frequency of orbitally driven climate change from ~500 ka has been argued to have presented an important selective force for greater behavioral plasticity among Acheulean hominins (Potts 1998). This time frame also corresponds to a significant change in hominin life history clearly embodied in increased cranial capacities (Rightmire 2015) that may have enabled or been enabled by new forms of social relations (e.g., Foley and Gamble 2009). Regional differences in the expression of orbital climate change may explain the late persistence of Late Acheulean populations in South Asia. For

instance, the tempo of changes related to monsoonal intensity, the particular mosaic of habitats the region sustains, or the nature of population structures they enable could have buffered subsistence stresses, offsetting the need for innovation. However, what changes may have occurred that led to a local innovation of Middle Paleolithic technology remains obscured.

Significant changes in the hominin demography of Asia are coincident with the transition from Late Acheulean to Middle Paleolithic technologies in the Indian subcontinent. Resolving between the fossil and genetic records of Asian hominins is complicated by a small number of fossils yielding Denisovan aDNA from North Asia and the diversity of South and East Asia fossil hominins that lack suitable aDNA preservation. This is particularly pertinent as mixed morphologies resulting from interbreeding have become a reality (Ackermann, Mackay, and Arnold 2015). Direct or indirect changes to the wider demography of Asia, such as through population or cultural diffusion, may have promoted conditions in which premodern human populations in South Asia locally developed Middle Paleolithic technologies.

Combined evidence from the fossil and archaeological record clearly illustrates that *Homo sapiens* were responsible for the production of Late Paleolithic industries in South Asia. For

some researchers, this co-occurrence clearly indicates the earliest arrival of modern humans within South Asia supported by uniparental genetic studies of contemporary populations (Mellars et al. 2013; Mishra, Chauhan, and Singhvi 2013). Typological comparisons between material culture in southern Africa and South Asia have been suggested to indicate direct cultural inheritance between these regions as a proxy for human dispersals (Mellars 2006; Mellars et al. 2013). However, neither direct technological comparisons of lithic technologies (Lewis et al. 2015) nor wider interregional syntheses (Groucutt et al. 2015a, 2015b) support any form of cultural inheritance from MSA Howiesons Poort technologies in southern Africa or East African Later Stone Age industries with Late Paleolithic technologies in South Asia (contra Mellars 2006; Mellars et al. 2013). A variant of such models advanced by Mishra and colleagues (Mishra, Chauhan, and Singhvi 2013) suggests that earlier human expansions may have colonized other regions in Asia but that modern human populations were unable to outcompete South Asian archaic populations. While both populations used Middle Paleolithic technologies, it is argued that the resilience of South Asian archaics is due to existing adaptations to the region's ecology. Only armed with Late Paleolithic technologies were modern humans able to successfully supplant extant South Asian populations. This model is unable to explain apparent gradual changes in Middle Paleolithic industries in which key Late Paleolithic technological approaches first become manifest. Nor is this model consistent with the heterogeneous appearance of Late Paleolithic technologies within South Asia across time and space.

Population dispersals associated with Middle Paleolithic technologies were first mooted to explain the spread of Levallois technologies across the Old World (Lahr and Foley 1994). The dispersal of modern humans using Middle Paleolithic technologies is well attested to by the Levantine record with the presence of *H. sapiens* during MIS 5 evident at Skhul and Qafzeh (Mercier et al 1993; Grun et al. 2005). The expanding Middle Paleolithic record of Arabia during this time frame is also thought to document expansions of modern humans based on the appearance of technologies with direct antecedents in North and East Africa, such as at Jebel Faya (Armitage et al. 2011). Environmental approaches highlight the more northerly position of the ITCZ during interglacial conditions in MIS 5 resulting in significantly enhanced precipitation in the desert belt that may have enabled modern human dispersal at this time (Boivin et al. 2013; Groucutt and Blinkhorn 2013). Comparative studies have indicated significant similarities between South Asian Middle Paleolithic technologies and those attributed to *H. sapiens* in Africa and the Levant, leading to arguments for modern human dispersals into South Asia during MIS 5 (Clarkson, Jones, and Harris 2012; Petraglia et al. 2007). Critically, these analyses indicate no continuity between South Asian Late Paleolithic and those industries found to the west of the region.

While the appearance of modern humans in the Levant is coincident with the last securely dated Late Acheulean sites in South Asia, the appearance of Middle Paleolithic industries during MIS 5a now coincides with dated evidence for modern humans in East Asia, best known from Fuyan Cave (Liu et al. 2015). Similarly, the sole use of Middle Paleolithic technologies in South Asia overlaps with the appearance of modern humans in South East Asia (Mijares et al. 2010) and Australia (Clarkson et al. 2015; O'Connell and Allen 2015). The association between modern humans and Middle Paleolithic technologies cannot be verified without the enrichment of the South Asian fossil record. However, current fossil evidence from adjacent regions, environmental studies, and interregional technological comparisons point toward the early dispersal of modern humans into South Asia with Middle Paleolithic industries.

Conclusion

The results of interdisciplinary research in South Asia within the past decade have had a transformative effect on the archaeological record, enabling us to approach new questions regarding the timing and nature of major changes in hominin behavior and the dispersal of modern humans into the region. Increased chronological resolution has illuminated a spatially, temporally, and technologically heterogeneous transition from Middle to Late Paleolithic technologies. While the time frame for the Late Acheulean to Middle Paleolithic transition is not sufficiently resolved in the same level of detail, it now appears to occur at a time of demographic upheaval across South Asia. Converging lines of evidence both from South Asia and beyond point to the appearance of Middle Paleolithic technologies coinciding with the expansions of modern humans. In the absence of fossil discoveries that can decisively resolve current debate, formulating questions that can be resolved by investigating South Asia's rich Paleolithic heritage is important. Combining investigations into technological diversification, ecological adaptation, and population structure in South Asia opens up the possibility of understanding what factors promote creativity and innovation among Late Pleistocene populations and comparing how this is expressed at an interregional level.

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The Chronological Factor in Understanding the Middle and Upper Paleolithic of Eurasia

by Katerina Douka and Tom Higham

For more than half a century, prehistorians have grappled with radiocarbon-based chronologies that are often contradictory and imprecise. Several key debates in the Paleolithic have their roots, at least partially, in basic issues of chronology. When did Neanderthals disappear? When did *Homo sapiens* disperse across Eurasia? How long was the overlap among several hominin groups? Without reliable time control, these questions are unanswerable, and unravelling the Paleolithic remains a distant and virtually unachievable goal. It is only recently that the extent of the problems with the application of radiocarbon dating near the limit of the method has become understood. Major challenges have arisen, ranging from inadvisable and poor selection of samples, on the one hand, to the analytical, chemical, and instrumental challenges of dating the low amounts of residual radiocarbon in these samples, on the other. Recent work has led to significant developments in the field. In this paper, we briefly review some of these developments, drawing on recent work undertaken at two sites, Bondi Cave (Georgia) and Kostenki 14 (Russia). By comparing new radiocarbon determinations against previous results, it is possible to begin to quantify quite how erroneous some of the previous chronometric models were.

The Middle to Upper Paleolithic transition, dating broadly to between 50,000 and 30,000 years BP, marks a pivotal point in late human evolution. In Europe and western Asia, it involves the latter stages of the dispersal of anatomically and behaviorally modern humans (AMH) outside of Africa, the replacement of Neanderthal populations, and the emergence of what is widely termed as the Upper Paleolithic—a period often associated with novel, symbolically loaded artifacts suggested to represent an important change in the cognitive abilities of modern humans (e.g., Bar-Yosef 2002; Klein 1995; Mellars 1989, 1991, 2005). Other authors have pointed out the occurrence of such artefacts in Africa much earlier (McBrearty and Brooks 2000) and the possible production of symbolic artefacts by European Neanderthals (e.g., Zilhão et al. 2010), yet the latter is not a universally accepted behavioral trait.

Similar—but not identical—processes affect Central and East Asia (and Australasia), leading to the wider establishment of AMH from the tropical rainforests of Sri Lanka and Thailand to the Siberian steppes and from the arid plains of Uzbekistan to the savanna of the Australian Northern Territory. However, the situation in this part of the world is far more complex, given the presence of archaic humans living in the continent (Denisovans, *Homo floresiensis*, possible late *Homo erectus*, and archaic *Homo sapiens*). These humans, we now know, have coexisted and in some cases interbred with incoming AMH, leading to a degree of genetic and potential cultural mixing.

So far, the vast majority of archaeological and chronometric research concerned with the Middle to Upper Paleolithic transition outside Africa has largely focused on one particular area: western Europe. Elsewhere, and possibly with the exception of Australia, not only is the archaeological record less abundant, but chronometric data are often minimal or absent.

Asia is critical to human evolution, particularly because AMH leaving Africa appear to have initially dispersed there before moving onward to Europe, Australia, and the Americas. Exciting new evidence is just beginning to rival in importance the better-known paleoanthropological records of longer- and better-investigated regions of Europe and Africa. The identification of Neanderthal presence beyond Europe and well into Siberia (Krause et al. 2007), along with growing fossil and archaeological evidence for the possible presence of AMH in China earlier than originally thought (e.g., Liu et al. 2015, but see also Michel et al. 2016), as well as confirmation that incoming AMH admixed genetically with indigenous archaic Asian populations (Fu et al. 2014; Green et al. 2010), reveals the Late Pleistocene record of human evolution to be much more complex than previously recognized. Most surprising has been the discovery, in 2010, of a new human group, the Denisovans,

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known almost exclusively from the genomic sequencing of DNA and four tiny bone fragments recovered at the eponymous cave site in southern Siberia. The lack of significant Denisovan remains has been seen as a paradox and has led to them being referred to in the popular science press as the "genome in search of a fossil."

Despite the importance of these recent findings, our understanding of archaic human presence in continental Asia remains unclear and lags behind information collected and synthesized from other continents. Among the reasons for this lag are the difficulties encountered so far, at a continental scale, in the recovery and identification of well-excavated and fully analyzed archaeological sites containing in situ fossils. One important component within this uncertainty is the lack of a reliable chronology, the challenge in directly dating precious human fossils, and the difficulty in comparing dates of specific lithic traditions across space. This paper outlines how novel chronometric developments and approaches offer the opportunity to improve this situation significantly.

Approaches in Chronology Building

Radiocarbon (^{14}C) dating is the most widely used scientific methodology for absolute dating of archaeological remains. Its effective limit, ~50,000 years ago, means that most significant events of late human evolution can be directly dated. The use of accelerator mass spectrometry (AMS) for the measurement of the residual ^{14}C in a sample also means that very small samples (between 0.5 and 2 mg of carbon) can be measured. There are three principal areas of development one can trace over the past 10–15 years. First, there have been several technical improvements, including higher measurement precision, lower backgrounds in particle accelerators, and more accurate subtraction of laboratory-derived ^{14}C backgrounds using sample-specific standards (Bronk Ramsey, Higham, and Leach 2004; Wood, Bronk Ramsey, and Higham 2010). To reach 50,000 BP, a measurement precision of $\pm 0.1\%$ is required. Before the mid-2000s, this was not achievable, and therefore the maximum age limit broached 40,000 BP or younger in some laboratories. Second, a calibration curve that stretches back to the limit of radiocarbon (the latest iteration is Reimer et al. 2013) not only allows calibration into sidereal time but offers the opportunity of building Bayesian age models, incorporating results from other dating techniques, and enabling tentative comparison against climate records, such as those from the Greenland ice cores (e.g., Andersen et al. 2006). It was not possible to do this with confidence until as late as 2009, when the first internationally agreed-upon 50,000-year-long calibration curve became available (Reimer et al. 2009). Third, significant improvements in chemical pretreatment and sample decontamination have resulted in superior purification of bone proteins, shell carbonates, and charcoal samples, which are the main items targeted for dating during this period. This has led to an increasing number of samples predating 40 ka BP and being reproducible at that age. In this paper, we examine the effects of sample decontamina-

tion and the application of Bayesian statistics in the chronostratigraphy of two Paleolithic sites in Russia and Georgia.

The radiocarbon dating of old (>10-ka) samples has proven to be particularly challenging for the radiocarbon community. Contamination with external carbon from modern or quasi-modern sources will alter a radiocarbon age by hundreds or sometimes thousands of years. It is well known, for example, that a sample whose actual age is 30,000 years, will, if contaminated with 2% C of modern origin, return an AMS measurement 5,000 years too young. A sample with a "true" age of 40,000 years, with the same amount of unremoved carbon contamination, will return an age of 29 ka, which is 11,000 years too young. For this reason, chemical protocols aiming at removing exogenous carbon from a sample before AMS dating are constantly being developed and improved to minimize and reduce the effect of contamination.

When dating bones, the organic fraction (collagen), rather than the diagenesis-prone inorganic matrix, is extracted and analyzed. In the early 2000s, the development and broader application of ultrafiltration as an additional step in the radiocarbon dating of Paleolithic-age bone (based on Bronk Ramsey et al. 2004; Brown et al. 1988; Higham, Jacobi, and Bronk Ramsey 2006) significantly improved our ability to purify collagen on a routine basis. An ultrafilter is a molecular sieve that separates high from low molecular weight fractions of the collagen. High-molecular-weight components will include nondegraded collagen, while low-molecular-weight components, which may contain degraded amino acids and peptides as well as soil-derived particles, all of which may be contaminants, are discarded. When ultrafiltration is applied to Pleistocene-age bones, it produces dates that are more reliable and often older than previous measurements. In addition, the extracted bone collagen is improved in terms of quality. In previously published work (e.g., Higham 2011; Higham et al. 2014), we have found that between 70% and 100% of previously obtained radiocarbon results were inaccurate after the same sites were reanalyzed using the ultrafiltration protocol. The new results are more consistent with site stratigraphies and have often changed significantly our understanding about human presence and occupation patterns at a site and a region as a whole.

For highly contaminated bones, even more stringent methodologies are currently being developed, tested, and applied to ensure contaminant-free radiocarbon dates. An advanced method involves extracting single amino acids from bones using high-performance liquid chromatography (HPLC). This technique ensures that the measured carbon comes only from the collagen amino acids and no other external contaminants. We have applied single amino acid dating to highly contaminated human bones from two key Mid-Upper Paleolithic sites in Russia, at Sungir and Kostenki 14 (Marom et al. 2012). These are two important burial sites of AMH that had not been dated reliably due to contamination of the bones with organic preservatives while in museum storage. The Kostenki 14 skeleton was previously dated three times (Hoffecker 2011; Sinitsyn 2004), but all determinations were much younger than anticipated (~3,700,

4,700, and 13,600 BP), leading to serious doubts over whether the specimen was actually Paleolithic. Krause et al. (2010) obtained a complete mitochondrial DNA genome from the skeleton, but no new dating was forthcoming because of the contamination present in the sample. Instead of trying to date bulk collagen, in 2012, members of our team extracted and purified the single amino acid hydroxyproline (HYP) from the tibia of the specimen and obtained a date of 33,250 $\pm$ 500 BP (Marom et al. 2012). This age is much older than the previous contaminated measurements and consistent with the stratigraphic position of the burial in the Kostenki 14 site, as we show below, making it the earliest directly dated modern human associated with a secure archaeological context anywhere in Eurasia. Isolation and dating of a single amino acid guarantee that there is no interfering contamination and are essentially a "gold standard" ^{14}C measurement.

The Sungir case disclosed a similar result. Previously, the Sungir double burial and the remains of Sungir 1, an older male, were radiocarbon dated with less robust methods (Dobrovolskaya, Richards, and Trinkaus 2011; Kuzmin et al. 2004; Pettitt and Bader 2000) that produced results that were at odds with the archaeological evidence, which suggests that the individuals probably died at the same time. New radiocarbon HYP results, however, produced a series of dates that were not only significantly older but also consistent and statistically identical (Marom et al. 2012, 2013). In the future, it will be very important to apply these types of methods to problematic cases; important human fossils, such as in the recent case of the Vindija Neanderthal fossils (Devièse et al. 2017); and low-collagen bones, which have usually proven impossible to date so far.

Other dating materials have also seen developments and significant improvements. Charcoal samples may now be pretreated using rigorous acid-base oxidation followed by stepped combustion (ABOx-SC) methods (Bird et al. 1999; Wood et al. 2012 and references therein). Like ultrafiltration, the new charcoal protocols remove organic contaminants from the samples and have led to significant revisions of previously established chronologies. We have spearheaded the application of this technique to the European Paleolithic record—for example, in sites in Russia (Douka et al. 2010) and Italy (Brock and Higham 2009; Wood et al. 2012)—and have demonstrated its applicability to cold, temperate, and tropical environments (e.g., Higham et al. 2009; Sutikna et al. 2016).

When archaeological sites and materials are near to or beyond the limit of radiocarbon (>50 ka) or where organics preservation is poor, optically stimulated luminescence (OSL) and infrared-stimulated luminescence (IRSL) dating of sediments can provide the best means of establishing a chronological framework. OSL and IRSL dating offer an estimate of the time since grains (usually on quartz or feldspar, respectively) were last exposed to sunlight. These methods can routinely measure the age of sediments from 0–200,000 years of age, but the upper limit (lower or much higher) varies locally, because it depends on the rate of saturation of the luminescence signal with dose. It is crucial that, at a broad timescale and when a site is occupied

over a long period of time, multiple methods are adopted. A good example of what is possible is provided by recent work at the site of Haua Fteah in Libya (Douka et al. 2014), where a suite of different chronological methodologies (^{14}C, OSL, tephra studies, and electron spin resonance) were used to build a reliable temporal framework for human occupation at the site covering the last 100,000 years.

Interpretation of the results of multiple methods of absolute dating like this is made possible by formal Bayesian statistical modeling. This approach has strengthened and formalized the interpretation of chronometric results by incorporating absolute data (e.g., the radiocarbon and luminescence measurements) with "prior" beliefs based on our knowledge of the archaeological site, information on the relative ordering of events, the position of a sample in the stratigraphy, and our estimated confidence in the dating results. Bayesian modeling provides the framework to help answer questions regarding the spatiotemporal relationships of hominin groups, the duration of overlap, the exact timing of their presence in an area, and the date of last appearance. Previous approaches, in which dates are compared "by eye," often increase the chances of interpretative errors involving the overestimation of temporal range due to problems decoding the natural statistical scatter of radiocarbon measurements and the influence of variations in the calibration curve. Bayesian modeling provides the mathematical and statistical framework for reliably interpreting chronometric data.

Case Studies

The impact of these new approaches to archaeological sites can be shown with recent work we have undertaken in Georgia at two Eurasian sites, Kostenki 14 (Markina Gora) in Russia and Bondi Cave in Georgia (fig. 1). The site of Bondi Cave documents a key period of the Middle to Upper Paleolithic sequence of the region (Tushabramishvili et al. 2012). The site is located in the Imereti region of northwestern Georgia (fig. 1) and comprises a well-stratified >3-m-thick late Pleistocene sequence. Layers VIII and VII, over 60 cm thick, are attributed to the Middle Paleolithic and are topped by a long Upper Paleolithic sequence that includes layers V to I, about 150 cm thick. Layer VI, a level of ceiling fall debris block, separates the Middle Paleolithic and Upper Paleolithic sequences. The Upper Paleolithic part, and especially layers II, IV, and V, was the richest of the sequence. In earlier archaeological work, a partial human tooth was recovered from sublayer Vb, which has been identified as *Homo sapiens*.

Previous radiocarbon determinations from the site have been obtained from two different laboratories (Saclay and Beta Analytic). These are shown calibrated in figure 2 in depth order—layer VII is the oldest, and layer III is the youngest (after Tushabramashvili et al. 2012). One can immediately appreciate that there is a lack of coherence in the sequence, and the results are characterized by a great degree of variability (fig. 2).

The Middle Paleolithic level VII appears to date to 40–43 ka cal BP, while the Upper Paleolithic levels seem to start after
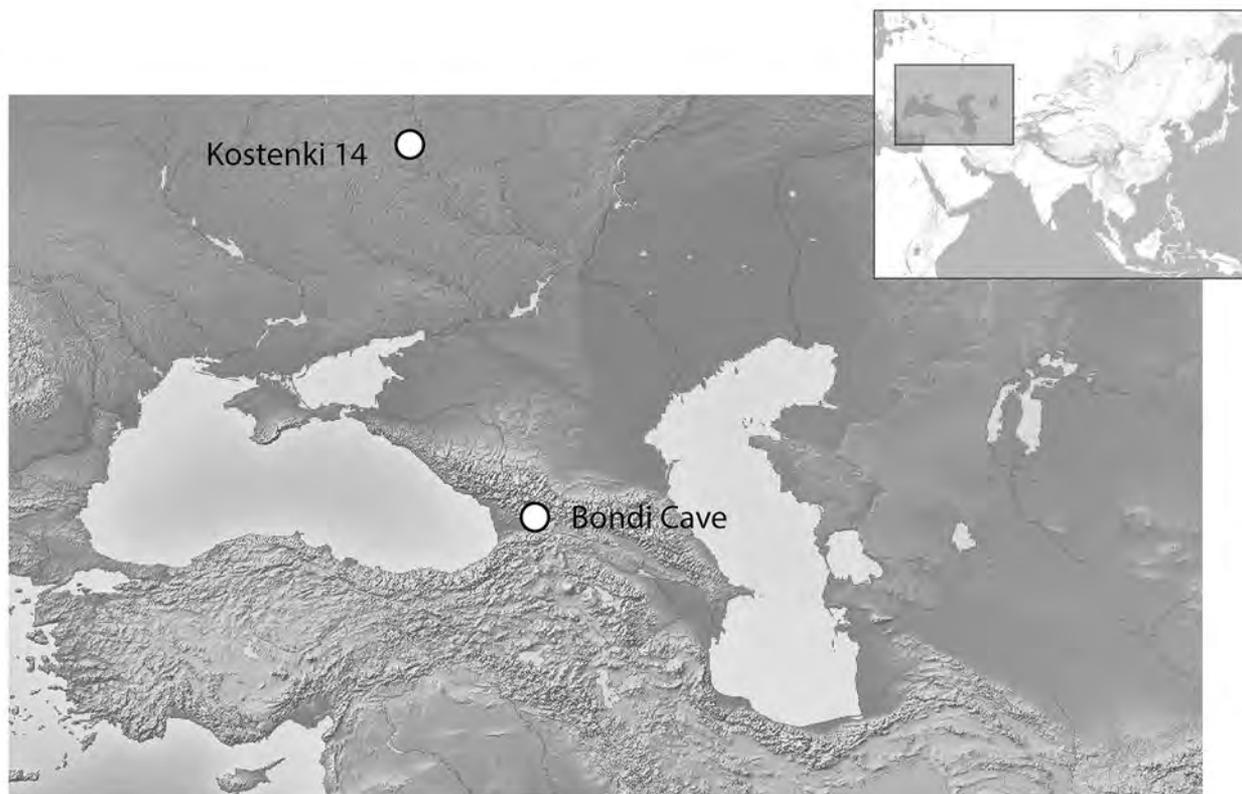
Figure 1. Map of northwest Asia showing the location of the two sites discussed in the text, Bondi Cave in Georgia and Kostenki 14 (Markina Gora) in Russia. A color version of this figure is available online.

30 ka cal BP. Layer VI is a distinct lithological phase representing roof collapse, and questions remain over whether it is an earlier Upper Paleolithic occupation dating to 35 ka cal BP or if the Upper Paleolithic material it contains is intrusive from layer V above. Precisely why there appears to be much variation in the previous dates likely revolves around two possibilities. First, it could be due to stratigraphic mixing of material to a degree that was not identified in the excavation. This could also include the possibility that material selected for dating was not properly identified as being humanly modified and hence not certainly linked to human presence at the cave. Second, the results are due to incomplete decontamination and pretreatment chemistry of the samples. This is now an oft-repeated theme in the chronology of the Paleolithic (Higham 2011) in which we usually see underestimates of the real age of the materials.

To test these hypotheses, we obtained new samples of animal bone from the site. All samples selected were humanly modified (cut-marked or smashed during procurement) bones. Before collagen extraction and radiocarbon dating, we tested selected bones with percentage nitrogen methods (Brock, Higham, and Bronk Ramsey 2010) to ensure that they had sufficient remaining collagen for analysis. We selected 28 new samples from 8 layers and sublayers of the site. The samples were dated using ultrafiltration preparation in the Oxford Radiocarbon Accelerator Unit (ORAU).

We obtained 23 new AMS determinations. These new results suggest that the previous dates are indeed almost certainly significant underestimates. Samples from Middle Paleolithic layer VII, which were previously producing conventional radiocarbon ages of 35,000–37,000 BP (40,000–43,000 cal BP), were all greater than the radiocarbon age limit (i.e., >50,000 BP). Layer VI, which represents a major phase of cave collapse, previously dated at 32,000 BP, produced an age very close to the radiocarbon limit as well (47,500 ± 2,600 BP). All material from Middle Paleolithic layers VII/VIII, therefore, date to beyond 50,000 years ago. All of the AMS dates from Upper Paleolithic level V were consistent and produce results that span the period 40–37 ka cal BP. Here, too, they are much older than the previous chronology would suggest, by up to 10,000 years.

To properly interpret results such as these, it is crucial to use a Bayesian modeling approach, as described earlier. We used OxCal4.3 software (Bronk Ramsey 2009) and the INTCAL13 calibration curve (Reimer et al. 2013) to construct a statistical model for Bondi Cave (fig. 3). The model priors comprise the detailed evidence obtained from the excavation and the discrete layers and sublayers identified. The phases of each ex-
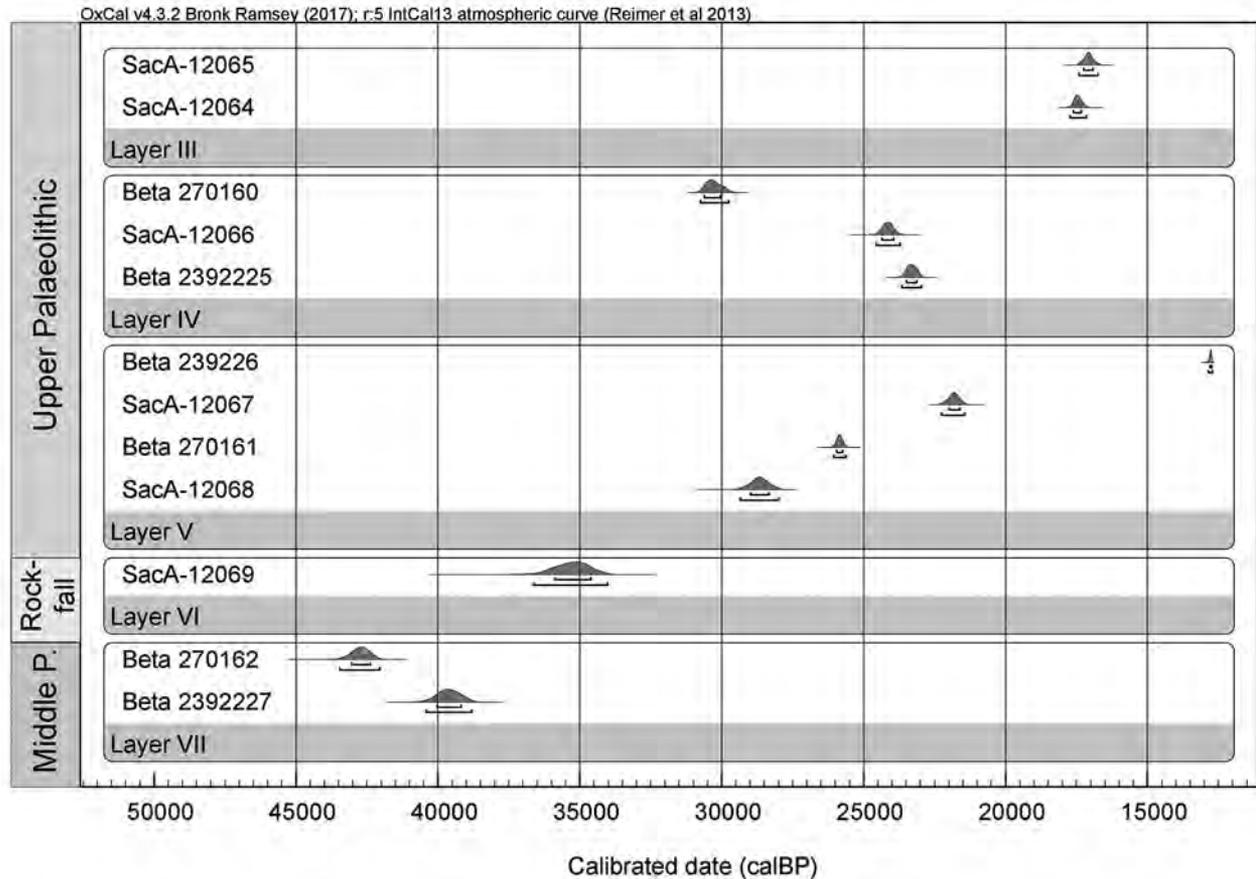
Figure 2. Previous radiocarbon chronology from the Bondi Cave site, from Tushabramashvili et al. (2012). The results show a great deal of variability and are therefore difficult to interpret. Middle P. = Middle Paleolithic. A color version of this figure is available online.

cavated layer contain the radiocarbon results obtained with no order assumed between them. Phases in sequence, from earliest to latest, are assumed to lie in order of stratigraphic superposition. The posterior results, from the output of the Bayesian modeling, are shown in the figure in darker outline. These suggest that the occupation of level V starts around 40,000 cal BP and ends by 33,000–34,000 cal BP. The results are in complete contrast to the previous chronology, and the data appear robust and reproducible, because there are no significant outliers identified in the sequence. Given our initial objective, to determine whether the chronological variability obtained in the previous series of dates was due to severe material mixing in the site's sequence or due to inadequate chemical pretreatment, we may now assume that the latter was the reason.

In addition, we can use this Bayesian age model as a means to estimate the age of material within different contexts in the sequence, even when such material is not directly dated. The human tooth, for instance, which was excavated in layer Vb, can be estimated to date between 38,700 and 35,300 cal BP (95.4%; see fig. 3), making it the earliest evidence for modern humans in the southern Caucasus mountain region. Such an estimate assumes no or very little postdepositional movement

of material; given the consistency of the new dates from Vb, as well as all other layers from Bondi Cave, we argue that this seems to be the case.

Another key advantage in using Bayesian approaches is the ability to integrate archaeological chronologies built from different radioisotopic and trapped-charge methods. We consider an example below from the site of Kostenki 14 (Markina Gora), one of the key sites in the Kostenki-Borschevo complex of sites in western Russia (fig. 1).

Kostenki 14 is an open-air site located on the west bank of the Don River, and most importantly for studies of the chronology of the site, it contains the Campanian Ignimbrite tephra, which lies in direct association with an Upper Paleolithic cultural horizon, the so-called "layer in volcanic ash" (LVA; Anikovich et al. 2007; Douka, Higham, and Sinitsyn 2010; Hoffecker et al. 2008; Sinitsyn 2003b). Although in parts of the site the tephra is clearly redeposited and subject to solifluction and slope movement, there are deposits that are considered to be in situ. LVA is considered to have been largely covered by the tephra fall and comprises typical Aurignacian lithic elements, including artefacts that evoke Roc de Combe twisted bladelets of the western European Aurignacian (Sinitsyn 2003a, 2003b).
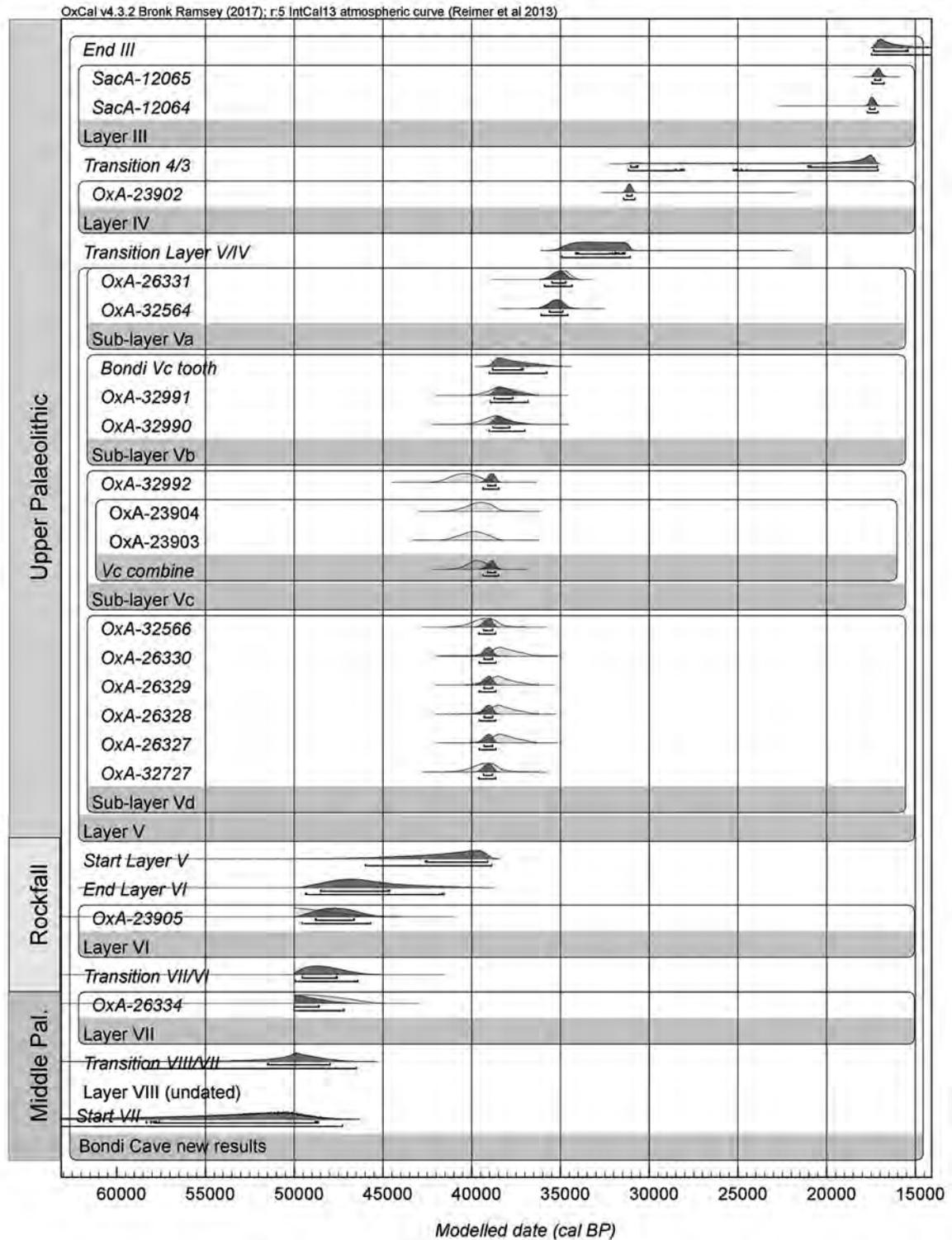
Figure 3. Bayesian age model for the site of Bondi Cave, Georgia. The model was produced using OxCal 4.3 (Bronk Ramsey 2009) and the INTCAL13 calibration curve (Reimer et al. 2013; for the data used in the model, see Pleurdeau et al. 2016). Middle Pal. = Middle Paleolithic. A color version of this figure is available online.
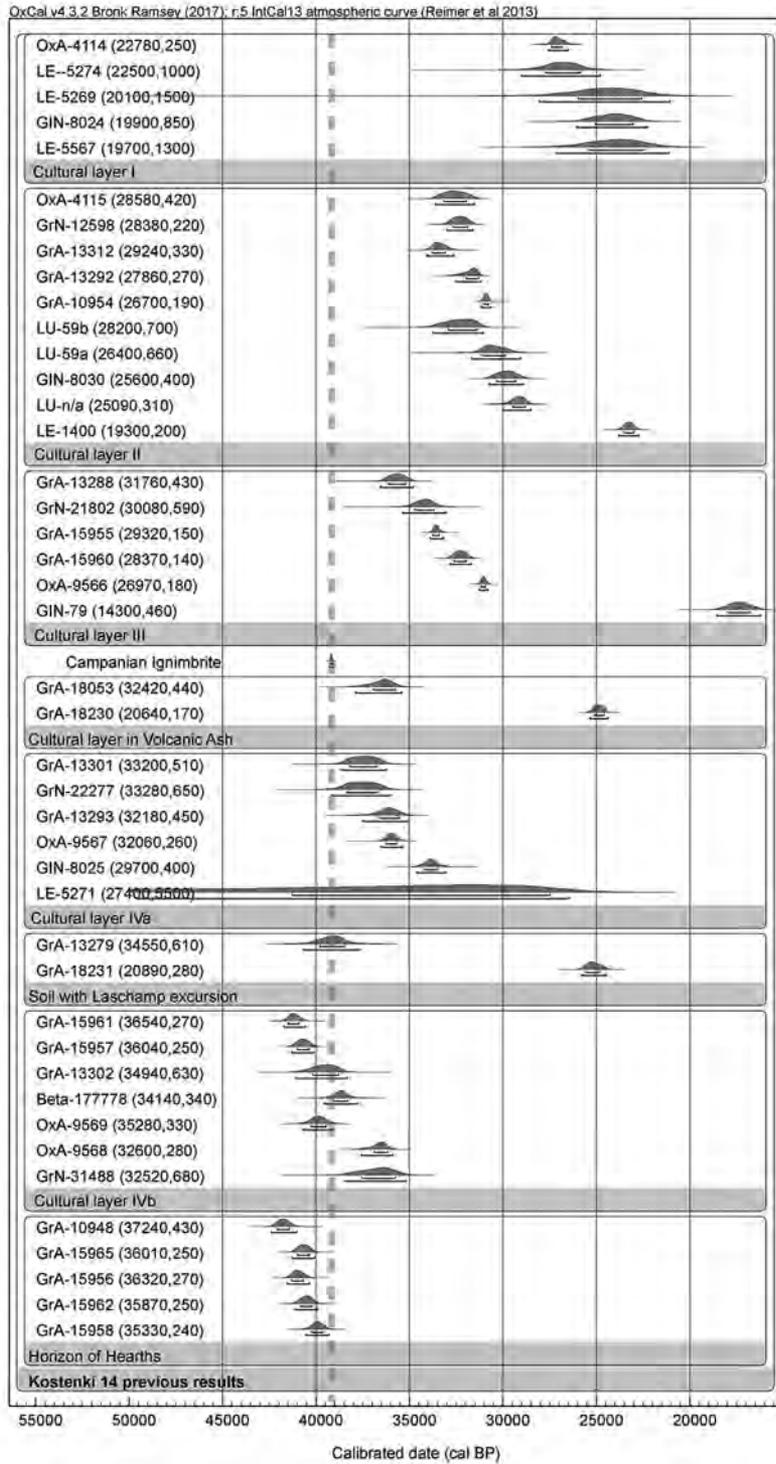
Figure 4. Previous radiocarbon chronology from Kostenki 14, based on the determinations published by Sinitsyn and Hoffecker (2006). The Campanian Ignimbrite is indicated in the sequence as a dashed gray line. It is clear that several results from layers superimposed by the tephra (layer in volcanic ash, IVa, and IVb) postdate the age of this marker by several millennia and hence must be considered erroneous. The ages for the lowermost cultural horizon, Horizon of Hearths, fall very close to the age of the tephra despite stratigraphic separation of the two horizons by as much 3 m at places. A color version of this figure is available online.

Layers below this, including IVa and IVb, are of early Upper Paleolithic affinities; the latter, for instance, contains items of early human sculpture, decorated bone tools, and a fossil shell pendant of probable Mediterranean origin (Hoffecker et al. 2008; Sinitsyn 2003a).

Once again, serious problems have arisen in the previous radiocarbon dating of the sequence, with dates of bone and charcoal prepared using the routine acid-base-acid (ABA) protocol producing results inconsistent with the age estimate for the tephra fall and exhibiting serious variation (e.g., Giaccio et al. 2006; Haesaerts et al. 2004; Sinitsyn and Hoffecker 2006). In figure 4, 11 of the 17 dates coming from layers clearly superimposed by the tephra (LVA, IVa, and IVb) postdate the age of this independently dated marker. In addition, all results from the Horizon of Hearths, the lowermost cultural layer at the site, sit very close to the age of the tephra despite the fact that they were produced on material found stratigraphically much deeper, at least 1.5–3.0 m below the tephra.

Over the past 5 years, we have obtained several new AMS dates from the site using more robust methods of pretreatment chemistry than previously was the case. The results include ABOx-SC determinations on charcoal (Douka et al. 2010; Wood et al. 2012), determinations on skeletal material based on the single amino acid HYP method (Marom et al. 2012), and new ultrafiltered collagen results of bones collected at the site between 2009 and 2014.

We built a new Bayesian age model for Kostenki 14, including these recent radiocarbon results. In addition to the AMS determinations, we also included the Campanian Ignimbrite calendar age and four luminescence (IRSL) ages obtained previously from level IVa/b (see Hoffecker et al. 2008). The dates of the Campanian Ignimbrite deposits are well known and reliable, being based on a series of $^{40}Ar/^{39}Ar$ determinations on sanidine crystals obtained from proximal deposits of the ash with the age extrapolated to the Don River sites (Giaccio et al. 2017). In our age model, the estimated age of the Campanian Ignimbrite was based on a weighted average of these dates after De Vivo et al. (2001) and Rolandi et al. (2003; see Wood et al. 2012 for discussion), providing an age estimation of 39,180 ± 45 years (before 1950).

The model is shown in figure 5. A high level of agreement and consistency is attested by the fact that there are no outliers of statistical significance. There is strong agreement between the luminescence ages and the radiocarbon results, and the absolute methods sit closely with the estimated age for the tephra, too. Taken together, this allows us to be confident in diagnosing a precise age for the industries identified at Kostenki 14.

These case studies demonstrate what is possible if a concerted effort is made to use robust radiocarbon methods, combined with other dating techniques, such as luminescence dating, nested within a Bayesian framework. Such integrated approaches are all the more important when dating sites that lie near or beyond the limit of radiocarbon. This is often the case in Asian sites, where modern human presence has been now postulated to lie well beyond 50 ka or much earlier (e.g., Liu et al. 2015), while other forms of archaic humans (Denisovans, *Homo floresiensis*) appear to lie beyond the working limit of radiocarbon (e.g., Sutikna et al. 2016).

Finally, the archaeogenetics revolution is also starting to impact chronology studies. It has been shown recently that molecular dating, in the form of a quantitative approach that calculates genetic separation times estimated from deeply sequenced human genomes, is in broad agreement with the direct dating of samples using radiometric methods (e.g., Fu et al. 2014; Moorjani et al. 2016). Incorporating this kind of information, stemming from fossil material beyond and within the radiocarbon timescale, in Bayesian models along with traditional chronometric data is sure to influence the future understanding of human presence and interaction of various hominin groups in Paleolithic Eurasia.

Conclusions

To understand the proper sequence and process of cultural development during the Middle and early Upper Paleolithic of Eurasia, it is crucial that prehistorians have chronometric control. In the past, dating material from late Pleistocene sites using the principal method, radiocarbon, has been challenging. A series of advances in measurement technology and pretreatment chemistry has seen significant improvement that points to a way forward. Additionally, the application of Bayesian methodologies provides a robust framework for integrating age determinations from different methods that allow for more refined chronometric data sets to be obtained.

In this paper, we have given two examples of the type of chronometric work that we hope will become routine in Paleolithic archaeology. At Bondi Cave in Georgia, we demonstrated the significant changes that occurred to the understanding of the site's archaeological sequence when improved radiocarbon protocols were applied. Fossil remains within this sequence could be ascribed tentative age estimates, despite not being directly dated, with the help of Bayesian statistics. At the site of Kostenki 14 (Markina Gora), in Russia, we showed how age estimates obtained using different methods (radiocarbon and luminescence) could be incorporated into a single Bayesian age model and the precision that can accrue. Building age models across space and time will allow us to compare probability distributions for different archaeological technocomplexes and begin the task of exploring how these industries relate to one another. Desmond Clark (1979: 7) wrote that, were it not for radiocarbon dating, "we would still be foundering in a sea of imprecisions sometime bred of inspired guesswork but more often of imaginative speculation." The "sea of imprecisions" has hampered Pleistocene archaeology more than that of any other period in the radiocarbon timescale, but this is now improving. Our task is now to roll out these methods to many more sites across Asia.

OxCal v4.3.2 Bronk Ramsey (2017); r:5 IntCal13 atmospheric curve (Reimer et al 2013)

End I
OxA-27229 (22970,170)
I
Start I
End II
OxA-26770 (28470,300)
OxA-26769 (28400,290)
IRSL/UIC-1126 (26340,1920)
II
Start II
OxA-26315 (31300,400)
III
Start III
OxA-X-2395-15/Human Burial (33250,500)
IRSL/UIC-1127 (32230,2310)
Transition CI/III
Campanian Ignimbrite
Start of Campanian Ignimbrite
OxA-26313 (33300,500)
OxA-26314 (33600,500)
OxA-19021 (35080,240)
OxA-X-2642-8 (35210,400)
LVA
Start LVA
OxA-26771 (33550,550)
OxA-21872 (34240,360)
OxA-21871 (34900,340)
OxA-21873 (35270,350)
OxA-27228 (35250,700)
IVa
Start IVa
IRSL/UIC-1128 (47780,3480)
OxA-27230 (35450,700)
OxA-26839 (35550,700)
OxA-23749 (36400,330)
OxA-X-2395-18 (35700,900)
OxA-X-2395-22 (34800,550)
OxA-X-2365-11 (34200,550)
IVb-low (34741,358)
IVb
Start IVb
IRSL/UIC-749 (34170,2700)
IRSL/UIC-748 (44900,3800)
Horizon of Hearths
Start Horizon of Hearths
Kostenki 14 new results

65000   60000   55000   50000   45000   40000   35000   30000   25000

Modelled date (cal BP)

Figure 5. Age model for the Kostenki 14 sequence including only radiocarbon determinations prepared with the latest decontamination protocols as well as five infrared-stimulated luminescence (IRSL) dating ages. Bone dates of the amino acid hydroxyproline, dates of ultrafiltered bone collagen, and charcoal dates obtained using acid-base oxidation followed by stepped combustion (ABOx-SC) and a new alternative acid-oxidation (AOx) methodology are shown in varying shades of gray. The IRSL ages are in a shaded dark gray border. The age of the Campanian Ignimbrite is input as a calendar date before 1950 based on the de Vivo et al. (2001) and Giaccio et al. (2017) estimates. There are no significant outliers in the model, and all radiocarbon age estimates (whether based on charcoal or bone) are consistent with the independently dated Campanian Ignimbrite tephra at the site. A color version of this figure is available online.

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The Northern Dispersal Route

Bioarchaeological Data from the Late Pleistocene of Altai, Siberia

by Alexandra Buzhilova, Anatoly Derevianko, and Michael Shunkov

Archaeological evidence indicates that the original settlement of the Altai occurred by ∼800 ka. The next major wave of hominin migration occurred by approximately 500–400 ka, followed by another one at ∼300 ka. Archaeological findings indicate a continuous evolution of lithic industries between 80 and 10 ka across the Altai. At about 55–45 ka, a small group of Neanderthals appeared in the Altai, producing various forms of lithics at places such as Okladnikov Cave and Chagyrskaya Cave. In the case of Denisova Cave, we suggest that the probable assimilation of Neanderthals occurred without any significant changes in material culture. The current archaeological patterns are well matched with the paleogenomic data from the region. Genetic data suggest that Denisovans were present in the area during at least two separate occasions and over a long period of time, with their presence perhaps interrupted by Neanderthal occupation. The analysis of odontological data shows that Denisovans preserved some archaic morphological features. The archaeological data, along with fragmentary human remains, demonstrate significantly different patterns in comparison with contemporary sites in eastern Asia. The specific position of the Denisovans could possibly be explained as a result of the temporal and geographic isolation of the migrant groups over a long period of time, with the ancestral population originating from western Asia.

Important results for the emergence of modern *Homo sapiens* in Eurasia derive from the analysis of mitochondrial and nuclear DNA sequences retrieved from hominin remains excavated in Denisova Cave in the Altai Mountains in southern Siberia, Russia. The human fossils from Denisova represent an unknown type of hominin that shares a common ancestor with both *H. sapiens* and Neanderthals. As genetic studies have pointed out, the separation from the common ancestor could not have occurred earlier than 1.0 million years ago (Krause et al. 2010; Reich et al. 2010). The background of the Denisovan genome derives from a population that lived before the separation of Neanderthals, Denisovans, and modern humans (Prüfer et al. 2014). According to data from the mitochondrial genome, the level of genetic variety in this population was much lower than that among Neanderthals and anatomically modern humans (AMH; Meyer et al. 2012; Slon et al. 2015). The Denisovan nuclear genome from one of the fossils (the phalanx) appears to be less divergent, forming a sister group

with Neanderthals. The separation from the common ancestor of the Denisovans and the Neanderthals took place at about 430 ka (Meyer et al. 2016). Moreover, the data indicate that gene flow also occurred between Denisovans and the ancestors of certain modern populations from Southeast Asia (Lalueza-Fox and Gilbert 2011; Meyer et al. 2012; Reich et al. 2010).

Here we present the results of an analysis of available fossil remains and archaeological data from Denisova Cave. We evaluate this information in light of paleogenetic data, examining the evidence for a supposed northern dispersal route of hominins in the Late Pleistocene. Unlike the rich archaeological collections from the Altai caves, the collection from Denisova Cave includes few human skeletal materials. The cave, in general, yields only fragmentary human remains due to poor preservation, thus limiting analyses. Hominin teeth, however, are preserved in greater numbers than are other parts of the skeleton. As a consequence, here we examine metric differences between hominin molars from various archaeological sites, with a focus on the Altai region. Teeth are advantageous to study because they can be a close reflection of the genotype, more directly affected by the forces of natural selection (Bailey 2004; Bailey and Hublin 2006; Brace, Rosenberg, and Hunt 1987; Crevecoeur et al. 2010; Martinón-Torres et al. 2012; Quam, Bailey, and Wood 2009; Scott and Turner 1988, 1997; Stefan and Trinkaus 1998).

Material

We analyze archaeological and odontological data from the Altai region of Siberia (Denisova Cave, Okladnikov Cave, and

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Chagyrskaya Cave) and Central Asia (Grotto Teshik-Tash, Uzbekistan; fig. 1).

Denisova Cave

Denisova Cave is located in the Altai region of Russian Siberia. Excavations undertaken by the Siberian Branch of the Russian Academy of Sciences have been ongoing for more than three decades (Derevianko, Shunkov, and Markin 2014). We include here three molars from Denisova Cave. The oldest hominin remains from the site is a deciduous molar, Denisova 2, from level 22 (central gallery), associated with a thermal-optical date of about 280 ka BP (Derevianko 2009). The other two hominin fossils from Denisova are permanent upper molars from horizons 12–11.4 and 11.1, which correspond to the Middle-Upper Paleolithic transition at the site (Derevianko and Markin 2011). The Denisova teeth have been described recently in some detail elsewhere (Krause et al. 2010; Reich et al. 2010; Sawyer et al. 2015; Zubova, Chikisheva, and Shunkov 2017), and their description will not be repeated here.

The oldest deciduous molar, Denisova 2, was previously studied by Turner (1990). He determined that the tooth is a lower right first molar. However, Shpakova and Derevianko (2000) suggested that it is a lower left second molar, which was confirmed by Viola (2009). The preservation of the tooth is poor, and it is characterized by severe wear of the crown, postmortem fragmentation, loss of parts of the enamel, and an almost completely absent root (fig. 2). The root is mostly resorbed due to antemortem aging processes, and as a result, the pulp cavity is exposed. The condition of the root resorption and crown wear suggests a possible age of the individual of around 10 years (Bass 1995). No pathological condition was observed.

The molar from horizon 11.1 (Denisova 4) is a cynodont tooth, most likely a left upper second/third molar. Krause et al. (2010) have suggested that it is a left upper third molar. If the third molar had not yet erupted, this tooth could be the second molar (Sawyer et al. 2015; Zubova, Chikisheva, and Shunkov 2017). It is almost complete and is missing only the apical fragment of the distal buccal root. The crown is very high with bulging walls, and it is very large. The roots are relatively short. Based on the condition of the crown wear, the possible age of the individual is around 18–20 years (Bass 1995). No pathological condition was observed (fig. 2).

The molar from horizon 12–11.4 (Denisova 8) is likely a left upper molar. The identification of its position is rather problematic due to preservation. The largest part of the crown is preserved, and the root is broken just below the cervix; it is possibly a second or third molar ($M^{2/3}$; Buzhilova 2014; Sawyer et al. 2015). In occlusal view, the crown is rounded. The specimen is very large, similar to Denisova 4. Based on the crown wear (Bass 1995), the individual is likely to be an adult. No pathological condition of the preserved part of the crown was observed (fig. 2).

Previous comparative metric analyses have shown the same tendencies using the Denisova 4 and 8 specimens either as M^2 or M^3 (see results of analyses done by Buzhilova 2014; Reich et al. 2010; Sawyer et al. 2015). In this paper, we present the comparative analyses of Denisova 4 and 8 as M^2s, although we acknowledge that they may be M^3s.

Grotto Teshik-Tash

The Neanderthal attribution of the Teshik-Tash fossil initially defined the eastern extent of this group's geographic distri-

Figure 1. Sketch map showing Asian and Altaien Late Pleisocene sites discussed in the text.
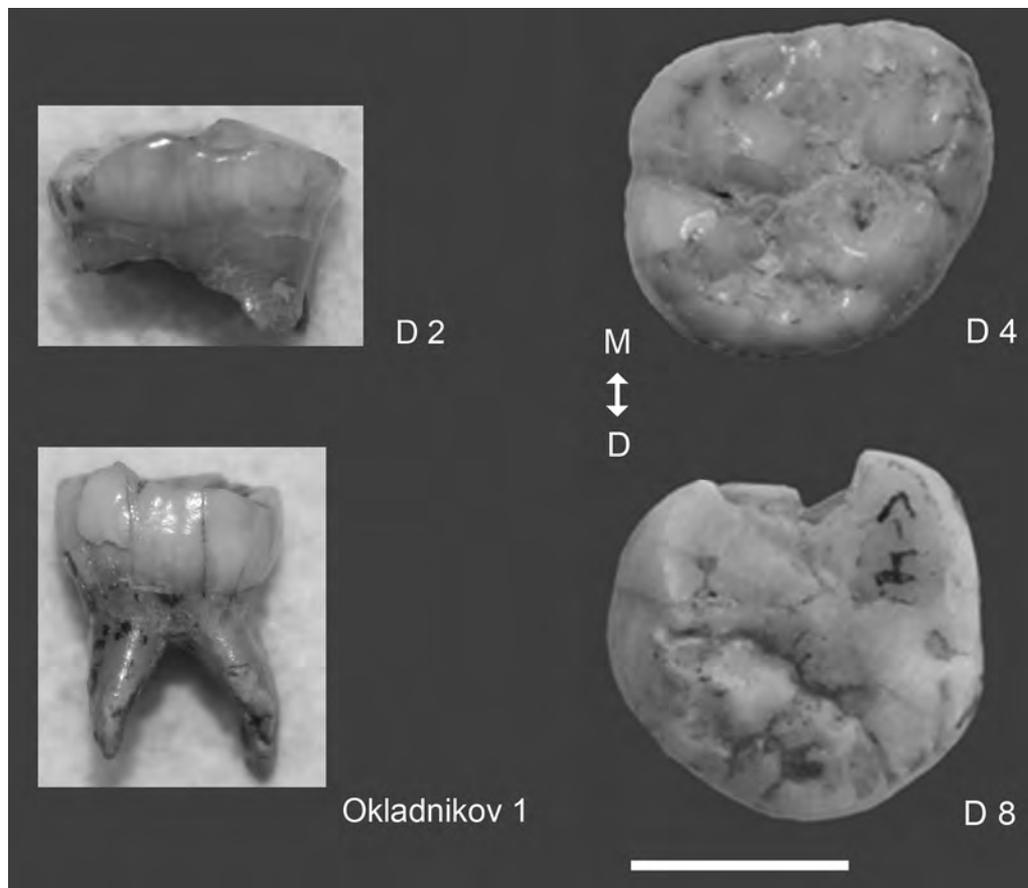
Figure 2. Molars from Denisova and Okladnikov caves. Deciduous m_2 of Denisova 2 (D2) and Oklandikov 1; permanent $M^{2/3}$ of Denisova 4 (D4) and Denisova 8 (D8).

bution (Okladnikov 1939). The history of the discovery of Teshik-Tash, its chronology, and the stratigraphic position of the grave and its ritual interpretation have been summarized by various authors (Movius 1953; Schwartz and Tattersall 2003; Vishnyatsky 1999). The analysis of the fossil remains and the taxonomical position of the Teshik-Tash materials have been discussed by local and foreign scientists (Alexeev 1973; Debetsc 1940; Glantz, Athreya, and Ritzman 2009; Gremyatskii 1949; Ullrich 1955; Weidenreich 1945).

The Teshik-Tash child consists of a hundred fragments that were reconstructed to produce a relatively complete cranium and mandible (Gerasimov 1949). The teeth are well preserved. According to Shaw (1928), two hypotaurodont m_2s of the lower jaw are available for measurements. The mesiodistal dimension (MDD) of the M^2 from Teshik-Tash could be determined only from the left side (fig. 3). The vestibulolingual dimension (VLD) was obtained with use of computed tomography (CT).

Okladnikov and Chagyrskaya Caves

Mousterian habitation horizons associated with Neanderthals were discovered in the Okladnikov and Chagyrskaya Caves, which are located in the piedmont zone of northwestern Altai.

Okladnikov Cave (formerly Sibiryachikha, named after a nearby village) was discovered in 1984 by A. P. Derevianko and V. I. Molodin. V. T. Petrin's excavations in the same year revealed isolated human postcranial remains and several teeth. Based on the results of uranium-series and radiocarbon dating analyses, all habitation horizons were determined to date to 45–40 ka (Derevianko 2011). In 2007, Chagyrskaya Cave was discovered by S. V. Markin. In 2008 and 2009, the lithics from that cave were shown to be similar to those from Okladnikov Cave (Derevianko and Markin 2011). Like the Okladnikov Cave assemblage, the lithics of Chagyrskaya Cave were described as Mousteroid (Derevianko and Markin 2011; Derevianko, Markin, and Zykin 2009). Both cave sites have typical Mousterian artifacts, which is suggestive of the presence of Neanderthals in the Altai. The excavators' views concerning the presence of Neanderthals in the Altai as well as the observations made by dental anthropology specialists were supported by the results of DNA sequencing, which confirmed the presence of distinct Neanderthal genes in the Okladnikov hominins (Krause et al. 2007; Viola 2009).

As a result of the ongoing excavations at Chagyrskaya Cave, the number of dental remains has increased substantially over time. Human remains from Chagyrskaya represent several in-

Generally, certain traits, both metric and qualitative, link the Okladnikov and Chagyrskaya hominins with both Neanderthals and Upper Paleolithic humans, whereas other traits indicate definitively Neanderthal affinities. This combination of archaic and more derived traits may be a distinctive characteristic of the Altaian Neanderthals.

Methods

The MDD and VLD of the teeth were measured with a standard sliding calliper and were recorded to the nearest 0.1 mm (Zubov 2006). Comparative samples were culled from the literature and presented in table 1. Metric data were evaluated using the Statistica 10.0 package. To evaluate the between- and within-group variation, one-way analysis of variance (ANOVA) was used. A post hoc test with a Bonferroni correction was used to determine whether any of the individual groups were significantly different from each other (Maxwell and Delaney 2003).

The Teshik-Tash specimen was examined with use of a different method. In this case, we collected CTs obtained at the Radiological Department of the Moscow State Medical University (Philips Brilliance 64 T; 120 kV, 300–400 mAs, rotation time: 0.4–0.5 s; voxel size: 0.363 mm, 0.363 mm, 0.45 mm; slice thickness: 0.5 mm; slice overlap: 0.3 mm). The thin-slice stacked Digital Imaging and Communications in Medicine (DICOM) sets were uploaded into Amira (Visualization Sciences Group, FEI) for automated image segmentation and isosurface model generation. The CT method follows closely similar fossil teeth studies (e.g., Kono 2004; Olejniczak et al. 2008; Smith et al. 2007; Spoor, Zonneveld, and Macho 1993).

We admit that there are a number of limitations with this comparative metric analysis and that a metric study in concert with approaches that evaluate nonmetric traits (e.g., Irish 1998; Zubova, Chikisheva, and Shunkov 2017) and/or shape variation of occlusal surfaces (e.g., Bae et al. 2014; Gómez-Robles et al. 2012) can produce substantially more confident results. However, even basic comparative metric analyses, such as are presented here, can inform on general variation between the different populations.
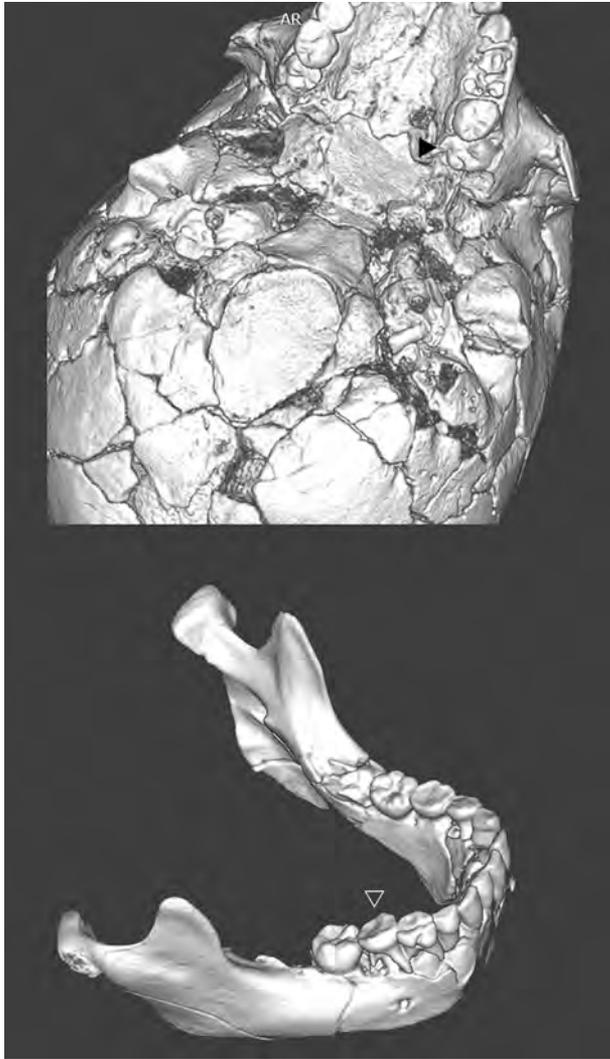

Figure 3. Teshik-Tash skull and mandible. Three-dimensional virtual reconstruction.

dividuals of various ages. The total number of fragments currently exceeds 50. Four or five fragments that were initially identified as human may have been inaccurately identified. Other samples include about 25 skeletal fragments representing one or more adults, two fragments representing an immature individual or individuals, two deciduous teeth, 10 isolated permanent teeth, a left maxillary fragment with molars, and a partial mandible with the right corpus and five teeth (a canine, two premolars, and two molars; Buzhilova 2013).

The dimensions of the deciduous teeth crowns place the Altai Neanderthals in between European/Southwest Asian Neanderthals and *Homo sapiens*. The permanent teeth from Okladnikov and Chagyrskaya caves could not be confidently assigned to a specific taxon. Newly discovered fossils from Chagyrskaya reveal a distinctly Neanderthal trait combination: anterior fossa and epicristid on the lower molars, a metaconid and crest on the premolars (Buzhilova 2013; Viola et al. 2012).

Results

Deciduous Lower Second Molars

The differences in crown diameters of the permanent teeth of the fossil dentitions are far better known than the deciduous dentition. In general, *Paranthropus* has larger deciduous cheek teeth, followed by *Australopithecus* and other hominins (Hillson 2002). No details are available concerning evolutionary divergences of hominins through the analysis of deciduous molars. As a result, we used statistical tools to identify any significant differences in the m_2 between the groups of hominins ($n = 151$ molars).

Table 1. Molars analyzed in this study

Species	Archaeological sites	No. comparative samples/specimen	Reference(s)
Australopithecus afarensis, Australopithecus africanus, Paranthropus robustus, Paranthropus boisei, Australopithecus sediba	Hadar, Makapansgat, Sterkfontein, Swartkrans, Chesowanja, Olduvai, West Turkana, Malapa	m_2, $n = 39$; M^2, $n = 130$	Frayer 1976; Wood 1991
Homo habilis, Homo rudolfensis	East Rudolf, Olduvai, Swartkrans, Omo	m_2, $n = 0$; M^2, $n = 4$	Frayer 1976; Tobias 1991; Wood 1991
Homo ergaster (Homo erectus, Africa)	East Rudolf, Turkana, Nariokotome, Konso, Swartkrans	m_2, $n = 0$; M^2, $n = 1$	Wood 1991; Brown and Walker 1993; Suwa et al. 2007
Homo georgicus (H. erectus, Caucasus)	Dmanisi	m_2, $n = 0$; M^2, $n = 3$	Martinón-Torres et al. 2008
H. erectus (Asia)	Zhoukoudian, Hexian, Chaoxian (Chaohu), S. Officinalis, Lantian, Trinil, Sangiran	m_2, $n = 8$; M^2, $n = 29$	Weidenreich 1937; Wood 1991; Grine and Franzen 1994; Wu and Poirier 1995; Xing et al. 2015
Atapuerca SH	Sima de los Huesos	m_2, $n = 0$; M^2, $n = 32$	Martinón-Torres et al. 2012
Homo heidelbergensis	La Chaise, Biache, Arago, Petralona, Steinheim1	m_2, $n = 0$; M^2, $n = 15$	de Lumley and de Lumley 1982; Condemi 2001; Rougier 2003
Homo neanderthalensis	Hortus, Monsempron, Petit-Puymoyen, Arcy sur Cure (Grotte du Bison), Archy, Krapina, Le Moustier, Vindija, Amud, Chateauneuf, St. Brelade, La Croze de Dua, La Quina, Le Moustier, Saccopastore, Shanidar, Spy, Tabun, Vergisson la Falaise.	m_2, $n = 36$; M^2, $n = 53$	Suzuki and Takai 1970; Frayer 1976; Tillier 1979; Trinkaus 1983
Asian *H. neanderthalensis*	Obi-Rakhmat, Okladnikov, Chagyrskaya, Teshik-Tash	m_2, $n = 2$; M^2, $n = 3$	Glantz et al. 2008; Viola 2009; Okladnikov, Chagyrskaya, Teshik-Tash (this article)
Late Pleistocene teeth, China	Xujiayao, Lunadong	m_2, $n = 1$; M^2, $n = 2$	Xing et al. 2015; Bae et al. 2014
Denisovans	Denisova	m_2, $n = 1$; M^2, $n = 2$	Krause et al. 2010; Reich et al. 2010; Sawyer et al. 2015
Early AMH	Skhul, Qafzeh	m_2, $n = 6$; M^2, $n = 8$	McCown and Keith 1939; Vandermeersch 1981
Paleolithic *sapiens*	Abri Pataud, Brno, Cro-Magnon, Combe Capelle, Dolni Vestonice, Cro-Magnon, Fontechevade, Isturitz, Le Rois, Grotte des Enfants, La Rochette, Leuca, Mladec, Oase, Predmosti, Sungir, Listvenka, Strashnaya Cave	m_2, $n = 58$; M^2, $n = 87$	Frayer 1976; Sladek et al. 2000; Trinkaus et al. 2003; Zubov 1984; Shpakova, Derevianko, 2000; Listvenka and Strashnaya caves (this article)

Note. For deciduous teeth, $n = 151$; for permanent teeth, $n = 369$. AMH = anatomically modern humans; SH = Sima de los Huesos.

One-way ANOVA indicated significant differences in crown diameters among the hominin groups (MDD *P* value for $F = 20.15$ is <0.01, $R^2 = 0.47$; VLD *P* value for $F = 9.35$ is <0.01, $R^2 = 0.28$; and the "area" [MDD × VLD] *P* value for $F = 17.28$ is <0.01, $R^2 = 0.43$). To determine which specific groups differed from each other, a post hoc test with a Bonferroni correction was used (table 2).

In general, the variability of MDD and VLD of m_2 confirms the well known picture of biological relationships between australopiths and various *Homo* taxa. As a consequence of the ANOVA results, a few points can be highlighted: (1) Asian *Homo erectus* differs significantly from Neanderthals and Paleolithic *Homo sapiens* by having a longer m_2; (2) the VLD of the m_2 does not have the power to differentiate between groups of Asian *H. erectus* and other hominins; and (3) European Ne-

anderthals do not differ significantly from groups of early AMH, such as from Paleolithic *H. sapiens*, by both diameters of the m_2 (table 2). It appears that the morphology of the deciduous m_2 does not have the statistical power to distinguish between different hominin types. Yet, at the same time, it has the possibility to indicate their common biological roots. The last conclusion is also important for an evaluation of the northern dispersal route.

Unfortunately, the odontological phenotype of the m_2 is unknown in regional groups of the Altai and in other parts of Asia as a consequence of having few fossil remains. The area (MDD × VLD) of the m_2 places Okladnikov 1 in the border of minimal teeth dimensions of Neanderthals and Paleolithic *H. sapiens* (fig. 4); it is closer to the average level of the known range of m_2 of modern humans (Buzhilova 2013; Viola 2009). Thus, the m_2 of Okladnikov 1 is modest in size, but the Teshik-

Table 2. Post hoc test with a Bonferroni correction for m_2

	Area, mm^2							
	Australopithecines	*Homo erectus*, Asia	Early AMH	*Homo neanderthalensis*	Paleolithic *Homo sapiens*	Teshik-Tash	Oklandikov 1	Denisova 2
Comparative species	124.86	112.71	104.93	97.48	95.12	105.60	86.00	95.79
Australopithecines	...	0.79	**0.04**	**<0.01**	**<0.01**	1.00	0.21	1.00
H. erectus, Asia	0.79	...	1.00	0.18	**0.03**	1.00	1.00	1.00
Early AMH	**0.04**	1.00	...	1.00	1.00	1.00	1.00	1.00
H. neanderthalensis	**<0.01**	0.18	1.00	...	1.00	1.00	1.00	1.00
Paleolithic *H. sapiens*	**<0.01**	**0.03**	1.00	1.00	...	1.00	1.00	1.00

Note. Area is defined as mesiodistal dimension (MSD) × vestibulolingual dimension (VLD) (mean square [MS] = 199.23). $n = 151$. Analysis of variance with statistical significance set at $P < 0.05$. Boldface type indicates statistical significance. AMH = anatomically modern humans.

Tash sample presents an exceptionally large molar and has dimensions closer to those of early AMH. The Denisova 2 sample is part of an average group that is formed by European Neanderthals and Paleolithic *H. sapiens* (fig. 4).

The differences noted between the studied samples could be the result of individual variation. Yet the differences in sizes and proportions of the crown of the m_2 do not exclude them from belonging to different hominin taxa. The genotypes of all three species are available: Denisova 2 represents a Denisovan genome, Okladnikov 1 is a Neanderthal genome, and Teshik-

Tash is a Neanderthal based on mitochondrial DNA (mtDNA; nuclear DNA remains unknown; Krause et al. 2007; Slon et al. 2015).

As was shown by genomic analysis of the Sima de los Huesos (SH) remains, the mtDNA indicated ancestry close to Denisovans, and the nuclear DNA indicated a relationship close to Neanderthals, but the morph (phenotype) of the remains is closer to that of Neanderthals (Gómez-Robles et al. 2015; Meyer et al. 2016). If the phenotypes of Okladnikov 1, Teshik-Tash, and Denisova 2 present possibly different biological relations,
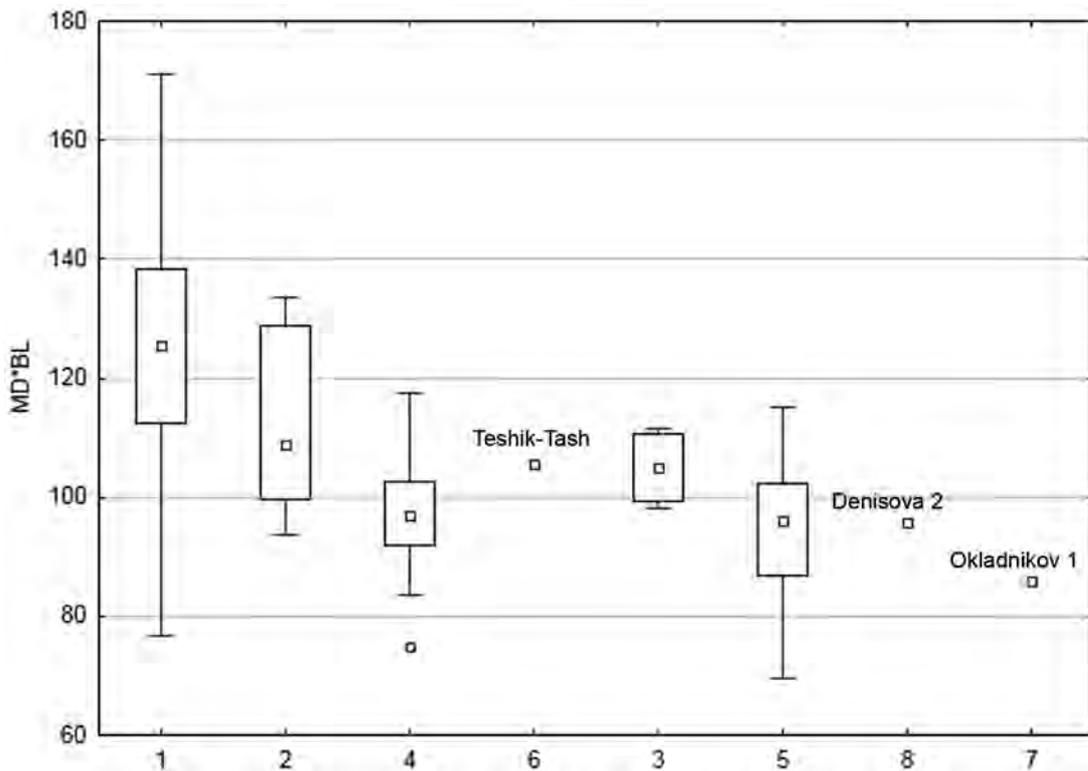
Figure 4. Box plot of Denisova 2, Okladnikov 1, and Teshik-Tash m_2 and comparative sample molar "areas" (mesiodistal dimension [MD] × vestibulolingual dimension [BL] in square millimeters). Comparative samples or specimens are australopithecines (1), Asian *Homo erectus* (2), early anatomically modern human (3), *Homo neanderthalensis* (4), Paleolithic *Homo sapiens* (5), Teshik-Tash (6), Okladnikov 1 (7), and Denisova 2 (8).

this should be reflected in nuclear DNA, as it was in the case of the SH fossils. Although Okladnikov 1 and Denisova 2 have been assigned to different hominin taxa, the Teshik-Tash fossil taxon designation remains unclear.

Permanent Upper Molars

The most diagnostic of the upper molars is the first one; the sizes of the other upper molars are more variable (Hillson 2002). For this analysis, we used only the M^2 data. The M^2 of australopithecines are large, including both linear measurement and geometric morphometric analyses of the tooth occlusal surfaces (Bae et al. 2014; Hillson 2002; Xiao et al. 2014). Different groups of other members of *Homo* demonstrate a reduction in molar sizes through time (Frayer 1976; Kieser 1990). Nonetheless, dental reduction of the cheek teeth is not a simple trend, and some increases in the crown diameters have been recorded (Hanihara and Ishida 2005; Harris and Rathbun 1991; Pilloud et al. 2014).

ANOVA results indicated significant differences in M^2 diameters among the hominin groups ($n = 369$ molars; MDD P value for $F = 72.16$ is <0.01, $R^2 = 0.68$; VLD P value for $F = 57.09$ is <0.01, $R^2 = 0.63$; and the area [MDD × VLD] P value for $F = 72.76$ is <0.01, $R^2 = 0.68$). A post hoc test with a Bonferroni correction provided the possibility to observe some significant differences between groups: (1) australopiths differ from groups of *Homo* species, except groups of *Homo habilis* sensu lato and African *H. erectus*; (2) African groups of *Homo* species differ from Paleolithic *H. sapiens*; (3) *Homo heidelbergensis* and Asian *H. erectus* differ from groups of Atapuerca SH, European Neanderthals, and Paleolithic *H. sapiens*; (4) the Atapuerca SH and European Neanderthals demonstrate differences from *H. heidelbergensis* and Asian *H. erectus* as well as from Denisovans; (5) early AMH differ from Denisovans; and (6) Paleolithic *H. sapiens* differ from African groups of *Homo* species, *H. heidelbergensis*, Asian *H. erectus*, and Denisovans (table 3).

In general, intergroup differences among the hominins reflect variability in time, except for the Denisovans. Both individuals from Denisova Cave, due to their large molar dimensions, are placed near the groups of *H. heidelbergensis* and Asian *H. erectus* and, interestingly, are also close to the australopiths. The Teshik-Tash M^2 demonstrates more or less the same tendency and is similar to the Oase 2 molar from Romania (fig. 5).

Archaeological Data

Due to systematic archaeological investigations over the past three decades (Derevianko, Shunkov, and Markin 2014; Derevianko and Rybin 2003), the Altai region has become one of the most well-investigated regions in northern Asia. All investigated archaeological sites examined here are stratified and multilayered, some containing up to 20 culture-bearing hori-

zons. The maximum thickness of sediments is 14 m at Denisova Cave and up to 8 m at open-air sites. Development of primary flaking techniques is best demonstrated by finds from Denisova Cave and the Ust-Karakol-1 and Kara-Bom open-air sites (see fig. 1).

Lithic materials from Denisova Cave were produced primarily on poor-quality sedimentary and effusive rocks. A small number of tools were manufactured on high-quality jasper and hornfels. A considerable number of cores of various types, especially from the lower strata, demonstrated an irregular flaking pattern. The cores in the lower portion of the cultural horizons at Denisova Cave were mostly Levallois, obtained using a generalized reduction strategy. The upper portion of the profile (strata 14 and 13) contained distinct double-platform cores; from stratum 12 and above, narrow-faced cores, blades, and microblades appear (Derevianko and Rybin 2003; Derevianko, Shunkov, and Markin 2014).

Materials recovered from the Ust-Karakol-1 culture-bearing horizons complete the gaps in primary reduction strategies observed at Denisova Cave. These sites are located at a distance of 3 km from each other. Ust-Karakol-1 has revealed Levallois cores in horizons 18a–10 and narrow-faced cores in horizons 11a–9a (Derevianko 2009).

The Anui-3 open-air site is located between Denisova Cave and the Ust-Karakol-1 site. The lowermost portion of the Pleistocene sediments (strata 18–13) produced a collection of typical Middle Paleolithic artifacts. The Middle Paleolithic strata are overlaid by the early Upper Paleolithic sediments with chronological dates no earlier than 54 ka (Derevianko 2009). The small collection of artifacts provides evidence for the presence of a well-developed technique of parallel reduction of prismatic cores.

The archaeological materials from the sites demonstrate a gradual change in lithic industries. The Middle to Upper Paleolithic transition in the Altai has been examined in detail (see review in Derevianko, Shunkov, and Markin 2014). Archaeological materials recovered from the Kara-Bom site, located in the middle-elevated zone of the Central Altai, demonstrate a different variant of the Middle to Upper Paleolithic transition. The Kara-Bom site has revealed two Middle Paleolithic and six Upper Paleolithic habitation horizons with chronological dates no earlier than 33 ka. Primary flaking techniques of both the Ust-Karakol and Kara-Bom traditions demonstrate a continuous development from the Levallois to the Upper Paleolithic. At the same time, a period when both strategies coexisted can be clearly identified. The evolution of primary flaking strategies within the Ust-Karakol and Kara-Bom early Paleolithic traditions is attributed to the same chronological period; however, they were aimed at producing blades through different techniques. The Kara-Bom variant resulted in the production of regular elongated blades from narrow-faceted cores, and the Ust-Karakol trend (Denisova Cave, Anui-3, and Ust-Karakol-1) developed into the microblade tradition. The technocomplex from Denisova Cave presents some differences as compared

Table 3. A post hoc test with a Bonferroni correction for M^2

	Australopithecines	*Homo habilis, Homo rudolfensis*	*Homo erectus*, Africa and Caucasus	*H. erectus*, Asia	*Homo heidelbergensis*	Atapuerca SH	*Homo neanderthalensis*, Europe	Early AMH	Paleolithic *Homo sapiens*	Denisovans	*H. neanderthalensis*, Asia	Late Pleistocene, China
					Area, mm^2							
Comparative species	206.60	166.45	167.02	163.17	160.91	121.44	135.55	133.41	120.69	201.39	138.18	147.48
Australopithecines	…	0.12	0.14	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	1.00	**<0.01**	0.07
H. habilis, H. rudolfensis	0.12	…	1.00	1.00	1.00	0.05	1.00	1.00	**0.03**	1.00	1.00	1.00
H. erectus, Africa and Caucasus	0.14	1.00	…	1.00	1.00	0.05	1.00	1.00	**0.02**	1.00	1.00	1.00
H. erectus, Asia	**<0.01**	1.00	1.00	…	1.00	**<0.01**	**<0.01**	0.21	**<0.01**	1.00	1.00	1.00
H. heidelbergensis	**<0.01**	1.00	1.00	1.00	…	**<0.01**	**0.04**	0.85	**<0.01**	1.00	1.00	1.00
Atapuerca SH	**<0.01**	0.05	0.05	**<0.01**	**<0.01**	…	0.83	1.00	1.00	**<0.01**	1.00	1.00
H. neanderthalensis, Europe	**<0.01**	1.00	1.00	**<0.01**	**0.04**	0.83	…	1.00	0.05	**0.02**	1.00	1.00
Early AMH	**<0.01**	1.00	1.00	0.21	0.85	1.00	1.00	…	1.00	0.05	1.00	1.00
Paleolithic *H. sapiens*	**<0.01**	**0.03**	**0.02**	**<0.01**	**<0.01**	1.00	0.05	1.00	…	**<0.01**	1.00	1.00
Denisovans	1.00	1.00	1.00	1.00	1.00	**<0.01**	**0.02**	0.05	**<0.01**	…	0.41	1.00
H. neanderthalensis, Asia	**<0.01**	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.41	…	1.00
Late Pleistocene, China	0.07	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	…

Note. Area is defined as mesiodistal dimension (MSD) × vestibulolingual dimension (VLD) (mean square [MS] = 632.19). $n = 369$. Analysis of variance with statistical significance set at $P < 0.05$. Boldface type indicates statistical significance. AMH = anatomically modern humans; SH = Sima de los Huesos.
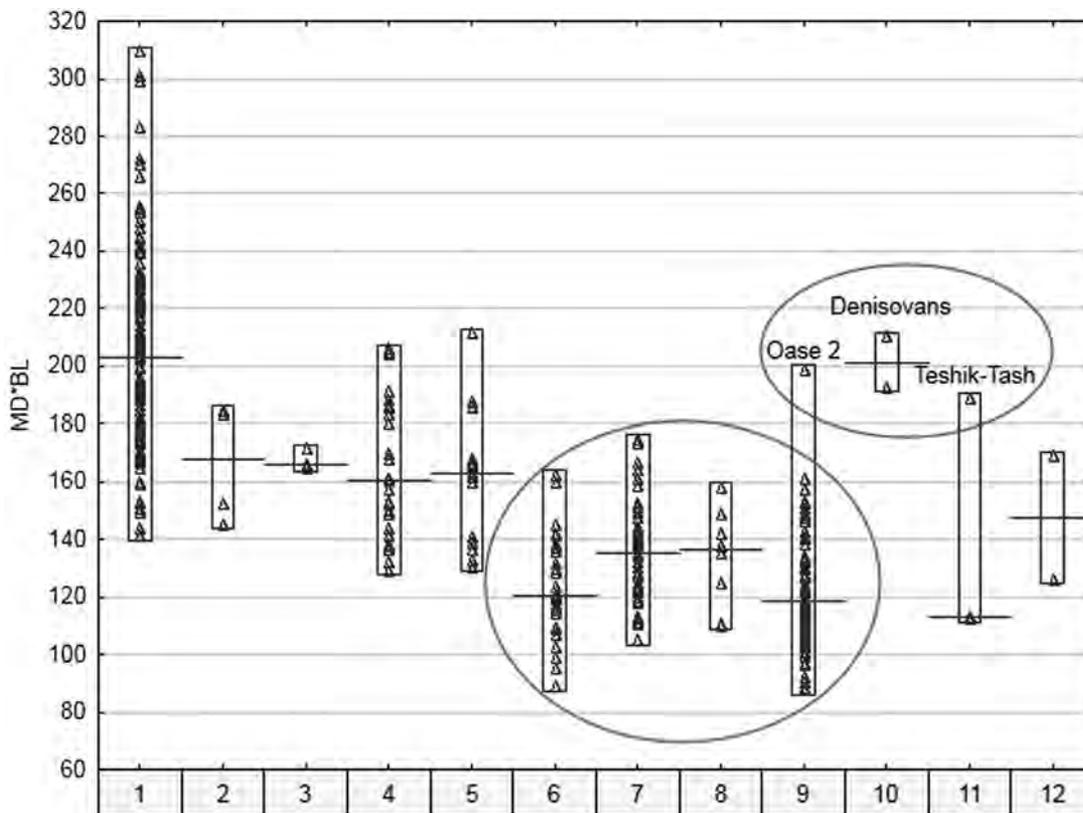
Figure 5. Box plot of Denisova 4, Denisova 8, and Teshik-Tash M^2 and comparative sample molar "areas" (mesiodistal dimension [MD] × vestibulolingual dimension [BL] in square millimeters). Comparative samples or specimens are australopithecines (1); *Homo habilis*, *Homo rudolfensis* (2); *Homo erectus*, Africa and Caucasus (3); *H. erectus*, Asia (4); *Homo heidelbergensis* (5); Atapuerca Sima de los Huesos (6); *Homo neanderthalensis*, Europe (7); early anatomically modern humans (8); Paleolithic *Homo sapiens* (9); Denisovans (10); *H. neanderthalensis*, Asia (11); and Late Pleistocene molars from China (12).

with the assemblages from Ust-Karakol-1, which might result from different behavioral and adaptive strategies (Derevianko 2009).

In-depth studies of lithic industries at Kara-Bom and Ust-Karakol provide evidence for developmental trends during the final stage of the Middle Paleolithic (i.e, between 70 and 50 ka). The divergent industries appear to evolve from a single Middle Paleolithic culture, giving rise to two variants of the early Upper Paleolithic industries around 50–43 ka. The evolution of the Middle Paleolithic industry and its development into the Upper Paleolithic was a continuous process based on a local technological tradition.

Discussion

Several studies of human fossils have suggested that there is no clear temporal gradient in ancestral versus derived dental morphology, implying a much more complex evolutionary scenario. Retention of ancestral traits in younger specimens may be due to evolutionary stasis associated with an isolated living environment (Xing et al. 2015). This scenario has also been suggested for the Javanese and Zhoukoudian *Homo erectus* populations (Anton 2002, 2003; Kaifu 2006; Kaifu et al.

2005). It is therefore possible that the preservation of archaic proportions and large tooth sizes observed in the Denisovans is due to relative isolation. In this case, the archaic pattern present in the Denisovan hominin fossils is understandable.

Sawyer and colleagues (2015) reported that Denisova 8 is different from Neanderthal and Middle Pleistocene European groups due to the presence of a large metacone, large hypocone, and very large cusp 5 that extends the crown distally. In addition, the Denisova 8 tooth lacks distal tapering, and the large cusp 5 is a feature not found in *H. erectus* populations. Strong expression of cusp 5 is rare in modern humans. The tooth of Denisova 4 presents a lingually skewed hypocone and metacone and large talon basin (features that are more similar to those of Neanderthals) as well as massive and flaring roots (Reich et al. 2010). Zubova and coauthors (2017) report affinities of both Denisovan molars with *H. erectus* of Sangiran and the Middle Pleistocene hominins of China, such as Xujiayao. Thus, the specific archaic position of the Denisovans observed by the metric analysis of M^2 is also supported by qualitative odontological features.

It is of interest to recall that the Middle Pleistocene fossils from SH show a very strong reduction in the size of the second and third molars, even more marked than the reduction ob-

served in Neanderthals and modern human populations. As researchers have noted, the highly derived shape of the SH molars points to an early acquisition of typical Neanderthal dental traits by pre-Neanderthal populations and to a deviation of this population from mean morphologies of other European Middle Pleistocene groups (Gómez-Robles et al. 2012). At the same time, in the Altai region, other groups, such as the Denisovans, exhibit large teeth. In both cases, the accumulation of idiosyncratic features in a certain geographical place can be explained by the same mechanisms influencing populations living in an isolated environment (Shmalgauzen 1946). Interestingly, despite a sharp contrast in odontological variants of both the SH and Denisovan populations, the two groups share a more or less similar mitochondrial genome that indicates the common root of the groups (Meyer et al. 2014). Moreover, the Denisovans display the development of discrete odontological traits, which are seen in more archaic Asian *H. erectus* groups (Zubova, Chikisheva, and Shunkov 2017).

The archaeological record, as summarized by Derevianko, Shunkov, and Markin (2014), confirms that, between 1.5 and 0.3 Ma, populations from eastern Asia developed different lithic industries in comparison with populations in adjacent regions. Unfortunately, archaeology cannot speak directly to the biological mechanisms of development and the formation of various hominin populations in any particular region. However, no radical changes have been observed in the material culture of the Sino-Malayan zone (Seong and Bae 2016). According to Lycett and Norton (2010), during much of the Pleistocene, a combination of biogeographical, topographical, and dispersal factors resulted in relatively lower effective population sizes among East Asian hominins compared with western groups. Thus, small populations originating from Africa and the Levant may have become isolated because of various barriers once they reached regions like Southeast Asia (Derevianko, Shunkov, and Markin 2014).

For Northern and Central Asia, the archaeological data confirm that the original settlement of the Altai and, most likely, southern Siberia in general, happened by ∼800 ka. The next wave of migration occurred at approximately 500–400 ka, and the territory was populated once again by Middle Eastern populations by approximately 300 ka. All available archaeological remains indicate a continuous local evolution of the lithic industries until approximately 80–10 ka (Derevianko, Shunkov, and Markin 2014).

Having integrated data from different sources, we propose that the highly derived odontological forms of Denisovans could be the result of long periods of isolation. Metric data on the permanent molars show the relationship of the Denisovans with premodern populations from Africa and Asia. Archaeological data suggest that the first Denisovans arrived in the Altai around 300 ka, with continuous cultural development for a long time. The genetic data confirm that Denisovans were present in the area at least twice and possibly over a long period of time. Thus, we have adequate data to evaluate the hypothesis of continuous cultural and physical development of Deni-

sovans over time. The similar morphology of two upper hominin molars from Denisova Cave, separated by a thick deposit and tens of thousands of years, also supports this idea.

At about 55–45 ka, a small group of Neanderthals appeared in the Altai (Chagyrskaya and Okladnikov caves). Derevianko, Shunkov, and Markin (2014) underlined that these Neanderthals possibly originated from Central Asia, and their lithic industry was different from the material culture found in other sites of the Altai. This group of migrants was possibly assimilated, and their arrival did not result in long-lasting changes in the material culture of the local Denisovan population. This model matches the genetic data. The genetic difference between the two Denisovan molars as well as their similar morphology suggest that Denisovans were present in the area at least twice, with their occupation perhaps interrupted by a Neanderthal migration between 55 and 45 ka (Sawyer et al. 2015). The genetic diversity of late Eurasian Neanderthals across their entire geographical range was lower than that of present-day humans, and there is evidence suggesting that Neanderthal populations may have been small and isolated from one another (Castellano et al. 2014).

It is important to note that geneticists do not exclude the possibility that the Denisovans may have been present in neighboring regions, from where they may have periodically extended their range to the Altai (Sawyer et al. 2015). This idea is interesting in the context of the unclear taxonomic position of the Teshik-Tash child. The extremely large dimensions of the M^2 place Teshik-Tash close to the Denisovans. If we were to look into the archaeological and anthropological context of the findings, V. P. Alexeev (1978, 1985), who studied the Teshik-Tash remains, suggested that the parietal and the inclination of the frontal are similar to those of the Skhul and Amud hominins. According to Alexeev, it is possible to identify a transitional European and southwestern Asian morph. Later, A. Haeussler (1997) stressed the existence of gene flow between European and Central Asian populations during the Middle Paleolithic. This idea is supported by a new finding of the M^2 of from Oase 2 in Romania. As H. Rougier and coauthors note (2007), Oase 2 exhibits an unusual molar size progression for an early modern human and unique combinations of traits resulting from the blending of previously divergent gene pools. The close position of the Oase 2 M^2 to the Asian molars of Teshik-Tash and Denisovans does not exclude the idea of existence of gene flow between Europe and Asia. The comparative odontological data of Teshik-Tash and other hominins further indicate the addition of Near East *Homo* to the list of possible participants in the gene pool (Haeussler 1997). More recently, the equivocal background of the origin of the Teshik-Tash hominins was reevaluated by Glantz and colleagues (2009). The paleogenetic data indicate similarities with the Neanderthal mitochondrial genome of Teshik-Tash, which does not exclude its relation to the Neanderthal morph; but at the same time, the nuclear genome remains unknown.

From the same region, material from Grotto Obi-Rakhmat is known. A subadult, Obi-Rakhmat 1, represented by part of a

permanent maxillary dentition and a fragmentary cranium, expresses a relatively Neanderthal-like dentition coupled with a more ambiguous cranial anatomy (Glantz et al. 2008). Most of the features that can be assessed suggest archaic or Neanderthal affinities for the Obi-Rakhmat 1 remains. Additional study of the upper first molar of this individual shows that cusp areas, angles, and relative cusp positions provide a strong Neanderthal signal (Bailey et al. 2008). This sample shows the same tendency that we noted on examples of Altaian Neanderthals, which demonstrate a combination of archaic and more advanced traits.

Taken together, the new findings of Middle Paleolithic hominins show that population dynamics in Central Asia were more complex than simply characterizing this region as the eastern border of the Neanderthal distribution. Indeed, we still do not have a firm evolutionary model to explain population dynamics or the relationship of hominin groups from Central Asia to those of the rest of the Old World. Central Asian fossil records are fragmentary and are represented predominately by subadults. In such cases, the archaeological data assume some importance. Derevianko (2009) has subdivided the Middle Paleolithic or Mousterian industries of Central Asia into two developmental trends, the Teshik-Tash and Obi-Rakhmat variants. Different researchers have subdivided the Middle Paleolithic cultures of the region into 3–5 variants (see Derevianko, Shunkov, and Markin 2014). All of the variants could be the result of different adaptive strategies in different ecological environments across the huge and diverse territory of Central Asia.

The techno-typological features of the industries associated with the human fossils of Teshik-Tash and Obi-Rakhmat are different. Derevianko, Shunkov, and Markin (2014) note that the Obi-Rakhmat and Mugharan cultures (Levant) are based on the same industry, whereas Teshik-Tash illustrates the development of different Middle Paleolithic industries, which were based on more ancient autochthonous traditions.

The Paleolithic assemblages from Chagyrskaya and Okladnikov caves, attributed initially to the Sibiryachikha variant, are comparable to the Mousterian industries recorded in regions of southeast Europe, Transcaucasia, and the eastern Mediterranean (Derevianko, Shunkov, and Markin 2014). These comparisons correspond well with the odontological data, which show that the two permanent molars from Chagyrskaya Cave and a deciduous molar from Okladnikov Cave are close to those of Neanderthals. In general, the genetic and anthropological data from these caves suggest that the Sibiryachikha variant is associated with Neanderthals (Buzhilova 2013; Krause et al. 2007; Mednikova 2013; Viola et al. 2011, 2012).

The archaeological data, along with the fragmentary human remains from the Altai and Central Asia, allow us to put forward a hypothesis to explain Middle Paleolithic human dispersals in the region between migrant Neanderthals and an earlier dispersal of Denisovans. The Denisovans formed from one of the dispersal waves of *Homo* species (mid-Pleistocene *Homo*? *Homo heidelbergensis*?) from the West to the East. The region that these hominin populations originated from must have been larger than and outside of the Altai region.

Conclusion

Although great strides have been made in understanding the evolution of hominins in the Altai region, little information is yet available about the biological and demographic history of Middle and Upper Paleolithic populations. Our analyses show that highly derived odontological forms of Denisovans could be explained as a result of the temporal and geographic isolation of the migrant groups over a long period of time, with the ancestral population originating from western Asia. It is possible that some elements of an archaic local population from Central Asia and Southern Siberia have been preserved in Middle Paleolithic individuals, such as the Teshik-Tash child. The Altai Neanderthals from Chagyrskaya and Okladnikov cave dental morphologies are similar to the teeth of *Homo neanderthalensis* (Buzhilova 2013; Viola 2009; Viola et al. 2012). The sample of teeth from Upper Paleolithic contexts of Strashnaya Cave shows some similarities to the Sinodont morphological pattern, which is seen in present-day North Asians and Native Americans (Viola et al. 2011).

Acknowledgments

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Late Pleistocene Human Migrations in China

by Youping Wang

Many archaeological and paleoanthropological discoveries have been made in China over the last 2 decades. Among these findings, I particularly note the recently excavated Late Pleistocene sites in the loess plateau in northern China and others found in a number of river basins in southern China. They all provide significant new information concerning Late Pleistocene human migrations across this vast region. A result of these excavations is the confirmation that flake- and pebble-tool industries dominated the region before the late marine isotope stage (MIS) 3. Small-flake-tool assemblages emerged suddenly during the late MIS 3 in South China. Blade industry first arrived in northwest China at the end of MIS 3, and microblade assemblages appeared in the loess plateau and the surrounding areas at a later stage. In this paper I briefly introduce the progress in Chinese Paleolithic archaeology and discusses Late Pleistocene human migrations and related issues.

For decades, Pleistocene China has been regarded as a vast and relatively isolated land at the eastern part of the Eurasian continent. Regardless of the geopolitical border, the natural boundaries are set by the Qinghai-Tibet Plateau, the northern and western deserts, and the subtropical lands in the south that stretch into Southeast Asia. Since the 1920s, thousands of Paleolithic localities have been found in this vast region, but only a few are known to Western scholars. Many sites remain unpublished or have been reported in regional journals and have material stored in local museums and work stations. Paleolithic research increased dramatically during the last 2 decades, leading to the discovery of numerous Late Pleistocene sites found across the loess plateau in northern China and at several river basins in South China. The new localities currently provide important new information concerning Late Pleistocene cultural changes and human dispersals. Below I review the new developments of Chinese Paleolithic archaeology and discuss the evidence for Late Pleistocene human migrations and related issues.

The Archaeological Record of the Early and Middle Pleistocene

The Earliest Occupations in China

In the early twentieth century researchers working around the area of the Nihewan village, located in a basin of northwest Hebei Province, recognized several Pleistocene sequences and other prehistoric occurrences. Based on surveys and excavations,

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the ongoing investigations in Nihewan identified an important core area for early hominin sites. The excavations at Majuangou, Xiaochangliang, Donggutuo, Banshan, Feiliang, and Cenjiawan yielded artifacts and animal bones attributed to the activities of such early hominins. Majuangou is identified as the earliest hominin occupation in China, dated to ca. 1.66 mya (Bar-Yosef and Wang 2012; Dennell 2013; Wei 1997; Wu, Wu, and Zhang 1989; Xie 2006, 2008; Zhu et al. 2004). Other sites are also dated to the time period between 1.6 and 1.0 mya. These early occupations are located along paleolakeshores and wetlands that supplied sources of vegetal and animal food as well as drinking water. Studies of knapped lithics found together with animal bones indicate that Early Pleistocene hominins obtained their food by hunting and scavenging (Y. P. Wang 2005). In addition, the basic operational sequence for manufacturing flakes with sharp edges is not much different from the industry revealed at the earliest site of western Asia, namely, Dmanisi in the Republic of Georgia (Ferring et al. 2011).

One of the most important findings from this period is the hominin skull from Gongwangling, Lantian County (Shaanxi Province). The initial paleomagnetic dating placed the fossil in the period between 1.1 and 1.15 mya, but more recent research suggested an earlier date of 1.63 mya (Zhu et al. 2014). The associated faunal remains indicate warm and wet climatic conditions similar to those of southern China today (Y. P. Wang 2005; Wu, Wu, and Zhang 1989).

The aforementioned archaeological records indicate similarities in the biological and cultural evolution of early hominins during the late Pliocene and the earliest Lower Pleistocene between China and western Asia. The common core chopper or core and flake industries reflect the earliest dispersals of hominins from Africa into Eurasia. Geography, climate, vegetal association, and the local fauna in East Asia did not present major obstacles to the migrating and colonizing groups. The region north of the Qinghai-Tibet Plateau was covered by spo-

radic dunes instead of the large sandy desert of today (Cui et al. 1996; Shi et al. 1996). In addition, paleolakes and wetlands were widely present across the vast land in northern China, providing favorable conditions for early hominin survival (Dennell 2009; Y. P. Wang 2005).

Hominin Adaptation during the Middle Pleistocene

The Middle Pleistocene period was a time for flourishing hominin evolution and cultural development in China. Numerous fossils of *Homo erectus* with associated lithics and animal bones have been discovered across China. The records present a variable occupation pattern: caves are commonly occupied in the north, while in the south open-air sites on lakeshores or riverbanks are more common.

Zhoukoudian Locality 1 is, to a large extent, the best example of human adaptation during this time period. Locality 1 was a cave site preserving very thick deposits, with thousands of lithics and a large number of animal bones. Most notable is the location where six *H. erectus* craniums (commonly known as Peking Man) were unearthed. Important but controversial was the evidence indicating the use of fire at the site (Zhang 1987). The initial dating by uranium series, thermoluminesence, electron spin resonance (ESR), and paleomagnetism indicated that the lower unit dated to around 500 ka and the upper unit to 230 ka. The occupation of *H. erectus* at the site may have continued for more than 200,000 years (Wu, Wu, and Zhang 1989). A more recent dating attempt suggested an even earlier start of the occupation at Locality 1 from 700 ka onward (Shen et al. 2009). Several layers contained rich cultural remains, while others yielded only very few lithics or hominin remains. This may indicate changes in the intensity of occupation of the cave. The hominins of Zhoukoudian Locality 1 exploited locally available raw materials such as quartz cobbles from the nearby river and the surrounding hills. The lithic assemblage includes large heavy tools such as choppers and small-flake tools including scrapers and points. The larger choppers seem to have played an important role in the early phases of the occupation, but lighter tools became more common in the upper, younger layers of the site (Pei and Zhang 1985).

Important evidence of human adaptation during the late Middle Pleistocene comes from Jinniushan cave at Dashiqiao city (Liaoning Province). The site is located on the plain of the Liao River, and the excavations retrieved abundant lithics, animal bones, hearths, and a human burial (Lu et al. 2011). Ashes of variable thickness dispersed throughout the cave document the use of fire in this northern cold region at about 250 ka (Chen et al. 2004). Several of the fireplaces appear to have been encircled with rocks. Intentionally broken long bones and burnt bone fragments indicate exploitation by hominins. The small scrapers and the large quantity of animal bones, in particular the processed ones, indicate a great degree of human reliance on meat resources (Norton and Gao 2008a; Zhang 1996). The lithic industry of Jinniushan resembles that of Zhoukoudian

Locality 1 by its medium- and small-size scrapers of quartz and the use of bipolar technique. The archaeological record from both Zhoukoudian and Jinniushan is a clear demonstration of the success of the subsistence and adaptation strategy of humans living in higher-latitude areas with cold temperatures and steppe vegetation.

In southwest China, Guanyindong Cave, in the area of Yunnan-Guizhou Plateau, is located in a well-developed karst landscape. Uranium-series dating of the residual sequence ranges from the late Middle to the Late Pleistocene (Wu, Wu, and Zhang 1989). The lithic assemblage is dominated by medium- and small-size scrapers, which are considered very effective for the acquisition and consumption of meat. Stone tools were made on siliceous rocks with the adoption of direct percussion by hard hammer (Li and Wen 1986). A large number of percussion-marked bones also reflect the importance of animal resources. Similar lithic technology can be observed in other caves in the southwest—for example, at Panxian Dadong—and is considered by many a regional adaptation trait of early humans (Karkanas et al. 2008).

From the southern part of northern China to the valleys in the southeast, many open-air localities or clusters of sites were discovered. The sites spread along the rivers, mainly along the upper-middle part of the Han River and the middle-lower area of the Yangzi River as well as the Baise Basin in the very south of China. These sites exhibit a highly distinct lithic industry compared with those of the regions mentioned above. Stone artifacts are made of cobbles, and the tool kit is characterized by large, heavy choppers and points but very few small tools. This type of lithic assemblage appears to fit the wood and bamboo resource exploitation and processing and could be perceived as an adaptive strategy for living in an environment with rich vegetation (Wang 1998; Y. P. Wang 2005).

One of the significant findings from this period is the human fossils and cultural remains from Quyuanhekou site, Yun County, Hubei Province, on the terrace of the Han River. The site yielded two relatively well-preserved skulls and some stone artifacts. The lithic assemblage includes scrapers made of quartzite as well as choppers and large points made of quartz or sandstone cobbles. A large group of animal fossils are identified as fauna typical of subtropical South China (Li et al. 1998).

Another concentration of sites is located along the Yangzi River, where many localities in the middle-lower Li River valley were surveyed and excavated. The sites are deposited in red sediment and are widely spread on the different level terraces in this region. Huzhaoshan, Hunan Province, is a typical example of this period, located on the fourth terrace of the Li River. It was excavated in 1988 and yielded several stone artifacts. The lithic assemblage can be assigned to the traditional cobble-tool industry, with large points made from long, loaf-shaped cobbles (Wang 1997). Besides Huzhaoshan, several other locations with similar lithic technology were recovered from the third and second terraces.

In the region of the Shuiyang River, a tributary of the larger Yangzi River, several sites have been discovered. Chenshan,

for example, a site formed in the red soil under the lower part of the "Xia Shu" loess, yielded more than 1,500 lithic pieces. Based on the local geological sequence, the site is considered to have been occupied since the late Early Pleistocene until the end of the Middle Pleistocene, from around 900 ka to 150 ka. The cobble-tool industry had been present at the site throughout this long period. Lithics do not show changes in terms of technological organization. Locally available cobbles of quartzite and sandstone were exploited as raw materials. Cobble blanks were simply knapped into choppers and large points. Small-size flake tools were used in low frequency (Fang et al. 1992).

The Middle Pleistocene archaeological record of China and East Asia is dominated by core and flake industries, or Mode 1 technology, revolving around the production of cores and flakes or cobble tools. Based on up-to-date observations and analysis, the handaxes reported from East Asia so far are different from those of the West in terms of absolute numbers, frequency in the assemblages, and technological system of production (Norton et al. 2006; Wang et al. 2014). Some scholars have argued that new discoveries of handaxes in East Asia indicate the dispersal of populations bearing the Acheulean technological concept (Hou et al. 2000; Huang 1987; Li, Li, and Kuman 2014; Li et al. 2014; Lu et al. 2011; S. J. Wang 2005; Wang et al. 2012; Xie and Boden 2007). However, it is clear that the issues of how handaxe technology appeared in China and its role in early human evolution and adaptation in East Asia require further investigation.

The Transition to the Early Late Pleistocene

The cultural evolution in China is best recorded during the period marking the end of the Middle Pleistocene through the early Late Pleistocene, to about 50–40 ka. Notably, the number of sites increases, and their geographical distribution extends significantly. The regional differences seen previously in the lithic industries continue to be present. In northern China, a typical example comes from the open-air site of Xujiayao, Shanxi Province, which was dated by uranium series to 125–100 ka. The cultural remains are dominated by tens of thousands of stone artifacts. The raw material includes quartz, chert, volcanic rock, and quartzite, all of which can be obtained locally. Direct percussion is the major knapping method, whereas bipolar technology is used only occasionally. The tool assemblage is composed of small-flake tools such as scrapers, points, awls, and burins. The scraper category accounts for more than 50% of all tools. Importantly, spheroid is a characteristic tool type, and over a thousand such tools have been discovered at the site. The lithic assemblage indicates persistence in the traditional small-flake industry. However, a transformation in lithic production is evidenced by the presence of prismatic cores and elegant round scrapers, which are commonly regarded as a signature of the Upper Paleolithic (Gao and Norton 2002; Jia et al. 1979; Norton et al. 2009).

In the southern part of northern China, the tool industry is based on large cobbles. At Dingcun, for example, large points and choppers played a major role in the tool kit. However, in many other sites in this region, for example at Dali, heavy-duty large tools were replaced with medium- and small-size scrapers and points (Y. P. Wang 2005).

In southern China, the lithic industry does not exhibit noticeable differences from the earlier period. Persistence in the traditional cobble-tool industry is indicated both in raw material acquisition and tool production. The systematic excavation of the Jigongshan site, Hubei Province, revealed in its lower layer an activity surface covering about 500 m² that yielded several thousand lithic pieces and cobbles. The site is interpreted as a base camp where stone knapping occurred on a regular basis. Supporting evidence is offered by the presence of piled cobbles and a large concentration of lithic tools and other artifacts (Liu and Wang 2002).

At the same time, the Mousterian culture appeared in western Eurasia and replaced most of the Acheulean tradition with the adoption of the Levallois technique. Although the influence of Levallois techniques reached Xinjiang and Inner Mongolia—that is, the boundary between central and northeast Asia—during the late marine isotope stage (MIS) 3 period, foragers in East Asia continued to produce tools on flakes and cobbles using simple core and flake technology (Gao 2013; Gao and Norton 2002). This cultural division may be attributed to the lack of interaction between populations caused by the Qinghai-Tibet Plateau, a significant physical barrier (Wang 2003).

The Late Late Pleistocene

North China

Until very recently the emergence of modern humans in East Asia was considered a local evolutionary process taking place at around 50–40 kyr BP (Liu, Wu, and Xing 2016). This hypothesis derived from the study of human fossils. On the other hand, various archaeological assemblages indicate the presence of novel technological features and new behavioral traits usually associated with modern humans (Norton and Jin 2009). Below, I present the innovations and changes in human adaptations observed in the Chinese archaeological record of the period.

Some of the most abundant evidence comes from Upper Cave, Zhoukoudian (Norton and Gao 2008b). Three well-preserved skulls surrounded with decorations and ochre were discovered at the site, suggesting an intentional burial. Only a few stone artifacts were found, knapped by direct hard-hammer percussion and bipolar techniques. The tool assemblage is composed of scrapers and choppers, produced in a simple and crude manner. Bone and antler artifacts are also present, most notably an eyed bone needle and a polished antler with a broken tip. In addition, various types of body ornamentation were discovered, including beads (perforated pebbles, shells, animal teeth, fish bones) and an incised bone shaft. Some ornaments are covered with ochre. In other areas of the world—for example, in West-

ern Europe and East Asia—the production of similar organic objects and ornaments has been suggested to serve as an important mark of modern behavior (Mellars 2006; Norton and Jin 2009; Pei 1990; Qu et al. 2013).

A similar cultural complex is attested at Xianrendong Cave, Liaoning Province, in northeast China. The cave yielded stone artifacts, bone objects, ornaments, human-modified (percussed) bone fragments, and ashes. Compared with Zhoukoudian Upper Cave, the lithics are more numerous but follow the same basic knapping technology. The artifacts are made of quartz pebbles. The tool kit is diversified and includes scrapers, points, awls, burins, choppers, and spheroids. Of all, scrapers are found in the highest frequency. The osseous industry includes one harpoon, one projectile point, and a couple of well-shaped needles. The body ornaments include perforated teeth and shell beads (Zhang et al. 1985).

This technocultural complex is widely spread in the caves and open-air sites of the northeast, for example, in Sifang Cave, Tashuihe, and Xiaonanhai. They are estimated to date to the early phases of the Upper Paleolithic and display a new subsistence pattern in this region (An 1965; Chen 1989; Y. P. Wang 2005).

In the northwest, a series of open-air sites, dated around the Last Glacial Maximum (LGM), are spread throughout the region, but the main concentration appears post-LGM. The landscape is covered with grassland or desert/grassland with limited plants. Hunting is viewed as an important method for food acquisition, and some lakeshore sites of this region are identified as base camps of hunter-gatherers. For example, Salawusu (Inner Mongolia) is a cluster of localities that yielded small-size stone tools made on the pebbles of siliceous rock. The tools are intensively and well retouched into various types, including side scrapers, end scrapers, points, burins, and awls. Scrapers dominate the tool assemblage, but end scrapers are the most standardized type. Knapping is practiced with simple core and flake technology as it was in earlier periods. Evidence for specialized hunting has been recovered from Salawusu (Huang 1989; Y. P. Wang 2005). For example, in the Fanjiagou locality alone, 300 horns of antelopes were uncovered.

The site of Shiyu in the same region provides further evidence of specialized hunting. The site yielded rich faunal remains including over 200 individuals of wild horses and wild donkeys. The lithic industry is similar to that of Salawusu. Raw material was directly knapped with hard hammer. Irregular flakes with triangular- and trapezoid-shaped ones were also produced. It has been suggested that the lithic industry and the subsistence patterns of the human foragers at the site indicate persistence in traditional technologies along with the emergence of new behaviors; the latter is best reflected in the discovery of a body ornament in the form of a pendant (Jia et al. 1972).

Technological and behavioral transformations become evident in the Yellow River basin around 30,000 years ago. These are best reflected in the cluster of the Shuidonggou (SDG) sites 1–12 (Li 2013; Pei et al. 2012). In SDG Locality 1, the earliest layers contain assemblages composed of Levallois and

blade techniques (Boëda et al. 2011), whereas the upper layers are dominated by the core and flake industry that is common in North China. A somewhat similar situation was recorded in SDG Locality 2, where in two of the earliest layers—dating to 34.4 to 32.6 kyr cal BP—the lithic industry is dominated by cores and flake production, and yet rare blades and blade cores are also present. Ostrich eggshell beads appear in the later deposits dating to 31.3–29.9 kyr cal BP (Li et al. 2013). In SDG Locality 7, dated by optically stimulated luminescence (OSL) between 30,000 and 22,000 years ago, the basic industry is represented by cores and flakes, although it was subjected to fluvial disturbance.

In all SDG localities, good-quality raw materials, including dolomite and chert, were exploited. The tool assemblages are made up of end scrapers, notches, points, and various type of scrapers. Given the absence of such a technocultural complex from the previous period, it is commonly accepted that material culture from the earliest layers in SDG Localities 1 and 2 were produced either by migrating populations or as a result of cultural exchange between immigrants and local people (Bae and Bae 2012; Gao et al. 2002). In regions to the northwest, such as Mongolia, lithic assemblages were dominated by the Levallois technique. Within China the effect of these techniques has been noted only occasionally (Li et al. 2013). The persistence of the core and flake industry means that the local tradition and possibly the indigenous population eventually dominated.

During the LGM, microblade technology appeared in the north and northwest and broadly spread throughout the north of China, surviving there until the end of the Pleistocene. The earliest microblade evidence was found at the sites of Xiachuan, Dingcun, and Shizitan in Shanxi Province (Qu et al. 2013). Two types of microblade cores were present. One is labeled as "boat-shaped," the other as prismatic; in addition, other types, such as wedge-shaped cores, were present. Bladelets removed from these cores were sometimes retouched. The tool kits also include end scrapers, occasionally backed knives, burins, and small bifacial foliates (Y. P. Wang 2005).

Major examples of microblade technology are concentrated in the Nihewan Basin, for example, at the sites of Hutouliang, Youfang, and Jijitan. Hutouliang was discovered in the 1960s, and the sequence contained a large number of lithics, especially microblades and wedge-shaped microblade cores. The site was dated to about 15,000 years ago by ^{14}C and OSL methodologies. End scrapers dominate the tool assemblage, but scrapers, notches, points, and burins are also present. Tools are elegantly retouched. Abundant ornaments including perforated shells, pebbles, ostrich eggshells, and bird bones are present in the assemblage. Fireplaces were discovered at all sites, often with bone fragments scattered around them. Many sites in the Nihewan Basin display similar technological traditions and material culture (Wang 2000; Y. P. Wang 2005). I should note that the wedge-shaped core technology is very different from the former boat-shaped or prismatic core technology and is closely related to the microblade technology of northeast Asia and North

America. This is the industry of (one of) the migrating waves of humans arriving first in the Japanese archipelago and later in North America (Bae 2010; Ono 2004).

Central China

During the last 2 decades, many new Paleolithic sites have been excavated in Central China, including Zhijidong (Wang 2008*b*), Zhaozhuang (Zhang et al. 2011), Laonainaimiao (Peking University, School of Archaeology and Museology of Peking University, Institute of Archaeology of Zhengzhou 2012), Xishi (Wang et al. 2011), and Lijiagou (Peking University, School of Archaeology and Museology of Peking University, Institute of Archaeology of Zhengzhou 2011). These sites are located in the region of Zhengzhou, the capital of Henan Province, immediately south of the Yellow River. The region, traditionally referred to as a part of the "Central Plains of China," is situated on an assumed main crossroad of early human migrations between

the East and the West as well as between North and South China (fig. 1). Except for Zhijidong Cave, these localities are open-air sites embedded in the loess, forming the well-known loess plateau of northern China.

Zhijidong Cave is located in the hilly region within the Mount Song range. The sedimentary sequence is over 20 m thick. The recently excavated area near the cave entrance is divided into nine layers. The lower unit (layers 8 and 9) yielded cobble tools (Wang 2008*a*) and is characterized by a higher frequency of heavy-duty tools such as choppers. Large pieces of quartzite and sandstone from locally available cobbles were primarily used, while quartz and chert are rare. On the other hand, layer 7 in the upper unit is characterized by flake tools. This layer was dated to ca. 40,000–50,000 years ago by ^{14}C and OSL. The lithics are mainly made of quartz and chert, and only a few quartzite and sandstone cobbles were used. It is worth noting that chert and quartz were exploited and transported from places between 5 and 30 km away from the site. Cores are directly knapped and
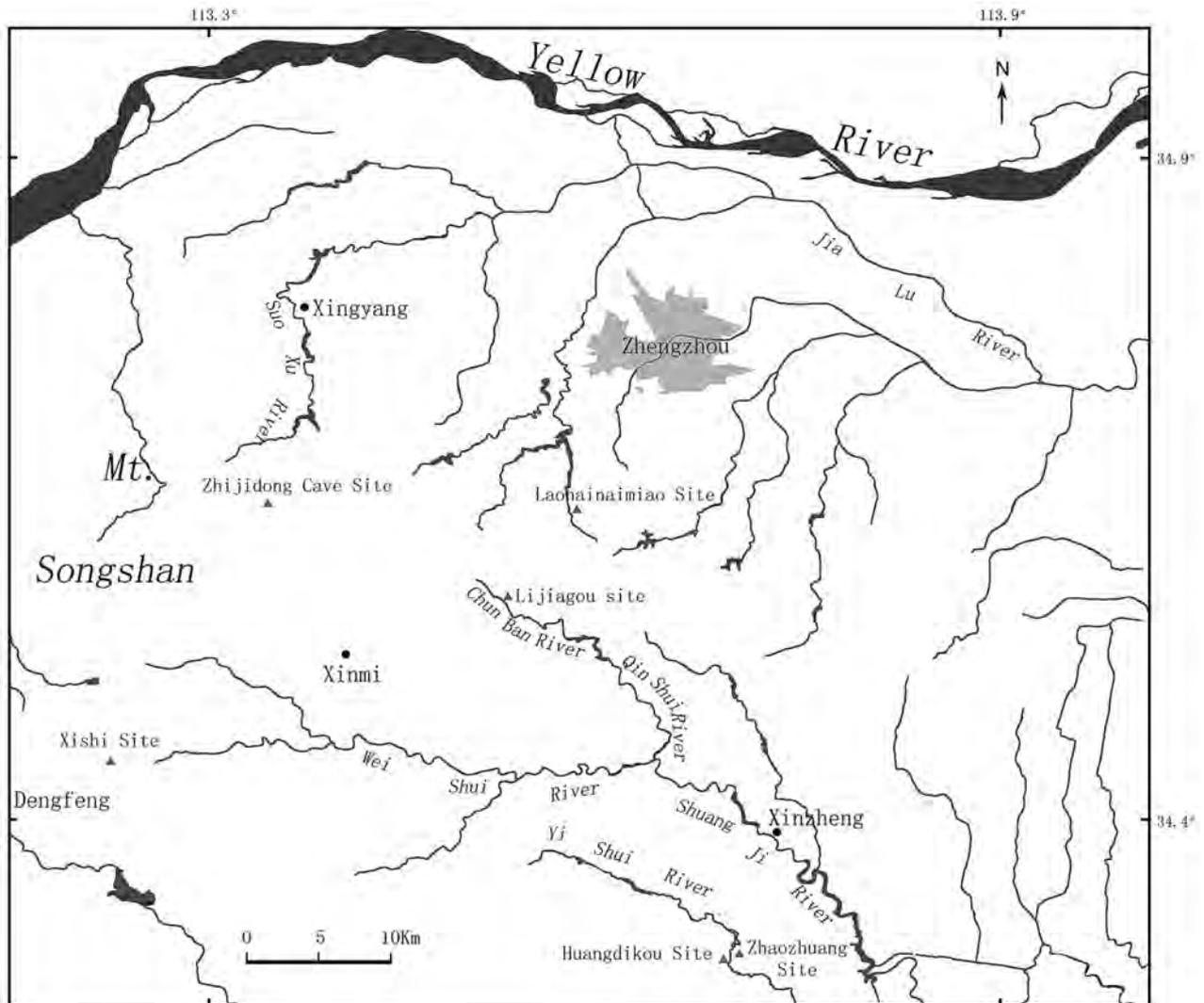

Figure 1. Geographic distribution of sites in Central China (triangles). A color version of this figure is available online.

are mostly of irregular shape. A few of them were produced by the bipolar technique. Several thousands of retouched pieces, classified as side scrapers, end scrapers, notches, awls, burins, and choppers were discovered.

Laonainaimiao is situated on the loess plateau along the banks of the Jialu River. The site has been excavated since 2011, and the exposed sequence contains 13 layers, demonstrating a consistent human occupation from 45,000 years ago based on ¹⁴C and OSL readings. Layer 2 preserved a hearth rich in charcoal and ash and surrounded by animal-bone fragments and lithics. Layer 6 contained four fireplaces that formed a half-circular structure. The site has yielded a lithic assemblage of about 5,000 pieces characterized by the use of quartz sandstone and quartz. Quartz sandstone flakes are found in high frequency, but retouched pieces are less common. Most cores are multiplatformed and knapped by simple techniques without any indication of core preparation. The tool kit contains small-size side scrapers and points. In addition, over 10,000 fragments of animal remains were recovered, many of which are about 10 cm in length. The size and shape of the bones appear to be suitable for handheld use. Some fragments bear knapping scars and use wear. The primary identified faunal taxa include Equidae, Bovidae, and Cervidae. Several bones are human modified; carnivore and rodent gnawing marks are rarely seen. In addition to mammalian fauna, plenty of ostrich eggshells have been recovered from the site. Faunal analysis combined with the presence of over 20 hearths indicates that the site was a long-term base camp (Wang and Qu 2014).

Zhaozhuang is located on the third terrace of the east bank of the Yishui River. The stratigraphy is divided into seven layers, and the main body of the cultural unit is layer 7, which is composed of whitish-gray clay sand. It dates to about 35 kyr cal BP. The recovered lithics amount to over 5,000 pieces. Quartz and quartz sandstone were exploited for tool production, but quartz is the most dominant type. The quartz artifacts, the majority of which are smaller than 5 cm, include cores, flakes, chunks, and chips as well as scrapers, points, and choppers. Quartz sandstone artifacts are on average larger than 15 cm in length. Most quartzite material is knapped or broken into blocks, and only a few are retouched.

Next to the lithic workshop, a pile of stone blocks with an elephant skull on top was uncovered. The elephant skull, quartz sandstone, and quartz artifacts exhibit a south-north distribution. When it was recovered, the elephant skull was in a fragmented condition either as a result of postdepositional processes or by human activity. Most quartz sandstones underlie the skull, but some were also spread around it. Overall, it is possible that the stone pile was purposely erected to support the elephant skull. The large blocks of purple-red quartz sandstones were removed and carried to the site from the bedrock of Xing Mountain, about 5 km away. It is clear that the transport of these rocks was intended for the construction of the stone pile instead of producing stone artifacts.

Xishi is located on the second terrace of the upper Weishui River and was excavated in 2010. Dating to ca. 25 kyr cal BP,

it yielded 8,500 lithics with clear evidence of blade production. Blades were concentrated in an area of 6 × 4 m in the northeast part of the excavation. The lithic assemblage contains hammer stones, cores, flakes, blades, bladelets, retouched pieces, and chert nodules. The collection is dominated by incomplete flakes, chunks, and chips. Most blades and blade cores may have been carried away by foragers when they moved to other sites (Wang et al. 2011). Some cores and flakes can be refitted, shedding light on the blade-knapping process. The typological and technological attributes of the lithics as well as their spatial distribution document a clear operational sequence of blade production.

Thousands of flakes were recovered at Xishi, and the frequency of typical blades exceeds 20%. Flakes with rejuvenated platforms and what may be considered as "the first blade of blade-core knapping" characterize the assemblage. With regard to the cores, blade core and blade-core fragments are dominant. Retouched pieces are present but in low frequency. The tool kit is composed of end scrapers, side scrapers, burins, and points; end scrapers dominate the assemblage. The majority of the raw material is chert, which was easily obtained from the bedrock near the site.

South China

The Upper Paleolithic in the south developed along a different trajectory apparently due to the peculiarities of the natural environment. In the southwest, the number of sites increases remarkably, and the material culture diversifies with the addition of bone and antler objects in the assemblages. The lithic industry does not show major differences from that of the local tradition of simple core and flake production. The cave inhabitants in the area of Yunnan-Guizhou Plateau used small-flake technology to produce tools, and their tool kit is dominated by scrapers. On the other hand, foragers living nearby, in the Sichuan Basin, tended to directly knap and retouch large cobbles into choppers and scrapers (Wang 1998).

In the surrounding area of the Nanling Mountains, cobble-tool industry was produced in the early MIS 3. This lack of change in the production of lithic tools may be best explained as a human adaptive strategy to this favorable environment where food and wood or bamboo resources were plentiful. However, at Bailiandong Cave in Liuzhou (Guangxi Province), Xianrendong Cave (Jiangxi Province), as well as other caves and open-air sites, small-flake-tool assemblages emerged suddenly during the late MIS 3. The number of small-flake tools continues to increase until the beginning of MIS 2. The presence of small-flake-tool assemblages, with the same flaking technique and tool types as those found in North China, may indicate the southward arrival of new populations from the north of the country.

The small-flake-tool industries were replaced with cobble tools at the beginning of MIS 2. The new industry, dominated by choppers, is different from the earlier traditional local cobble-tool industry. For instance, disk-shaped choppers appear in

the assemblages, whereas large points are not present anymore (Wang 1997).

Discussion

The Qinghai-Tibet Plateau

The Qinghai-Tibet Plateau and the large desert area to the north of this high-altitude region appear to be almost isolated from the Eurasian continent during the Pleistocene. The Qinghai-Tibet Plateau was not as high as it is at present during the early Pleistocene (Fang and Li 1998; Li 1988*a*, 1988*b*; Pan et al. 1998), and early migratory populations along both sides of the plateau would have been able to cross this natural boundary. However, the uplift in the succeeding period seems to have made human migrations more difficult. This is often pointed out by scholars to explain why East Asia exhibits unique lithic technology, material culture, and patterns of human adaptation (Gamble 1993; Lycett and Norton 2010; Wang 1995, 2001, 2003; Zhou et al. 1991).

The tempo and intensity of the Qinghai-Tibet Plateau uplift as well as its effect on human adaptation and migrations has attracted numerous discussions over the years. Some researchers suggested that the plateau raised and reached its present height ca. 7–8 mya (Harrison et al. 1992). Recent evidence shows that the desertification of Asian hinterland at least 22 mya could have been the result of this uplift (Guo et al. 2002). However, dramatic plateau uplift is also recognized to have occurred during the Pleistocene based on a series of recent multidisciplinary research efforts. These point to the fact that the plateau reached its present height after three tectonic events during the late Cenozoic; the Qinghai-Tibet tectonic event (3.4–1.7 mya), Kunlun-Huanghe (1.1–0.6 mya), and the Gonghe tectonic event (0.15 mya; Pan et al. 1998). The plateau thus separated China and East Asia from the western part of Eurasia into a relatively isolated geographic region during the Pleistocene. This uplift is also believed to have led to the development of the Asian Monsoon, causing global climate change (Fang and Li 1998).

Based on current evidence, the earliest human occupation in China and East Asia took place at least ca. 1.66 mya. The Lower Paleolithic industries in North China follow the flake-tool tradition and consist of scrapers, points, and other light-duty tools made on flake blanks. The flake-tool technology continued to exist with no obvious change from the Early to the Late Pleistocene in north and southwest China. In the meantime, several hundred localities with core-chopper industries were found recently along the river valleys of central and southern China. These consist of choppers, picks, and spheroids as well as other heavy-duty tools. The core-chopper industries continued to develop from the late Early Pleistocene to the early Late Pleistocene.

Comparative studies of Paleolithic industries between China and the western part of Eurasia indicate that connections between the East and the West existed probably before 1 mya as evidenced by the appearance of similar, simple lithic techniques and similar components of the lithic assemblages, sometimes referred to as "Mode 1 technology." These sites offer evidence for the first human migrations from Africa to China and East Asia (Wang 2003).

Cultural and genetic bottlenecks between the two parts of the Old World must have occurred during the period from the late Early Pleistocene to the early Late Pleistocene. Mode 1 technology was quickly replaced by Acheulean industries (Mode 2) technology in the West, while the core-chopper and flake-tool industries continued to exist in the East for much longer. Such different technological trajectories persisted in the two sides of the Qinghai-Tibet Plateau until the early Late Pleistocene.

The Late Pleistocene Human Migration

With the onset of the early Late Pleistocene, Mousterian industries dominated many parts of western and central Eurasia while core-chopper and flake-tool traditions continued existing in China. The so-called Chinese Middle Paleolithic was, in fact, a continuation of the previous core-chopper and flake-tool traditions, different from the Mousterian industries in the West (Gao and Norton 2002). It seems, therefore, that two evolutionary paths succeeded the earliest Mode 1 technology: the Acheulean and Mousterian in the West, and core-chopper and flake-tool industries in the east of Eurasia.

It is also apparent that during the late phase of the Late Pleistocene, the simple core-flake technology still persisted in many regions of China. This cultural separation of China from the West comes to an end in this period evidenced by the emergence of blade and microblade industries in North China. The appearance of this new technology indicates a new cultural transformation that was either adopted by indigenous populations by means of cultural diffusion or was brought into this region as a result of demic diffusion, that is, with the arrival of new human migrants (Bae and Bae 2012).

It is often suggested that blade and microblade technology in East Asia was introduced by populations who entered northwest China and East Asia from Siberia (Bae 2010; Bar-Yosef 2015; Ono 2004; Qu et al. 2013). Given the barrier set by the Qinghai-Tibet Plateau and the vast desert of Central Asia, this means that the dispersal of modern humans must have taken place through the northern path, which was covered with grassland. However, deciphering migration routes and how the migrants succeeded in East Asia requires further evidence as well as consideration of the southern route for modern human dispersals, that is, the possibility of human movements south of the Himalayas.

In Central China, the paleoenvironmental record reveals a forest/steppe landscape between 50 and 40 kyr BP (Liu et al. 2008). The occupants at the lower and upper units of Zhijidong did not seem to witness an environmental change. Among the various markers of modern human behavior, the transportation of raw material over long distances, the high frequency of well-retouched tools, and the expansion of territory are clearly

identified in Zhijidong's upper unit. These new elements of human behavior and adaptation at Zhijidong are very likely to have emerged as a result of the arrival of new human groups in the area (Wang 2008b).

The replacement of large cobble tools by small-flake tools is also commonly seen at other sites in the southern part of North China as well as in South China. The same reason that explains the emergence of small-flake-tool industries in the surrounding area of the Nanling Mountains during the late MIS 3—that is, the expansion of modern human groups from the north of the country southward—applies here as well. Hence, it appears that the transition from the Middle Paleolithic and the emergence of the Upper Paleolithic in China and East Asia differs from that in western Eurasia (Wang 2003); in the former case this involves the transition from cobble tools to flake technologies, while in western and central Eurasia the transition is typified by the change from Mousterian to blade-based technologies.

Conclusions

China is a vast land where early humans survived since the Early Pleistocene, and the abundance of material culture demonstrates a biological evolution sometimes considered separate from the rest of Eurasia. Recent research on the Qinghai-Tibet Plateau provides a geographic boundary one needs to consider when reconstructing possible hominin dispersal routes into and through China. New archaeological discoveries include many Late Pleistocene sites, from the loess plateau in North China to a number of river basins in South China, and provide detailed information about human dispersals in this region.

Small-flake-tool assemblages suddenly emerged in the surrounding area of the Nanling Mountains during the late MIS 3 period. This could be interpreted as evidence of a late Late Pleistocene human dispersal from North to South China. In addition, blade industries from Siberia or northwest Asia first arrived in the northwest of China during the late MIS 3 and then reached Central China about 25,000 years BP. Similarly, the wedge-shaped microblade core industries found in the Nihewan Basin may represent another migration wave from Siberia and northeast Asia to North China. Summing up, based on the current archaeological record, several hominin dispersal episodes, mainly occurring from north to south, affected China during the Late Pleistocene.

Acknowledgments

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Late Pleistocene Human Evolution in Eastern Asia

Behavioral Perspectives

by Christopher J. Bae

A deeper understanding of the eastern Asian Late Pleistocene paleoanthropological record will contribute to some resolution of the modern human origins debate. Here, I review the current state of the Late Pleistocene behavioral record with a particular focus on the Korean and Japanese records. In addition to questioning the applicability of the three-stage (Lower/Middle/Upper) Paleolithic sequence in the region and advocating a two-stage model (Early/Late), I add a number of behaviors to the definition of the eastern Asian Late Paleolithic, traditionally defined based on the appearance of blade-tool technology. In particular, any definition of this cultural period for this region should include the appearance of tanged points, ground stone tools, trap-pit hunting, and importantly, watercraft. Tanged points and trap-pit hunting represent an expansion of the Late Paleolithic foragers' diet breadth and an increased effectiveness in hunting large game. As well, ground stone tools, which included ground axes used for felling trees and woodwork, probably contributed to the building of sturdy watercraft necessary to make oceanic voyages. Finally, I briefly discuss the arguments for and against the pre-50,000 ka occupation of eastern Asia by modern *Homo sapiens* with a focus on four specific sites that are proposed to support the pre-50 ka model: Huanglong Cave, Fuyan Cave, Luna Cave (all in China), and Callao (Philippines).

When, how, and by which route did modern *Homo sapiens* (MHS) move out of Africa and into the novel environments of regions such as eastern Asia continue to be points of major debate in paleoanthropology (Bae, Petraglia, and Douka 2017; Bae et al. 2014; Di and Sanchez-Mazas 2011; Kaifu, Izuho, and Goebel 2015; Liu et al. 2010*a*, 2010*b*, 2015; Michel et al. 2016; Norton and Jin 2009; Stringer 2002; Trinkaus 2005). In general, support seems to be waning for the traditional multiregionalism (Etler 1996; Pope 1992; Wolpoff, Wu, and Thorne 1984) and no interbreeding replacement models (Stringer and Andrews 1988). Questions still remain, however, as to what was the nature of the interactions between modern humans moving out of Africa and indigenous mid-Pleistocene *Homo* and other groups such as the Denisovans in Asia (generally, variations of the assimilation/hybridization models; C. J. Bae 2010; Bae et al. 2014; Liu et al. 2010*a*; Trinkaus 2005; Wu 2004). Recent genetic studies support the case for at least occasional, if not regular, interbreeding occurring between MHS, Neanderthals, and Denisovans, with the MHS genome containing an estimated 1.5%–2.1% Neanderthal DNA (Green

et al. 2010; Prufer et al. 2014; Reich et al. 2010). Although the assimilation/hybridization model or a more flexible version of the replacement model that allows for continuous gene flow between these different populations appears to have the most support from the genetic, archaeological, paleontological, and geochronological records, still not clear are which route, the timing, and whether a single dispersal event or multiple dispersals out of Africa best explain the Late Pleistocene human evolutionary record in eastern Asia.

According to traditional models, MHS did not arrive in eastern Asia until after 50 ka (Klein 2008). For instance, based on a purported absence of hominin fossils, Jin and Su (2000) argued that mid-Pleistocene *Homo* went extinct in China around 100 ka, and then following a 60,000 year gap, MHS suddenly arrived on the scene after 40 ka. Although the Jin and Su (2000) hypothesis has been contested based on hominin fossil findings from sites such as Huanglong Cave (Liu et al. 2010*b*), Luna Cave (Bae et al. 2014), and perhaps Fuyan Cave (Liu et al. 2015; but see Michel et al. 2016) and related archaeology (Norton and Jin 2009), similar arguments continue to appear in the literature. Indeed, Kaifu, Izuho, and Goebel (2015:545) recently concluded that "there is no compelling paleoanthropological/ archaeological evidence of *H. sapiens* prior to 50 ka anywhere in eastern Asia," suggesting there is not full support for the pre-50 ka appearance of MHS in eastern Asia. The question remains, however; is this evidence of absence or an absence of evidence?

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Although important not to confuse MHS morphology and behavior (Lieberman and Bar-Yosef 2005), one aspect of modern human origins models that is receiving increasing attention is the contribution of the hominin behavioral record. There is a wide diversity of archaeological signatures that are considered representative of modern human behavior that are outlined in detailed reviews elsewhere (Henshilwood and Marean 2003; McBrearty and Brooks 2000; Mellars 2015). These archaeological traces form what is commonly referred to as a trait list and include behaviors such as symbolism, long-range planning, a more sophisticated tool kit, and a more diversified diet breadth. Besides the relatively in-depth understanding of the Western Old World archaeological records, regionally focused reviews of the eastern Old World have been published over the past decade or so (e.g., Habgood and Franklin 2008; James and Petraglia 2005; Norton and Jin 2009). These regional reviews are contributing to a better understanding of the Late Pleistocene human behavioral record. Some questions these reviews answer or attempt to answer include the following: If modern humans were moving into a region occupied by other hominin populations, did the former group have a different behavioral package that perhaps gave them some type of advantage over the indigenous populations? Further, does the appearance of MHS coincide with the appearance of so-called modern human behaviors in eastern Asia?

There have been suggestions that paleoanthropologists need to move away from a trait list of traditionally accepted modern human behaviors and perhaps examine these data through a different lens (e.g., Henshilwood and Marean 2003; Marean 2015; Shea 2011). However, Mellars (2015) recently noted that at the end of the day these so-called more theoretical approaches still rely on the same data that form the foundation of any trait list (e.g., presence/absence of certain types of symbolic behavior). This raises the valid point that it is still important to identify so-called trait-list data before applying a different theoretical spin to try to answer broader-ranging questions. In other words, it is probably better to try to answer the what, when, and where questions before tackling the more difficult why query, though this certainly does not mean one should never attempt to answer the processual why question. In fact, it may even be argued it is a difficult task to apply a more theoretical approach to a geographic region where the human evolutionary record is not nearly as well known (e.g., eastern Asia vs. Africa and Europe; Kaifu, Izuho, and Goebel 2015; Norton and Jin 2009). Thus, there is still some utility in identifying the nature of the record of a specific spatial-temporal point before trying to apply novel approaches to answer the same questions.

Here, I focus my attention on the Late Pleistocene behavioral record of the Korean peninsula and the Japanese archipelago and where applicable, the Chinese mainland. The reason for the focus on the eastern edge of the Asian mainland is that there are many interesting findings in this region of the world that suggest perhaps a reformulation of the definition of the Late Paleolithic in the region may be necessary. In particular, in addition to the appearance of blade technology after

40 ka, additional tools and behaviors appear as well around the same time and often in the same contexts (e.g., tanged points, ground stone tools, oblique trapezoids, trap pits). Further, as pointed out by others (e.g., Kaifu, Izuho, and Goebel 2015; Norton and Jin 2009; Norton et al. 2010*b*), Japan was almost surely peopled initially by means of watercraft, which is generally considered evidence of modern human behavior (Davidson and Noble 1992). The locations of the primary sites mentioned in the text are found in figure 1.

In this paper I use the Gao and Norton–defined Early and Late Paleolithic to divide up the eastern Asian Late Pleistocene archaeological record, the primary trait being the appearance of blade technology after ~40 ka (Gao and Norton 2002; see also Norton, Gao, and Feng 2009). In fact, it is still common to see Middle and Upper Paleolithic in the eastern Asian prehistoric literature (e.g., Bar-Yosef and Wang 2012; Kaifu, Izuho, and Goebel 2015; Sato 2016), and arguments for the continued use of the European-derived three-stage behavioral model appear occasionally (e.g., Yee 2012). However, there is support for the two-stage behavioral sequence (e.g., Li 2014). Indeed, in reviewing the Korean Paleolithic record, Seong and Bae (2016) found that similar criteria used to define the Chinese Middle Paleolithic (e.g., presence or absence of mid-Pleistocene *Homo*; geochronology) are also used in Korean Paleolithic research. This led them to draw the conclusion that as with the Chinese record, the Korean record should also be divided into two stages: Early and Late Paleolithic (Seong and Bae 2016). Thus, it is not too surprising that a growing number of Western-trained Korean Paleolithic researchers support the two-stage model (Bae and Bae 2012; Bae and Kim 2015; Seong 2015; Seong and Bae 2016). Before continuing, it would be useful to briefly revisit the original Gao and Norton defined–Early and Late Paleolithic (Gao and Norton 2002).

Semantics in "Paleolithic" Studies in Eastern Asia

Ikawa-Smith (1978) was one of the first prehistorians to note that the three-stage behavioral model developed for the European Paleolithic record is not easily applied to the eastern Asian record. Gao and Norton (2002) examined this question more closely using the Chinese "Middle" Paleolithic record as a case study. They concluded that although there are changes between the Lower and Middle Paleolithic, these changes are subtle and not sudden as might be expected with a major behavioral transition. Further, they noted that there is an absence of a specific behavioral marker (e.g., the presence of Levallois technology that defines the Middle Paleolithic in the Western Old World) that can distinguish a distinct Middle from a Lower Paleolithic tradition in China. Even when the Levallois technology appears in northern China, it appears around the same time as the introduction of blade technology in the region. Gao and Norton (2002:410) concluded that "a distinct 'Middle Paleolithic' cultural period does not exist in China." Norton, Gao, and Feng (2009) further found that simply changing the chronology of a lithic assemblage could possibly
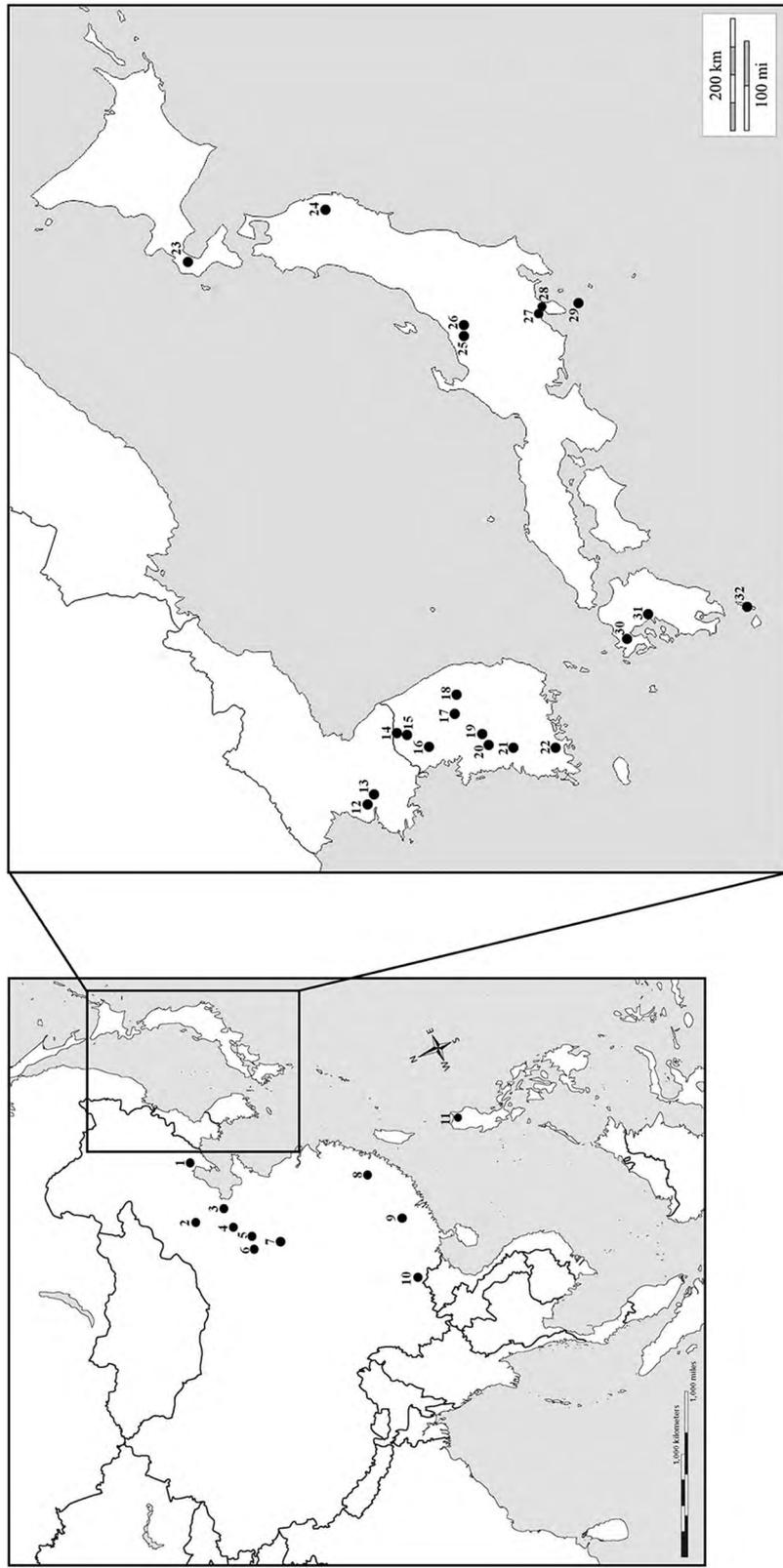
Figure 1. Locations of sites mentioned in the text. *1*, Xiaogushan; *2*, Xujiayao; *3*, Zhoukoudian Upper Cave, Zhoukoudian Locality 15; *4*, Dingcun; *5*, Dali; *6*, Longwangchan; *7*, Huanglongdong; *8*, Chuanfandong; *9*, Fuyandong; *10*, Lunadong; *11*, Callao; *12*, Ryonggok; *13*, Mandalli; *14*, Jangheun-ri; *15*, Hwadae-ri; *16*, Sam-ri; *17*, Songam-ri; *18*, Suyanggae; *19*, Yongho-dong; *20*, Yongsan-dong; *21*, Galsanri; *22*, Sinbuk; *23*, Pirika; *24*, Kanedori; *25*, Tategahana; *26*, Hinatabayashi B; *27*, Idemaruyama; *28*, Hatsunegahara; *29*, Kozushima; *30*, Hirasawara; *31*, Ishinomoto; *32*, Otsubobata.

move the site from the Middle Paleolithic to the Lower or Upper Paleolithic. The broad range of chronological ages from Zhoukoudian Locality 15, Dali, Dingcun, and Xujiayao were cited as examples. The primary conclusion drawn from the Norton, Gao, and Feng (2009) study was that geochronology cannot be used as a core criterion to define a behavioral stage. In their recent evaluation of the Korean Paleolithic record, Seong and Bae (2016) found many similar problems with the use of the term "Middle Paleolithic" by Korean archaeologists. They concluded, as others have, that Middle Paleolithic should be dropped from the eastern Asian literature until it is shown that it can be unambiguously defined. Clearly, these observations are applicable to broader eastern Asia and not just restricted to the Chinese and Korean Paleolithic records.

Unfortunately, archaeologists in other regions of eastern Asia appear to continue to use the terms "Middle" and "Upper Paleolithic" indiscriminately (Seong and Bae 2016). For example, any casual review of the Japanese Paleolithic literature will see the term "Upper Paleolithic" in the title of the paper for analyses focused on sites and materials that postdate 30 ka (e.g., Abe 2006; Suzuki and Yasuo 2006). Anything older than 30 ka is then assigned to the Middle or Lower Paleolithic (e.g., Sato 1992; Matsufuji 2001; Shimada 2010). Even papers that draw the conclusion that the Levallois method is not present in Japan assert that a Middle Paleolithic is present but just needs to be defined using other lithic criteria. For instance, Sato, Nishiaki, and Suzuki (1995:497) concluded that the "Levallois in Japan seems to be a myth created by a combination of inadequate artifact samples from old excavations and the presupposition that Levallois must have been used in the Middle Paleolithic." Granted, much of the data used by Sato, Nishiaki, and Suzuki (1995) to support a distinct Lower and Middle Paleolithic in Japan stemmed from the supposed "legitimate" sites from Miyagi Prefecture, sites and materials that were exposed in 2000 as a complete hoax. However, even some recent papers continue to include "Upper Paleolithic" in their titles (e.g., Ikeya 2015; Izuho and Kaifu 2015). Perhaps this is not that unexpected as Izuho and Kaifu (2015:292) note, "the principles of Paleolithic study [in Japan] were imported mainly from France." Thus, as with the cases of the European influence on the development of Paleolithic research in China and Korea, it is not that surprising that Japan also follows the three-stage behavioral model developed in France (Gao and Norton 2002; Seong and Bae 2016). Interestingly, not all Japanese researchers have supported the three-stage Paleolithic model even when the field of study was still in its formative stages. For instance, the founding father of Paleolithic research in Japan, Chosuke Serizawa, advocated early on for an Early and Late Paleolithic with the division around 30 ka, with others following suit (e.g., Ikawa-Smith 1978, 2008; Imamura 1996). Thus, it would be interesting for Japanese researchers to conduct a critical review of the data and formulate a new definition of how they define the Paleolithic, because as others have noted, the Western Old World definition of the Paleolithic may not be applicable to

much or even some of eastern Asia (e.g., Bae and Bae 2012; Gao and Norton 2002; Ikawa-Smith 1978; Seong and Bae 2016).

Following the two-stage behavioral model in eastern Asia as advocated here, the Early Paleolithic is represented by expediently made core and flake tools. These stone tools are usually produced by direct percussion on locally available quartz and quartzite river cobbles (Bae and Bae 2012; Gao and Norton 2002; Norton 2000; Olsen and Miller-Antonio 1992; Pei et al. 2013; Pope and Keates 1994; Zhang 1985). In addition to these simple core and flake tools, by the advent of the Middle Pleistocene, handaxes and later cleavers begin to appear sporadically in different regions of eastern Asia, although in certain morphological and metric aspects they appear different from traditional bifaces from the Western Old World (Corvinus 2004; Hou et al. 2000; Lycett and Bae 2010; Lycett and Norton 2010; Norton 2000; Norton and Bae 2009; Norton et al. 2006; Petraglia and Shipton 2009; Shipton and Petraglia 2010; Wang 2005; Wang and Bae 2015; Wang et al. 2012, 2014). No generally accepted bone-tool cultures or art and symbolic behavior are currently known from the Early Paleolithic (Norton 2000; Norton and Jin 2009; but see Gao et al. 2004 for one possible exception that dates to the Early Paleolithic).

After 40 ka, blade technology appears in the region, signaling the traditional introduction of the Late Paleolithic (Gao and Norton 2002; Izuho and Kaifu 2015; Pei et al. 2012; Seong 2009, 2015). Around 30 ka, microblades appear in the archaeological stone-tool kits in Korea and China, and combined with blades, they make up a dominant component of the stone-tool industries in the region (Bae and Bae 2012; Seong 2015). Microblades, however, do not appear on the Japanese archipelago until around the beginning of the Last Glacial Maximum (Imamura 1996; Kudo 2006; Nakazawa and Yamada 2015). During the Late Paleolithic, clear-cut evidence of symbolic behavior (e.g., perforated teeth and shells) and a diversified bone-tool industry, including a bone harpoon, appear at sites such as Zhoukoudian Upper Cave (Norton and Gao 2008*b*) and Xiaogushan (Norton and Jin 2009) in northern China. Bone artifacts, in association with microblades and a microblade core, are reported from the Late Paleolithic Mandalli site in North Korea, though other bone artifacts in South Korea have been questioned (Bae 2013, 2014; Norton 2000). As discussed below, additional behavioral components possibly specific to the eastern Asian record need to be included in any definition of the Late Paleolithic from the region.

The Uniqueness of the Eastern Asian Late Paleolithic

The advent of the Late Paleolithic in eastern Asia is normally associated with the appearance of blade technology ca. 40 ka. However, recent reviews have indicated that blade technology did not simply replace all of the traditional core and flake-tool industries in the region but in fact for the first 10,000 years or so made up only a small component of the overall lithic technology (K. Bae 2010; Bae and Bae 2012; Lee, Bae, and Lee 2017; Seong 2015). Only after 30 ka, with the initial ap-

pearance of microblades, do these types of stone tool appear more regularly and eventually phase out the more traditional Early Paleolithic–type large cutting tools and flakes. For further evaluation of the eastern Asian record, particularly when examining aspects of the Korean and Japanese records, other behavioral components should be considered a part of the Late Paleolithic; namely, watercraft, ground stone tools, tanged points, and trap pits. I discuss each of these in turn below.

Watercraft

Several sites from Japan (e.g., Kanedori, Sunabara, Ono) have been proposed to date to the first half of the Late Pleistocene and are considered to be among the oldest sites in the archipelago (Ikawa-Smith 2016; Kuroda 2016; Sato 2016; Uemine, Matsufuji, and Shibata 2016; Wada 2016). For instance, the Kanedori open-air site in Honshu that has basal dates placing it in marine isotope stage (MIS) 5 has been proposed as one the oldest sites in Japan (Kuroda 2016; Matsufuji 2010). Because there were no apparent land connections at that time between the Japanese archipelago and the Asian mainland, either through the Korean peninsula or eastern Siberia, Matsufuji (2010) proposed that the earliest evidence of hominin occupation of the archipelago could have been some time during MIS 6 when hominins may have been able to simply walk from the mainland to the archipelago. Indeed, Uemine, Matsufuji, and Shibata (2016:17) recently concluded that "so long as we find it unlikely that hominin migration to the Japanese archipelago took place over the open sea during the Last Interglacial stage, the hypothesis that they used the land bridge during the earlier glacial stage must be considered. These new discoveries in Shimane Prefecture would suggest that further exploration for archaeological sites dating to MIS 6 or even earlier is warranted." Nevertheless, questions do exist about the legitimacy of these proposed early sites in Japan. For example, questions have been raised about the legitimacy of the artifacts from the lowest level at Kanedori dated to between 84 ka and 68 ka based on associated tephra. To at least some observers, these artifacts appear to be geofacts (Norton and Jin 2009; Norton et al. 2010*b*).

The Kanedori case aside, there appears to be growing support that the earliest occupation of the Japanese archipelago occurred sometime during MIS 3, ca. 40 ka, which is clearly a time period when the only way to reach Japan would have been via the use of some type of watercraft departing from either the southern tip of the Korean peninsula or the eastern edge of Siberia (Kaifu, Izuho, and Goebel 2015; Norton and Jin 2009; Tsutsumi 2012). Further, this also includes the Ryukus island chain that does not appear to have been connected to either Taiwan or the main Japanese islands at any time during the Late Pleistocene (Kaifu et al. 2015). In fact, because of deep oceanic trenches separating the different groups of islands even within the Ryukus, watercraft were the only way to move between these different island groups. For instance, to move from Taiwan to the southern Ryukus would have involved a sea voyage of at least 105 km, and to travel from the southern to central Ryukus (Miyako to Okinawa) would have been a 220 km trip over open seas during MIS 3 (Kaifu et al. 2015). These long oceanic voyages would have been to destinations that may not have been visible from the points of departure.

Besides the clear evidence for an absence of any land connection during MIS 3 that may have connected the archipelago with the mainland, obsidian sourcing studies in Japan have also contributed to furthering our knowledge of early watercraft activity (Ikawa-Smith 2008; Ikeya 2015; Norton and Jin 2009; Suzuki 1974). In particular, obsidian sourced from Kozushima island, which currently lies some 50 km off the central-eastern side of Honshu, has been identified at the Idemaruyama site on the Izu peninsula that dates to 38 ka (Ikeya 2015). Because Kozushima was always separated from Honshu even during major glacial periods, the only way obsidian from that island could have reached Honshu is via human transport. Idemaruyama is one of the earliest accepted archaeological sites in Japan and roughly coincides with the earliest peopling of the peninsula. Interestingly, the Kozushima obsidian appears on Honshu for several thousand years then disappears for about 20,000 years only to reappear again during the Terminal Pleistocene (Ikeya 2015). This would suggest that different foraging groups, a focus on different obsidian sources, a loss of the knowledge of the Kozushima obsidian source, or some combination of the above reasons best explains the absence of this raw material from the archaeological record during this time period.

Ikeya (2015; see also Kaifu et al. 2015) also discusses the importance of understanding the influence of local sea currents on these earliest voyages, thus indirectly suggesting that the earliest occupants of the Japanese archipelago were fairly experienced seafarers by that time. These early sea voyagers may indeed have been looking for new resources. One such resource could have been megafauna, and the earliest peopling of the Japanese archipelago has been linked to the local extinction of various megafauna on the islands (Norton et al. 2010*b*).

Megafaunal extinctions in Japan. The extinction of the Late Pleistocene megafauna has been one of the most debated topics over the past few decades. In general, climate, humans, or some combination of both influences are cited for why megafauna disappeared from most regions of the Old and New Worlds, particularly in the past 50 ka (Barnosky et al. 2004; Burney and Flannery 2005; Martin 2005). Most evidence to support human-induced faunal extinctions are generally in geographically restricted areas such as small islands (Martin and Steadman 1999). Evidence for humans causing faunal extinctions in larger-sized islands (e.g., Madagascar, New Zealand) also exists (Burney, Robinson, and Pigott Burney 2003; Worthy and Holdaway, 2002). Continent-wide cases, though, are a bit more problematic as the evidence is not always as clear cut (Grayson and Meltzer 2002; Martin 2005). It may be possible

to link the effect of Late Pleistocene human dispersals across eastern Asia to the extinction of megafauna in areas like the Japanese archipelago (Norton et al. 2010*b*).

Japan is an interesting test case because there is fairly abundant evidence that humans only arrived there some time during MIS 3 (<50 ka), by boat, and at least initially in fairly small numbers (Norton and Jin 2009; Norton et al. 2010*b*). After 30 ka, there is a sudden proliferation of archaeological sites in the archipelago, where Paleolithic sites older than 30 ka number in the tens while Paleolithic localities younger than 30 ka are present in the thousands (Ikawa-Smith 2016; Sato 2016). The interesting point about the Japanese Late Pleistocene is that when human foragers first arrived, they encountered a diversity of megafauna, including *Paleoloxodon naumanni*, *Mammuthus primigenus*, and *Sinomegaceros yabei* (Hasegawa 1972; Iwase, Takahashi, and Izuho 2015; Kawamura 2007; Norton et al. 2010*b*; Takahashi and Izuho 2012). Earlier hypotheses (e.g., Kawamura 2007) suggested that megafaunal extinctions occurred during the MIS 2–1 transition and coincided at least in part because of the appearance of Jomon hunter-gatherers. However, more recent proposals, based on a better understanding of the dating of these fossils, indicate that these extinctions probably occurred during MIS 2 and possibly beginning during the MIS 3–2 transition. In all likelihood these megafaunal extinctions occurred well before the MIS 2–1 transition and the appearance of Jomon foragers (e.g., Iwase, Takahashi, and Izuho 2015; Iwase et al. 2012; Norton et al. 2010*b*; Takahashi and Izuho 2012). However, some of these studies have concluded that climate can singularly explain the extinction of the megafauna in Japan. Indeed, Iwase et al. (2012:122) concluded that "the process of Japanese megafaunal extinction can be explained *without* consideration of human influence" and "that the 'main' cause of [MIS 2] extinction on the Japanese Archipelago was climate-induced ecosystem changes" (emphasis added).

Nevertheless, not all agree that climate was the sole driver of megafaunal extinctions in Late Pleistocene Japan. For instance, Norton et al. (2010*b*) showed that the extinction rate between the Middle-Late Pleistocene and the Last Glacial Maximum–Early Holocene was significantly different in Japan, with a greater number of extinctions occurring during the latter transition ($\chi^2 = 5.562$, df = 1, $P = .017$). This raises the question, if climate was the primary driver causing megafaunal extinctions, then why did it not affect fauna as severely during the Middle to Late Pleistocene transition? Indeed, Norton et al. (2010*b*:116) proposed that "if extinctions were based primarily on climatic changes, we might expect there to be a higher extinction rate during MIS 6–5 than MIS 2–1 or at least a similar extinction rate." This is simply because the effect of the climatic transition during the former stage was as, if not more, persuasive than the latter. Thus, it is a bit surprising that none of the recent studies promoting a single-cause, climate-driven extinction model (e.g., Iwase, Takahashi, and Izuho 2015; Iwase et al. 2012; Takahashi and Izuho 2012)

attempts to address this pattern in the data. Another point that Norton et al. (2010*b*) raised and that is not addressed adequately by the climate proponents is the fact that after 30 ka, suddenly thousands of archaeological sites appear throughout the archipelago. Even if humans were not directly hunting these megafauna to extinction, the sudden human population increase could have indirectly caused their extirpation through contracting megafaunal home ranges and modifications to the environment, "which could have served to push said taxa into less hospitable regions" (Norton et al. 2010*b*:118) and presumably to eventual extinction, at least locally. This evidence suggested to Norton et al. (2010*b*) that clearly after 30 ka, human foragers were affecting megafauna in Japan and probably played a major role in causing their disappearance some time during MIS 2 and well before Jomon hunter-gatherers appeared. This should not be confused with cases of "rapid overkill" or even "overkill" as suggested by Iwase, Takahashi, and Izuho (2015) and never the idea proposed by Norton et al. (2010*b*). Needless to say, the earliest peopling of the Japanese archipelago does seem to have played some role in the eventual extinction of these megafauna.

Ground Stone Tools

Ground stone tools (axes and whetstones) were once considered restricted to and an important component of the Neolithic Revolution (Child 1958). However, we now know that ground stone tools have been identified in various areas of eastern Asia during the Late Pleistocene (Imamura 1996; Lee, Bae, and Lee 2017; Qu et al. 2013; Tsutsumi 2012). Paleolithic ground stone tools were initially found in the Japanese archipelago during archaeological reconnaissance and are by far the best researched and published in eastern Asia.

In Japan, more than 800 ground stone tools have been found from more than 200 archaeological sites (Tsutsumi 2012). Interestingly, these stone axes have only been found on Honshu and Kyushu but have yet to be identified in Hokkaido and the Ryukus. In general, these stone tools appear as early as 38 ka (Ishinomoto in Kyushu), disappear before the beginning of MIS 2, and then reappear during the Terminal Pleistocene (Imamura 1996), though slight variations on these dates are present (Tsutsumi 2012). Potential functions of these ground stone tools are debated. For instance, at the Hinatabayashi B site, 60 stone axes, with at least 36 identified as ground, were excavated. Microscopic use-wear analysis indicated the large axes were probably used for felling trees that would have contributed to the production of temporary settlements (Sato 2006). Microscopic analysis of the small axes suggests that they may have been utilized for scraping hides (Tsutsumi 2012). Interestingly, the small axes may have originally been large axes that were exhausted and could no longer function to fell trees, with the hypothesis that these spent large axes were purposely ground further down to create the small axes (Sato 2006; Tsutsumi 2012).

Late Paleolithic ground stone tools are beginning to be reported from the Asian mainland from countries such as China and Korea as well. For instance, in Korea, ground stone tools have been identified in at least nine Paleolithic sites to the point where the appearance of ground stone tools is no longer considered so unusual (Lee, Bae, and Lee 2017). Except for Galsanri, which dates to 40–30 ka, all of the sites in Korea date to MIS 2 (25–15 ka) and are found in association with blades, tanged points, and microblades. In the case of Galsanri, ground stone tools were found in association with blades and typical Early Paleolithic core and flake tools. Curiously, ground stones with cupholes, perhaps utilized in various grinding activities, were also identified at Galsanri (Lee, Bae, and Lee 2017). In China, ground stone tools were found at Chuanfandong (36–22 ka) and Longwangchan (>20 ka; Qu et al. 2013; Zhang et al. 2011). Chuanfandong is located in southern China, also a region where early plant domesticates appear. Thus, a reasonable functional interpretation for these ground stone tools may have been to process wild plants during the Late Pleistocene, though ground stone axes would certainly have a different function.

Although it is generally accepted that ground stone axes would have been used for felling trees to build settlement structures, it is also likely they served other functions. For instance, given the necessity to build sturdy watercraft to make these long oceanic voyages roughly 40 ka and the fact that the appearance of these ground stone axes roughly coincides with the earliest peopling of the Japanese archipelago, it would not be a great leap to suggest that the development of the latter facilitated the former. In particular, because ground stone axes in Korea appear to be penecontemporaneous with the earliest stone axes in Japan and because the earliest human dispersals to Japan probably originated from points of departure on the Korean peninsula, it seems reasonable that the technology could have been initially developed on the Asian mainland (e.g., in Korea) and used to facilitate the construction of the watercraft used to travel to Japan. The appearance of ground stone axes in such higher densities in the Japanese archipelago would simply be a function of the migrating human foraging groups that initially arrived on the islands including these tools among their regular tool kits.

Tanged Points

The appearance of blade technology in northern China, Korea, and Japan between 40 ka and 35 ka coincides with the introduction of tanged points in the latter two countries as well. This is clear evidence of a diversification of the tool kits that signals the advent of the Late Paleolithic in the region in addition to being very suggestive of interactions between different foraging groups and dispersals into new regions (Bae and Bae 2012; Chang 2013; Morisaki 2015; Norton and Jin 2009; Seong 2008, 2009).

More than 300 tanged points have now been identified from more than 30 sites on the Korean peninsula (Seong 2015). The primary raw materials are locally available hornfels and sili-

ceous shale, though a few bifacially worked tanged points produced on obsidian are known from the Suyanggae and Sam-ri sites (Seong 2008). The oldest tanged points in Korea are from the Yongho-dong site and date to 38.5 ka (Han 2002), while other slightly younger dated tanged points are from Songam-ri (ca. 33 ka) and Hwadae-ri (ca. 31 ka; Seong 2015). Interestingly, these early tanged points from Korea were produced on flakes rather than blades. Tanged points younger than 30 ka (e.g., Yongsan-dong), however, were produced on blades and often appear in the same context as blades and microblades (e.g., Jangheun-ri, Sinbuk). In Korea, tanged points appear continuously from 38 ka and then disappear from the archaeological record after the Last Glacial Maximum (Seong 2008, 2015). It is not clear whether tanged points are an indigenous development on the peninsula or the technology, as with general blades, originated from northern China, Mongolia, or Siberia.

A tanged point was initially identified in Japan at the Hirasawara site in Saga Prefecture in 1962 (Sugihara and Serizawa 1962). Since then, tanged points (in Japan, commonly referred to as "hakuhen-sentoki") have been found at many Paleolithic sites in Kyushu. Tanged points are also reported from multiple sites on Honshu and at least one site on Hokkaido (Pirika site in association with microblades; Chang 2013). The Kyushu tanged points, which are the best known in Japan, all postdate the appearance of Aira-Tn tephra ca. 30 ka but quickly disappear during the Last Glacial Maximum (Morisaki 2015). Although obsidian is readily available in Kyushu, these tanged points were also produced on other types of raw materials such as andesite, rhyolite, and chert (Morisaki 2015). Two primary hypotheses have been proposed to explain the appearance of tanged points in Kyushu: (1) the technology naturally developed from the indigenous blade technology (Sato 2000), and (2) the technology diffused from the Korean peninsula and probably reflects the movement of new foraging groups into the region (Matsufuji 1987). A recent analysis of the Kyushu tanged points and associated archaeology and dating suggests that the latter hypothesis is the correct one (Morisaki 2015). In particular, tanged points appear much earlier and the lithic industries are much more diversified in Korea, suggesting the technology moved to Kyushu, possibly carried by a second wave of foragers from the peninsula. Indeed, at sites in Kyushu that are closest to the Korean peninsula, the tanged points are morphologically very similar to Korean artifacts from sites such as Suyanggae (Chang 2013; Morisaki 2015).

Although evidence of fairly effective hominin predation dates to the late Middle Pleistocene at sites such as Xujiayao, which is associated with mid-Pleistocene *Homo* (Norton and Gao 2008b; Xiao et al. 2014), it is quite evident that the dietary breadth of Late Paleolithic foragers in the region was probably broader than during the Early Paleolithic (Norton and Gao 2008a, 2010b; Norton et al. 2007). The appearance of the tanged point in the archaeological record is thought to reflect an improvement in hunting technology primarily because hafting on to the ends of wooden spears probably provided a more effective killing capacity (Seong 2009; Shea 2006). Indeed, Seong (2008:878) noted that the "emergence of stone-

tipped spears marks an advance over organic ones, since stone-tipped spears can be thrown farther and penetrate deeper mainly due to their mass." Improvements such as these could have contributed to successful predation of larger game, including megafauna, in the region (Ellis 1997; Norton et al. 2010*b*; Seong 2008).

Trap-Pit Hunting

Directly related to the diversification of the hunting tool kit during the Late Paleolithic, trap-pit hunting appears in Japan during the MIS 3–2 transition (Sato 2012, 2015). Similar evidence has yet to be reported from Korea or China. Evidence of these archaeological traces was first identified in Japan at the Late Paleolithic Hatsunegahara site in Shizuoka Prefecture, southwest of Tokyo. To date, 397 trap pits are reported from 52 different localities (Sato 2015). The Late Paleolithic traps are all located in the southern half of Honshu and Kyushu, while similar traps dating to the Jomon are found throughout the archipelago (Imamura 1996; Sato 2012; Sato, Izuho, and Morisaki 2011). These archaeological traces have dates ranging from 38 ka to 15 ka based on associated tephra, with the oldest being from the Otsubobata site on Tanegashima Island off the southern coast of Kyushu (Sato 2015). Originally, these trap pits were thought to be restricted to people following a strictly sedentary lifestyle, but the identification of such deposits in Late Pleistocene sites suggested that they well predated the advent of the Jomon (Sato 2012).

These Late Paleolithic trap pits are considered to have been used for hunting because they are not found near residential or temporary camp locations and are usually found in clusters and on sloping hillsides, upper reaches of rivers, and open terrace areas (Sato 2012, 2015). In addition, they do not contain grave goods as might be expected if they served as burials. These trap pits are found in low density at any particular site but usually clustered in the former types of sites ("set arrangement") or arranged more linearly in the latter site types ("line arrangement"; Sato 2012). The arrangement of these Late Paleolithic constructions is similar to those found in the Jomon, which have also been interpreted to have functioned as trap pits specifically for hunting (Imamura 1996; Sato 2012). Sato (2012) suggests that the variation in the distribution of these trap pits may in part be due to variation in foraging group organization. The pits themselves are generally bucket shaped and about one meter deep, suggesting the goal may have actually been to capture live game such as deer and wild boar (Sato 2015). If that was the goal, it may be possible that the trap pits were only occasionally visited and that the Late Paleolithic foragers were indeed interested in capturing live game.

Discussion

Based on the current archaeological record from eastern Asia, there is little to no support for a clear Middle Paleolithic in the region. Instead, the Paleolithic of eastern Asia should be divided into a two-stage sequence: Early and Late (Gao and

Norton 2002; Ikawa-Smith 1978; Norton, Gao, and Feng 2009; Seong and Bae 2016). Although the onset of the Late Paleolithic in eastern Asia was originally identified specifically by the appearance of blade technology sometime after 40 ka (Bae and Bae 2012; Gao and Norton 2002), it appears that a number of additional novel human behaviors appeared in the region around that time as well (Norton and Jin 2009). As outlined above and found in figure 2, ground stone tools, tanged points, and trap pits all enter the archaeological record by around 40 ka and watercraft by at least that time period if not earlier. Interestingly, many of these novel behaviors appear in the Korean peninsula and the Japanese archipelago and could, in part, have facilitated the initial colonization of the latter area. It may also be possible that similar archaeological traces have yet to be identified in the broader Asian mainland. For instance, ground stone tools have been found in southern China that could be as old as some of the oldest ground stone tools found in Korea and Japan. Further analysis of these Chinese artifacts and their associated dates, in addition to supplementary field-work in the region, could potentially clarify this point. Fortunately, the increase in multinational, multidisciplinary research projects in the region is contributing to a better understanding of what the eastern Asian human evolutionary record can contribute to these scientific debates (Norton and Jin 2009).

There are currently no proposed sites in the Korea peninsula or the Japanese archipelago for a pre-50 ka occupation by MHS (sites such as Kanedori and Sunabara notwithstanding). Further, if the pre-50 ka record of modern humans from eastern Asia (e.g., Callao, Huanglong, Luna, Fuyan) is discounted (Kaifu, Goebel, and Izuho 2015), then it appears that MHS arrived in eastern Asia carrying with them a modern behavioral repertoire that included blades and tanged points, ground stone tools, trap pits, burials, art and symbolism, and watercraft (Norton and Jin 2009). However, this Late Paleolithic tool kit appears to some extent to have been regionally varied. For instance, blade and tanged point technology has yet to be identified in the Oriental biogeographic zone (region as defined by Norton et al. 2010*a* among many others). Further, trap pits have yet to be reported from the Asian mainland in Paleolithic deposits. The identification of ground stone tools in southern China in association with typical Early Paleolithic core and flake tools suggests Late Paleolithic foragers may have practiced different subsistence strategies than coeval foraging groups farther north in the Palearctic biogeographic zone, behaviors that resulted in a very different tool kit altogether from that found in northern China, Korea, and Japan (Bae and Bae 2012; Bar-Yosef et al. 2012; Norton and Jin 2009). This is not altogether surprising given the significant differences in faunas and floras between the Palearctic and Oriental biogeographic zones (Norton et al. 2010*a*).

Nevertheless, if the pre-50 ka record of MHS is accepted, then groups of MHS arrived before the development or appearance of these so-called modern human behaviors. Unfortunately, Huanglong and Fuyan are not associated with any archaeological traces (Liu et al. 2010*b*, 2015), and the Callao human metatarsal, directly dated to 67 ka, was not found in
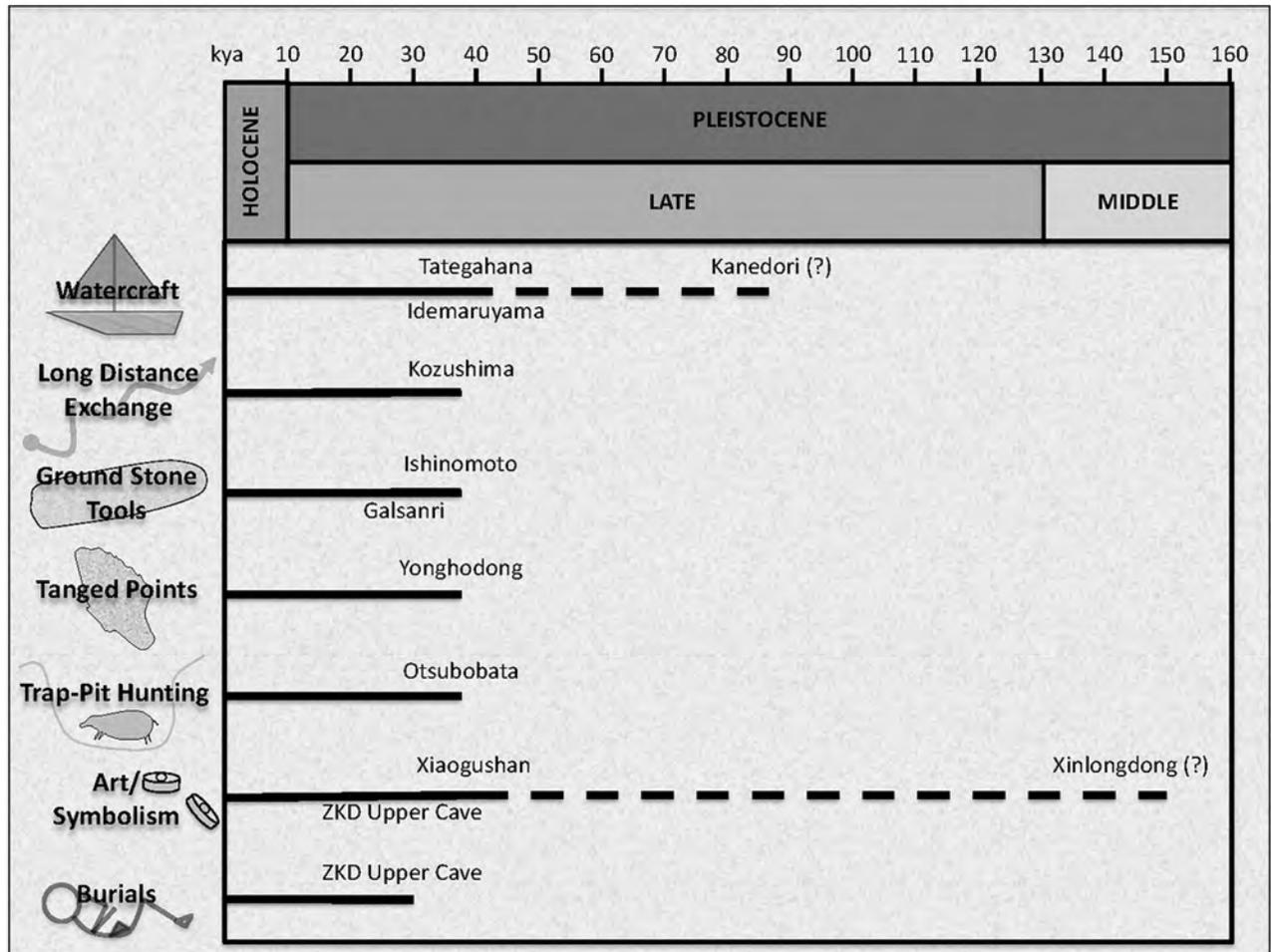
Figure 2. Appearance of various archaeological traces that signal the advent of the Early to Late Paleolithic transition in eastern Asia. A color version of this figure is available online.

association with any stone artifacts, though cut-marked bones appear to be present at the site (Mijares et al. 2010). Further, the human fossils from Huanglong and Fuyan are in fact found deep inside their respective caves, where it is possible fluvial transport or rodent collection may have served to produce a mixture of deposits from different time periods (see Michel et al. 2016 for further discussion of the Fuyan deposits). However, the 67 ka date for the Callao human metatarsal represents a time period where occupation of Luzon island could only have been via watercraft. This would be an early date for a modern human behavior to appear in the region. The discovery of additional hominin occupations/traces in Luzon and other areas of the Philippines as well as supplementary analyses should certainly be done to further test this hypothesis.

Questions about Callao, Huanglong, and Fuyan aside, the human teeth from Luna Cave (Guangxi, China) suggest that it is currently the only proposed pre-50 ka MHS site in eastern Asia that is found in association with clear archaeological traces (Bae et al. 2014). Perhaps the primary difference be-

tween Luna and the other Chinese sites in question is that in the case of Luna, the human teeth were found near the entrance of the cave in clearly dated stratified deposits. Indeed, a recent small-scale excavation conducted at Luna cave in the same area where the human teeth were discovered resulted in the discovery of additional Paleolithic flakes both in situ and surface collected as well as additional vertebrate paleontological materials. Approximately 5–10 m outside the current entrance of Luna cave are typical Neolithic ground stone tools that are clearly different from the chipped stone flakes found inside the cave. The sedimentary context of the Neolithic and Paleolithic deposits is different. A test pit excavated deeper inside the cave actually resulted in no additional findings, thus suggesting that all paleontological and cultural deposits in Luna will likely be in the front part of the cave. In fact, the original cave entrance is estimated to have been about 20 m wide and would have offered a commanding view of the basin because the entrance sits only about 30 m above the valley floor. Given the location, the secure dates, and the association of archaeological materials,

Luna perhaps offers one of the few pre-50 ka MHS sites in eastern Asia with relatively fewer questions.

Conclusions

It may be argued that there will only be resolution to the modern human origins debate when the eastern Asian paleoanthropological record is better understood (C. J. Bae 2010; Bae, Petraglia, and Douka 2017; Kaifu and Fujita 2012; Kaifu, Izuho, and Goebel 2015; Norton and Jin 2009; Stringer 2002; Trinkaus 2005). Fortunately, because of a recent increase in analyses of various Late Pleistocene deposits and fossils and archaeological materials in eastern Asia, the record is in fact becoming further appreciated (e.g., Bae and Bae 2012; Bae and Guyomarc'h 2015; Bae et al. 2014; Demeter et al. 2012; Li et al. 2017; Liu et al. 2010*a*, 2010*b*, 2015; Mijares et al. 2010). The primary points discussed here are as follows:

1. Based on the current archaeological data from eastern Asia, particularly China and Korea, there is little support to continue to use the three-stage Paleolithic sequence but rather it should be divided into two stages: Early and Late. It is recommended here that researchers in other regions of eastern Asia also closely evaluate this question for the sites and materials in their own country. For instance, many Japanese researchers appear to continue to use terms such as "Middle" and "Upper Paleolithic" indiscriminately. The question, though, is what defines this behavioral division except perhaps based on dating or the presence or absence of blade technology.
2. The eastern Asian Late Paleolithic should not be identified only by the appearance of blade technology but should also include other behavioral traces. In particular, watercraft, ground stone tools, tanged points, and trap pits for hunting should be included in any definition of the Late Paleolithic for the region. In part, some of these behaviors are related to a diversification of subsistence and mobility strategies. Better appreciation of the Korean and Japanese Paleolithic records has contributed to a reformulation of our definition of the eastern Asian Late Paleolithic. Closer evaluation of the Southeast Asian record may serve to reformulate this cultural period even further.
3. Because the early occupation of Callao (~67 ka) could only have been by watercraft, it may be possible that this particular behavior appeared earlier in island Southeast Asia than the earliest occupation of the Japanese archipelago. This may raise the prospect that MHS appeared first in Southeast Asia and then spread farther north. Alternatively, this may reflect multiple dispersals of MHS moving south through South Asia and north through Central Asia before arriving in eastern Asia. Future research should be designed to specifically test this hypothesis.
4. The increasing number of multinational, multidisciplinary research projects in eastern Asia is clearly contributing to a better understanding of what this region's record has to

offer to the modern human origins debate. Moving forward, it would not be surprising to see many additional important findings being reported from throughout the region.

Acknowledgments

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Early Modern Humans from Tam Pà Ling, Laos

Fossil Review and Perspectives

by Fabrice Demeter, Laura Shackelford, Kira Westaway, Lani Barnes, Philippe Duringer, Jean-Luc Ponche, Jean Dumoncel, Frank Sénégas, Thongsa Sayavongkhamdy, Jian-Xin Zhao, Phonephanh Sichanthongtip, Elise Patole-Edoumba, Tyler Dunn, Alexandra Zachwieja, Yves Coppens, Eske Willerslev, and Anne-Marie Bacon

Despite the importance of its geographical position for early modern human migration through Australasia, the Indochinese Peninsula has produced relatively few fossils or well-documented archaeological sites, resulting in a poor chronology for early occupation. Tam Pà Ling (TPL), a cave in northern Laos, is one of the rare sites yielding fossils contemporaneous with the earliest migrants into Australasia within a securely established chronology. From its discovery in 2008 until the most recently filed season in 2016, TPL has provided evidence of a modern human presence in the region by marine isotope stages 4 and 3. A partial cranium (TPL1), two mandibles (TPL2, TPL3), and assorted postcranial fragments (TPL4, TPL5) represent the earliest well-dated, anatomically modern humans in the Indochinese Peninsula and introduce new migration routes into the area. The sedimentary context of TPL is described and refined elsewhere, resulting in an approximate age of 44–63 ka for the TPL1 and TPL2 fossils and a maximum depositional age of 70 ka for the lowest layer containing the TPL3 mandible. This is 20 ka older than the depositional ages for the TPL1 and TPL2 fossils and establishes a new upper limit for sedimentary deposition at the site and for the associated fossil evidence. In this study, we review previously presented material (TPL1–TPL3), present unpublished postcranial material (TPL4 and TPL5), and provide dental metric analysis of the TPL1–TPL3 specimens.

Introduction

In 2003, archaeological research was resumed in the karstic landscape of the Annamite Mountains at the historical site of Tam Hang in Huà Pan Province, establishing a long-term human presence across northern Laos (Arambourg and Fromaget 1938; Bacon et al. 2008*a*, 2011, 2015; Demeter et al. 2009; Fromaget 1940*a*, 1940*b*; Fromaget and Saurin 1936; Kuzmin and Keates 2014; Patole-Edoumba et al. 2015). In 2007, new surveys began in the surrounding karstic areas for evidence of Pleistocene human evolution that yielded new sites for further study, including Tam Pà Ling (TPL; Cave of the Monkeys), which has been excavated annually since 2009 (Demeter et al. 2012, 2015; Shackelford and Demeter 2012; Shackelford et al. 2017). During this time, it has been the source of early modern human fossils from a secure stratigraphic context. As of December 2017, skeletal remains from at least five individuals have been recovered, and details of the cranial remains have been presented (Demeter et al. 2012, 2015; Shackelford et al. 2017). In this study, additional details about the dentition of these fossils are provided in an effort to contextualize the site of TPL and understand its significance.

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Context and Dating

TPL is located in Huà Pan Province, Laos (20°12′31.4″N, 103° 24′35.2″E; elevation: 1,170 m), in the Annamite mountain range, which is an extensive limestone karst landscape featuring a network of sinkholes, towers, caves, and caverns (Duringer et al. 2012). TPL is located at the top of the Pà Hang hill (fig. 1). The cave has one main chamber (L × W × H: 30 m × 40 m × 12 m) that is accessed by a single south-directed entrance. The 30-m length of the chamber is oriented along a north-south axis, and its 40-m width is oriented along an east-west axis. Upon entering the cave, there is a steep 65-m slope that descends to the chamber floor. The excavation site lies at the base of this slope at the east end of the gallery. Further details of the site can be found in Demeter et al. (2012, 2015).

The stratigraphy of the site (fig. 1) indicates formation by periodic slopewash deposition from the muddy slope at the entrance of the cave (Demeter et al. 2012, 2015; Shackelford et al. 2017). Sediments from the excavation show alternating brown sandy and silty clays interbedded with a dozen flowstone and moon milk layers (up to several centimeters thick). Limestone clasts measuring up to 1 m are present throughout the trench with a net increase in size toward the base of the

section. The clay-dominated deposits display a microstructure mainly made from millimeter-scale argillaceous pellets that are the result of reworking of consolidated clays from the sloped cave entrance. There is no evidence of an occupation surface within the stratigraphic section or within the cave. The source of the TPL fossils is unknown, but the state of preservation and the absence of water-rolling evidence suggest that they originated at or near the entrance of the cave before slopewash transport and burial.

Dating of the site has been detailed elsewhere (Demeter et al. 2012, 2015; Shackelford et al. 2017). U-series dating was performed on fossil remains (TPL1 and TPL2) and on a stalactite taken at a depth corresponding to the level at which these fossils were recovered. To determine the sedimentary history of the cave, single-grain luminescence dating of quartz was used to construct a stratigraphically consistent chronology, resulting in a steady increase in age from 2–48 ka. New preliminary dating results suggest that the age of the deepest layers may be slightly underestimated due to the saturation limits of quartz optically stimulated luminescence (OSL) dating that occurs at 3–4 m. This issue has been addressed in Shackelford et al. (2017) by applying postinfrared infrared-stimulated luminescence (pIR-IRSL) dating to feldspars to provide an independent age control for the quartz chronology. This new feldspar chronology is coeval with the established quartz chronology until ~3 m (sample TPLOSL-2) but then increases in antiquity to ~4 m (TPLOSL-3) and beyond. This new chronology agrees with the age of a stalactite, whose tip ceased being precipitated at ~64 ka due to the deposition of sediments (Demeter et al. 2015), but it also provides a new upper limit of 70 ± 8 ka to the depositional age at ~5 m. Other supporting evidence for the antiquity of the sediments includes U-series dating of the TPL1 frontal bone and a bone fragment from the TPL2 mandibular condyle. Neither of these samples provided the opportunity for U-series profiling to establish the integrity of the result and thus provided only minimum ages of >63 ka (Demeter et al. 2012) and 44–36 ka (Demeter et al. 2015), respectively. The source of the older skeletal material found in the cave has not yet been identified, but soil samples collected from excavations outside the cave at a depth of 3 m were revealed to be as old as the sediments that yielded TPL1 inside the cave. This work is ongoing.

As of December 2016, a grid measuring 12 m × 4 m has been excavated to a depth of 4.5–6 m (depths vary depending on large boulders located throughout the space). Micromammal, amphibian, and reptile remains have been recovered between 0.74 m and 6 m. These fauna are predominantly rodents, with three taxa (*Leopoldamys* cf. sabanus, *Niviventer* species, and *Rattus* species) comprising 80.7% of the identifiable remains. Additional details regarding the fauna can be found in Demeter et al. (2015) and forthcoming literature (Bacon et al., unpublished data). Human cranial fossils have been recovered at depths of 2.35 m (TPL1), 2.65 m (TPL2, TPL5), and 5 m (TPL3; Demeter et al. 2012, 2015; Shackelford et al. 2017). In 2015, a partial rib, TPL4, was recovered at a depth of 5.95 m (fig. 1). No artifacts have been found at the site.

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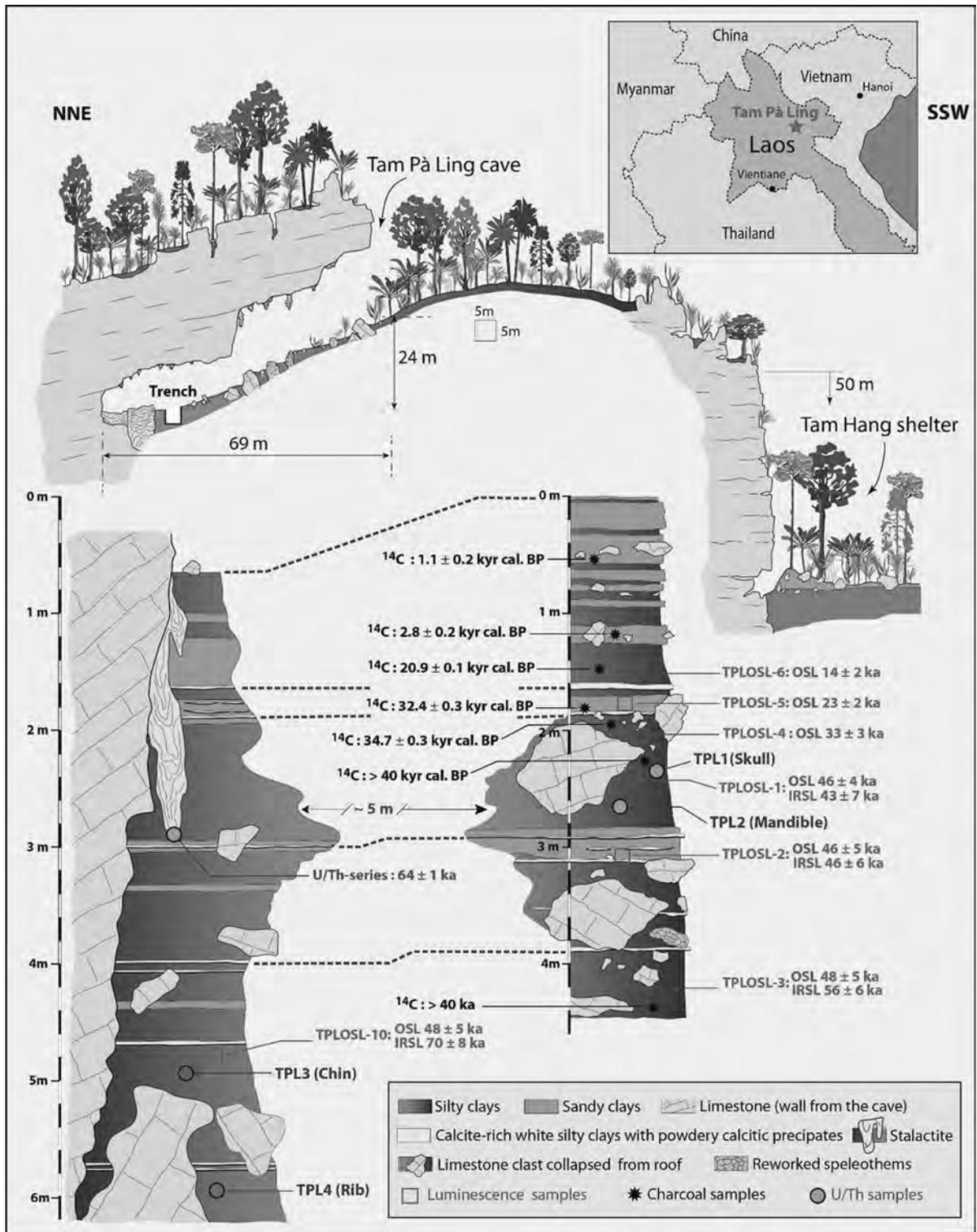
Figure 1. The 6.0-m stratigraphic section showing the accumulation of sandy and silty clay layers from the Tam Pà Ling (TPL) trench. Provenance of the charcoals sampled for carbon-14 (^{14}C) dating, soils sampled for optically stimulated luminescence (OSL) and postinfrared infrared-stimulated luminescence (pIR-IRSL) dating, and stalactite sampled for U-series dating is identified on the stratigraphy. The fossils were recovered from the following depths: TPL1, 2.35 m; TPL2, 2.65 m; TPL3, 5.0 m; and TPL4, 5.95 m. Inset is a map of Laos with the location of TPL identified. A color version of this figure is available online.

TPL Fossil Record

TPL1 partial cranium. The TPL1 cranium (Demeter et al. 2012) includes the frontal, partial occipital, right parietal and temporal, and right and left maxillae containing the right I^2–M^2 and left I^2–M^1 (fig. 2). A distal interproximal facet on the right M^2 indicates that the M^3 was in occlusion, and hence the individual was mature. Minimal wear on the molars suggests a young adult.

The TPL1 frontal lacks a supraorbital torus and has minimal postorbital constriction. Rather than a rounded skull in posterior view, as seen in East Asian late archaic humans from Maba and Xujiayao, the reconstructed calotte has a rounded sagittal suture with angled parietals that is characteristic of modern humans. The preserved occipital squama has a distinct external occipital protuberance; there is no suprainiac fossa or transverse nuchal torus as is typically found in western Eurasian Neanderthals. TPL1 has small anterior teeth despite little reduction in postcanine tooth size.

TPL2 mandible. The TPL2 mandible (Demeter et al. 2015) is largely complete, although broken at the midline symphysis; the right mandibular condyle and coronoid process as well as the left mandibular condyle are absent (fig. 2). Despite damage to the alveolar bone at the symphyseal plane, details of the bone allow the two halves to be rejoined in accurate anatomical position. All the teeth have been broken postmortem except M_3, which shows moderate occlusal attrition (grade 2 on the Molnar wear scale; Molnar 1972) and a small carious lesion on the distal occlusal surface. The eruption of both third molars and the degree of occlusal wear on the right M_3 indicate that the mandible represents an adult within the second half of the third decade.

The overall dimensions of TPL2 are small, well below that of all other Pleistocene archaic or early modern human samples (Demeter et al. 2015). The mandible has a chin with a protruding tuber symphyseos and lateral tubercles and has other discrete traits that align it with early modern humans (Dobson and Trinkaus 2002). The mental foramina in TPL2 are positioned below P_4–M_1 as seen in the majority of East Asian early modern humans. However, TPL2 has a relatively thick, shelf-like superior transverse torus and a relatively robust mandibular corpus, particularly at the M_1–M_3 level, that is most similar to robust archaic humans (Demeter et al. 2015).

TPL3 mandible. TPL3 is an anterior mandibular corpus preserving the alveolus of the right M_1 to the left P_1 (fig. 2). The crown and partial distal root of the right M_1 are present. Based on the height of the mandibular symphysis (32.9 mm), the overall dimensions of TPL3 are relatively small, although typical for an East Asian early modern human (Shackelford et al. 2017). It has a well-developed mentum osseum (Dobson and Trinkaus 2002), but it does not have a robust lateral corpus, as was seen in the TPL2 mandible. It is distinct from other early modern humans, however, in overall shape of the ante-

rior dental arcade, having a relatively broad anterior mandibular arch and large bimental breadth.

TPL4 partial rib. TPL4 is a left partial rib shaft that is highly fragmented from repeated cycles of heating and cooling (fig. 2; Pokines et al. 2016). It is in two pieces that have an articulated length of 76.2 mm. The fragment has virtually no curvature, but it can be oriented supero-inferiorly based on the clearly identifiable costal groove along the medial side of the inferior edge of the rib shaft. It has a maximum height of 17.3 mm toward the sternal (anterior) end of the fragment and a minimum height of 15.6 mm toward the vertebral (posterior) end of the fragment. The maximum breadth of the rib is 6.9 mm. Due to the lack of curvature and identifiable features, its position can be estimated only on the basis of general size; this fragment is most likely from between ribs 5 and 10.

TPL5 proximal pedal phalanx I. TPL5 is a right partial proximal hallucal phalanx that is damaged on both the proximal and distal ends (fig. 2). Despite this damage, it can be oriented and a total length measure can be taken, as there is no damage to the medial shaft and it maintains the anteromedial edge of the base, the medial portion of the metatarsophalangeal facet, and the medial edge of the head. The bone is stout with the typical mediolaterally compressed, hourglass silhouette of a proximal pedal phalanx. In lateral view, the dorsal surface is slightly convex, particularly toward the proximal end, and the plantar surface is concave. The fragment is 29.5 mm in length from the proximal facet to the fragmented distal end and measures 13.9 mm in width and 9.2 mm in height at the midshaft. It has marked pitting at the insertion site for the adductor hallucis and flexor hallucis brevis muscles near the proximal articular facet on the medial surface.

The Dentition of TPL: Material and Methods

The TPL1, TPL2, and TPL3 fossils each preserve variable dental remains that can be measured for comparisons with other available archaic and modern human specimens. TPL1 preserves the majority of the maxillary dentition, including the right I^1 through M^2 and the left I^2 through M^1. Although multiple tooth roots are preserved within the TPL2 mandible, only one tooth crown, the right M_3, is preserved. The TPL3 mandibular fragment retains a right M_1 that is intact but very fragile.

Dentition was measured by one of us (F. Demeter) using a digital caliper. The mesiodistal and buccolingual (labiolingual) diameters were taken at their widest points on each tooth. Analysis was focused on size variation, particularly in the molars, and measurements and indices are assessed for TPL and comparative samples. Linear measurements for the TPL dental remains are provided in table 1 and were graphed on bivariate scatterplots. Individual data points are graphed for all other specimens. Additional analyses of the dentition from TPL, including geometric morphometric analysis of the molars, are available elsewhere (Corny et al., 2017).

Figure 2. Human fossil remains from Tam Pà Ling (TPL). *Upper left*, TPL1. *A*, Frontal bone in norma facialis. *B*, Frontal bone in norma verticalis. *C*, Frontal bone in norma basilaris. *D*, Occipital bone in norma verticalis. *E*, Occipital bone in norma basilaris. *F*, Right parietal bone in norma verticalis. *G*, Right parietal bone in norma basilaris. *H*, Left temporal bone with partial mastoid in norma lateralis, external. *I*, Left temporal bone with partial mastoid in norma lateralis, internal. *J*, Maxillae in norma facialis. *K*, Maxillae in norma verticalis. *L*, Maxillae in norma basilaris. *Upper right*, TPL2. *A*, Mandible in norma lateralis, right side. *C*, Mandible in norma lateralis, left side. *D*, Mandible in norma facialis, external. *E*, Mandible in norma facialis internal. *F*, Mandible in norma basilaris. *G*, Occlusal view of the right M₃. *Lower left*, TPL3. Fragmentary mandible right lateral view (*A*), anterior view (*B*), left lateral view (*C*), superior view (*D*), and posterior view (*E*). *Middle right*, TPL4. Fragmentary rib anterior view. *Lower right*, TPL5. Proximal pedal phalanx I proximal view (*A*), plantar view (*B*), and dorsal view (*C*). A color version of this figure is available online.

Table 1. Crown dimensions and total crown area of Tam Pà Ling (TPL) teeth in millimeters

Tooth	TPL1			TPL2			TPL3		
	BL	MD	CBA	BL	MD	CBA	BL	MD	CBA
I^1:									
	7.4 (R)	9.1 (R)	...	...	...	...	...	...	...
I^2:									
	7.5 (R)	7.2 (R)	...	...	...	...	...	...	...
	6.9 (L)	7.4 (L)	...	...	...	...	...	...	...
C^1:									
	10.6 (R)	9.2 (R)	...	...	...	...	...	...	...
	9.2 (L)	8.6 (L)	...	...	...	...	...	...	...
P^3:									
	11.6 (R)	8.1 (R)	94.0 (R)	...	...	...	...	...	...
	10.2 (L)	7.7 (L)	78.6 (L)	...	...	...	...	...	...
P^4:									
	10.8 (R)	7.3 (R)	78.8 (R)	...	...	...	...	...	...
	11.2 (L)	7.7 (L)	86.2 (L)	...	...	...	...	...	...
M^1:									
	12.7 (R)	11.1 (R)	141.0 (R)	...	...	...	...	...	...
	...	12.2 (L)	...	...	...	...	...	...	...
M^2	13.3 (R)	11.0 (R)	146.3	...	...	...	...	...	...
M$_1$	...	...	...	...	...	...	10.4 (R)	10.3 (R)	107.1
M$_3$	...	...	...	10.8 (R)	11.0 (R)	118.8	...	...	...

Note. BL = buccolingual; C^1 = first canine; CBA = crown base area; I^1 = first incisor; I^2 = second incisor; L = left; M^1 = first molar; M^2 = second molar; M^3 = third molar; MD = mesiodistal; P^3 = third premolar; P^4 = fourth premolar; R = right.

Comparative data for these measurements come from Pleistocene archaic humans and Pleistocene and Holocene modern humans from eastern Asia and Australia as well as from similarly aged specimens from across the Old World. Samples from Europe and western Asia are identified by traditional archaeological designations; eastern Asian and Australian samples are identified on the basis of geological divisions, because the archaeological record of Australasia is inconsistent with these traditional designations. Comparative samples are divided into (1) East Asian archaic humans, which primarily include fossils dated from marine isotope stage (MIS) 5–3; (2) western Eurasian archaic humans (i.e., Neanderthals of Europe and western Asia); (3) East Asian modern humans from the Pleistocene and Holocene; (4) Upper Paleolithic modern humans, with the vast majority from western Europe and dating between 19 and 28 ka; (5) Middle Paleolithic modern humans from Qafzeh and Skhul; (6) Mesolithic humans spanning Europe and western Asia; and (7) Australian Aborigines from the terminal Pleistocene and Holocene. Details of these samples and sources of metric data can be found in the appendix (available online).

Results of the Dental Measurements Analysis

Measurements and indices for the TPL teeth are provided in table 1. Given that mesiodistal lengths are most affected by interproximal wear, comparisons between samples are between buccolingual (labiolingual) breadths. For the anterior teeth (incisors and canines), there is considerable overlap in the ranges of variation for labiolingual breadths of the comparative samples (table 2). The TPL1 incisors fall within the ranges of variation of all these samples, although at the low end (or just below in the case of the Neanderthals) of the archaic human ranges and the upper end (or just beyond in the case of the Mesolithic sample) of the modern human ranges. Differences between samples become more apparent with the canines, with the older samples (East Asian archaics and Neanderthals) having broader mean labiolingual breadths than the younger samples (East Asian, Upper Paleolithic, or Mesolithic modern humans), although again the ranges of variation broadly overlap. TPL1 is more closely aligned with the means of the archaic samples, but it does fall within the ranges of variation for multiple samples. The Australian sample is an exception to the above-stated rule, having larger crowns for all teeth than other modern human samples across the board (table 2).

The upper premolars and molars of the TPL fossils, however, are absolutely large (tables 2, 3). The buccolingual breadth of the right P^3 falls above the mean of all comparative samples and is equal to or above the ranges of variation of the East Asian, Upper Paleolithic, Middle Paleolithic, and Mesolithic modern human samples (table 2). The size of both P^{4}s are also more similar to the archaic samples than to any of the modern human samples, with the exception of the terminal Pleistocene/Holocene Australian sample, whose mean breadth (10.5 mm) is well above that of any other Pleistocene sample (table 2).

Figures 3a and 3b plot crown length against crown breadth of the maxillary molars. From figure 3a, there is considerable overlap between samples, and TPL1 falls near the upper limits of these samples with respect to mesiodistal length for a given crown breadth. Figure 3b differentiates the archaic samples from the modern human samples to some extent, with the ar-

Table 2. Buccolingual breadths of maxillary teeth of Tam Pà Ling 1 (TPL1) and comparative samples in millimeters

	I1	I2	C	P3	P4
TPL 1:					
Left	7.4	6.9	9.2	10.1	11.2
Right	…	7.5	10.6	11.6	10.8
East Asian archaics:					
Mean (±SD)	7.8 (.98)	7.0 (1.4)	9.1 (.98)	10.8 (.98)	9.9 (1.3)
Range	6.4–8.4	6.0–8.0	7.9–10.4	9.9–12.8	8.5–12.2
No. samples	4	2	6	7	6
Neanderthals:					
Mean (±SD)	8.0 (.47)	8.1 (.49)	9.5 (.55)	10.5 (.55)	10.0 (.51)
Range	6.9–9.3	7.1–9.0	8.4–10.7	9.8–11.8	9.2–11
No. samples	22	19	24	18	19
East Asian MH:					
Mean (±SD)	7.2 (.64)	6.9 (.52)	8.7 (.64)	9.7 (.65)	9.8 (.57)
Range	5.2–8.5	6.1–8.3	7.4–10.0	7.7–10.8	8.6–10.8
No. samples	22	22	27	29	28
Upper Paleolithic MH:					
Mean (±SD)	7.6 (.44)	6.7 (.51)	9.0 (.84)	9.7 (.72)	9.7 (.58)
Range	6.9–8.6	5.8–8	6.9–10.7	8.7–11.6	8.7–11.3
No. samples	31	32	47	44	54
Middle Paleolithic MH:					
Mean (±SD)	8.3 (.68)	7.5 (.67)	9.2 (.79)	10.1 (.98)	9.8 (1.35)
Range	7.3–9.8	6.2–8.5	8.0–10.3	7.9–11.1	6.9–11
No. samples	11	10	10	8	9
Mesolithic MH:					
Mean (±SD)	7.4 (.47)	6.5 (.46)	8.7 (.63)	9.5 (.53)	9.6 (.53)
Range	6.5–9.0	5.3–7.4	7.0–9.8	7.7–10.7	8.1–10.6
No. samples	94	74	118	117	130
Australian Pl/Holocene:					
Mean (±SD)	8.1 (.48)	7.6 (.45)	9.5 (.75)	10.6 (.56)	10.5 (.42)
Range	6.8–8.8	6.8–8.5	8.2–11.4	9.2–11.8	9.4–11.7
No. samples	21	26	31	23	30

Note. MH = modern humans; Pl = Pleistocene.

chaic samples having slightly smaller lengths for a given breadth than the modern samples. This may be due in part to underestimated mesiodistal lengths that result from interproximal tooth wear. TPL1 falls comfortably within the ranges of variation of all comparative samples. Figures 3*c* and 3*d* plot crown length against crown breadth of the mandibular molars. The lengths and breadths of the M_1s and M_3s vary considerably within each comparative sample, and TPL1 is difficult to reliably assign to one sample. It does, however, have a relatively narrow M_1, although in this respect it is similar to several other East Asian archaic fossils (fig. 3*d*; table 3).

In figures 4 and 5, the relative buccolingual diameters of teeth within the same tooth field are plotted for the premolars and molars, respectively. There is significant overlap between samples when looking at the relative sizes of premolars (fig. 4). In TPL1, the right P^3 is larger than the right P^4 (11.6 mm and 10.8 mm for the P^3 and P^4, respectively), whereas the left P^3 is smaller than the left P^4 (10.1 mm and 11.2 mm for the P^3 and P^4, respectively). In the molars, the archaic humans generally have larger M2s than M1s, whereas the early modern humans show the opposite pattern (fig. 5). TPL1 is more similar to the archaic humans in having an M^2 that is greater in breadth than the M^1 (13.3 mm vs. 12.7 mm for the M^2 and M^1, respectively).

Discussion

The most notable feature of all of the fossil material from TPL, including both cranial and mandibular material, is its relatively small overall size. The maximum frontal breadth of TPL1, a reliable size measurement available for comparison, is 106 mm, which is below the range of variation for East

Table 3. Buccolingual breadths of maxillary and mandibular molar from Tam Pà Ling 1 (TPL1) and comparative samples in millimeters

	M^1	M^2	M_1	M_3
TPL1	12.7 (R)	13.3 (R)	…	…
TPL2	…	…	…	10.8 (R)
TPL3	…	…	10.4 (R)	…
East Asian archaics:				
Mean (±SD)	12.0 (1.8)	12.7 (1.6)	10.3 (.57)	11.0 (1.5)
Range	10.2–14.1	10.5–15.6	9.7–11	9.4–13.6
No. samples	19	10	4	7
Neanderthals:				
Mean (±SD)	11.9 (.68)	12.3 (.74)	11.2 (.61)	11.3 (.6)
Range	10.4–13.4	10.7–13.8	10.5–12.5	10.5–12.4
No. samples	26	27	13	12
East Asian MH:				
Mean (±SD)	12.1 (.6)	11.9 (1.0)9	11.1 (.74)	10.3 (.7)
Range	10.4–13.5	9–13.7	9.4–12.4	8.6–12
No. samples	35	37	38	37
Upper Paleolithic MH:				
Mean (±SD)	12.2 (.69)	12.4 (.83)	11.0 (.62)	10.6 (.73)
Range	10.8–14.1	10.5–14.3	9.1–12.4	8.8–12.5
No. samples	85	77	95	65
Middle Paleolithic MH:				
Mean (±SD)	12.1 (.58)	11.0 (1.3)	11.5 (.64)	10.8 (.76)
Range	11.2–13.2	8.6–13	110.5–12.6	9.9–11.9
No. samples	16	10	7	6
Mesolithic MH:				
Mean (±SD)	11.9 (.58)	11.8 (.73)	10.9 (.49)	10.2 (.67)
Range	10.2–13.31	9.7–13.91	10–12.51	8.2–18.81
No. samples	84	92	82	84
Australian Pl/Holocene:				
Mean (±SD)	13.4 (.49)	13.5 (.84)	12.3 (.79)	…
Range	12.1–15.1	12–15.3	11.1–13.1	…
No. samples	29	30	15	…

Note. MH = modern humans; Pl = Pleistocene.

Asian Late Pleistocene humans (Demeter et al. 2012). Similarly, the TPL2 mandible has an inferior mandibular length of 77 mm and an estimated superior length of 87 mm, well below that of all other archaic or early modern human samples (Demeter et al. 2015). The overall dimensions of the TPL3 chin can be estimated only by the symphyseal height, but with a symphyseal height of 32.9 mm, it is only slightly larger than that of TPL2 (30.0 mm) and within the range of variation for East Asian early modern humans (Shackelford et al. 2017).

Found in the same stratigraphic unit, these specimens demonstrate a broad range of morphological variation that is not completely consistent with the typological features of any single population. The TPL1 cranium demonstrates morphology that is consistent with that of modern humans. However, the relative sizes of teeth within the same tooth field have been shown to be population-specific in some cases (Bailey and Liu 2010), and TPL1 has large cheek teeth that show a pattern of size progression that is more consistent with archaic than modern humans, although these features are present in both populations to varying degrees. In a majority of Middle Pleistocene hominins and some Neanderthals, the buccolingual breadth of the P^4 is larger than that of the P^3; conversely, the breadth of the

P^3 is larger than that of the P^4 in the majority of Late Pleistocene hominins (Neanderthals and modern humans; Bailey and Liu 2010). In TPL1, the right P^3 is larger than the right P^4, as is seen in the majority of Late Pleistocene hominins; however, the left P^3 is smaller than the left P^4, the configuration more common in Middle Pleistocene hominins (fig. 4). Molars follow a similar pattern, with *Homo erectus*, Neanderthals, and archaic humans most often having an M^2 with a larger breadth than the M^1, whereas molars decrease in size as you move posteriorly with modern humans (Bailey and Liu 2010). In this way, TPL1 follow the more archaic pattern, having an M^2 that is greater in breadth than the M^1 (fig. 5).

A previous geometric morphometric study of TPL2 (Demeter et al. 2015) has shown that this fossil was most similar to Middle and Late Pleistocene archaic human groups due to the size and shape of the lateral mandibular corpus, particularly with respect to the expansion of the internal aspect of the mandibular body superior to the mylohyoid line. This large lateral corpus combined with its small overall size makes it unique among fossil specimens. In contrast, a recent between-group principal component analysis of the TPL mandibles demonstrates that, when looking at only the anterior mor-
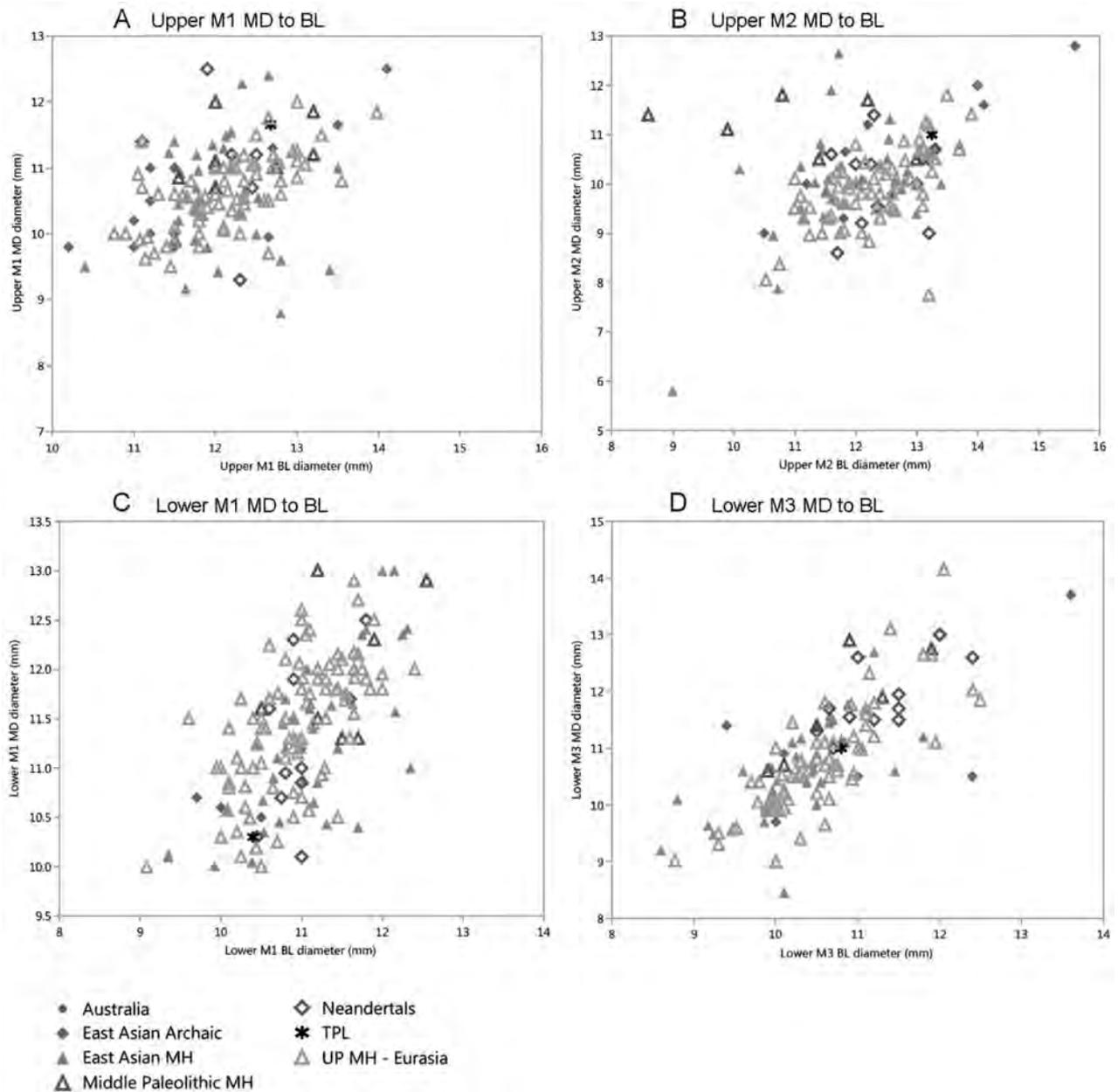
Figure 3. Mesiodistal (MD) lengths plotted against buccolingual (BL) breadths for molar 1 (M1; *A*), M2 (*B*), M1 (*C*), and M3 (*D*). Mesolithic humans are not shown so as not to obscure all other data points. MH = modern humans; TPL = Tam Pà Ling; UP = upper Paleolithic. A color version of this figure is available online.

phology of TPL2, this fossil is most consistent with early modern humans rather than with archaic humans. In the same way, the TPL3 mandibular fragment has a prominent mental protuberance, like early modern humans, but the large anterior arch and bimental foramen width clearly position this fossil among archaic rather than modern humans (Shackelford et al. 2017).

While these mixtures of features appear conflicting when looked at as characteristic of archaic versus modern human comparative samples, they are better understood as traits that are expressed across a continuum and expressed to some de-

gree in each of these populations. From this perspective, the fossils from TPL appear to demonstrate the wide range of variability that is typical of early modern humans in Southeast Asia at a relatively early time period. This is especially true when considering the growing body of fossils in East Asia during the previously barren periods of MIS 5–3 that have been described as mosaic or transitional (Bae et al. 2014; Chang et al. 2015; Curnoe et al. 2016; Liu et al. 2010, 2015). Like TPL, these may also present a combination of modern anatomy that retains some archaic features (Liu et al. 2010).
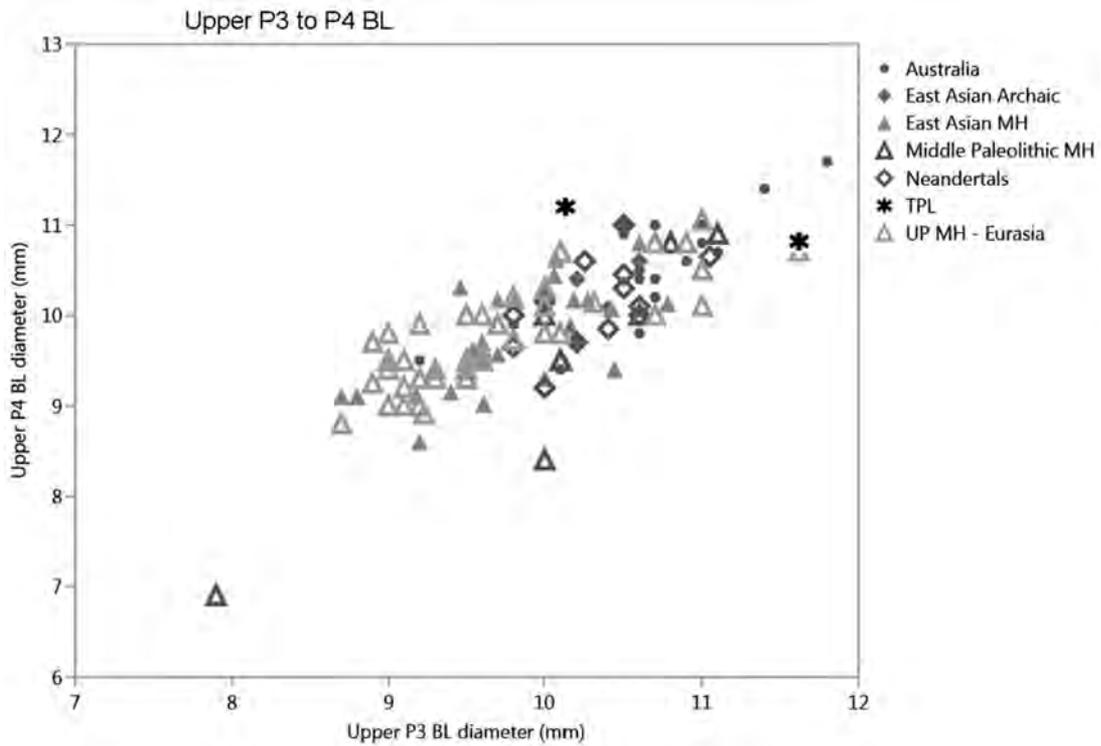
Figure 4. Buccolingual (BL) breadths of upper premolars (P) plotted. MH = modern humans; TPL = Tam Pà Ling; UP = Upper Paleolithic. A color version of this figure is available online.
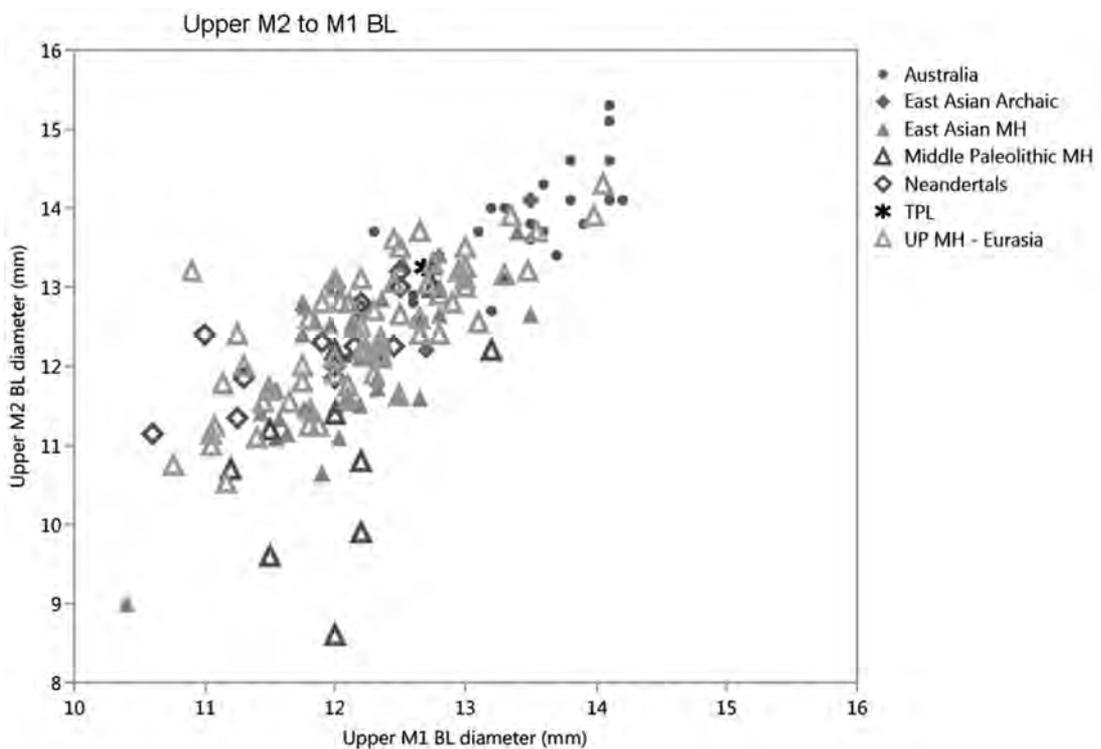

Figure 5. Buccolingual (BL) breadths of upper molars (M) plotted. MH = modern humans; TPL = Tam Pà Ling; UP = Upper Paleolithic. A color version of this figure is available online.

Conclusion

The warm and wet climate of the Indochinese Peninsula often prevents fossil evidence from being preserved. For this reason, the early modern human occupation history of the region is difficult to understand, since interpretations are based on only a handful of well-dated sites ranging from 74–10 ka, mainly from Malaysia (74 ka; Saidin 2012), the Philippines (67 ka, although the specific designation of these fossils is still debated; Salvador Mijares et al. 2010), Vietnam, and Laos (Bacon et al. 2008*b*; Demeter, Manni, and Coppens 2003; Demeter et al. 2005, 2012, 2015; Oxenham 2016; Shackelford et al. 2017). The newest dates from the deepest layers of TPL derived from feldspar pIR-IRSL techniques of ∼70 ka confirm the presence of early modern humans in Indochina by MIS 4, implying a more complex migration scenario than was originally thought. These dates can be combined with recent studies demonstrating an early modern human presence in the Levant, the Arabian Peninsula, and India by 74 ka (before the Toba eruption; Petraglia et al. 2007) to suggest that an MIS 5 migration out of Africa is equally—if not more—plausible than a single MIS 3 exit and that these early migrants may have followed multiple routes toward the East (Boivin et al. 2013; Liu et al. 2015; Michel et al. 2016; Reyes-Centeno et al. 2014). As such, these early dates for TPL and the variation in morphology demonstrated by the TPL fossils illustrate the overlap in traits and varying trait frequencies that could have existed among the earliest humans in the Indochinese Peninsula (Rosas 2001; Stefan and Trinkaus 1998; Trinkaus 2006) and that would have spread from Africa toward the East.

A recent genomic study on contemporary Australians and Papuans estimates a single African exit for all living non-African populations 60–100 ka (Malaspinas et al. 2016). The fossil record clearly shows more than one "Out of Africa" migration of anatomically modern humans, although it remains to be seen whether these early waves provided genetic signatures in the ancestors of living human populations. Some recent genetic studies suggest this may be the case (Pagani et al. 2016). Ancient DNA normally survives poorly in hot and humid regions, such as Southeast Asia (Willerslev and Cooper 2005), but recent technical advances provide some promises for future success (Orlando, Gilbert, and Willerslev 2015). Genetic studies on well-dated fossils like those described here will obviously shed light on the origins and evolution of anatomically modern humans in the region. They may also provide exciting possibilities for studying interactions with local archaic groups. The archaic admixture found in present day Australians and Papuans does not come directly from Denisovans, which so far are found only in Altai in Siberia, but from an unknown hominin distantly related to this group (Malaspinas et al. 2016). Ancient genomics on fossils such as the one from TPL may well be the only way to get direct insights as to the number of out of Africa migrations and the genetic nature and timing of possible admixtures between early human groups.

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On the Pleistocene Population History in the Japanese Archipelago

by Yuichi Nakazawa

This paper provides a current understanding of human population history in the Pleistocene Japanese Archipelago, particularly with respect to the routes and timing of hunter-gatherer migrations, by incorporating multiple lines of evidence from the records of archaeology, human paleontology, and genetic studies. The human fossil remains are concentrated on the Ryukyu Islands in southwestern Japan, suggesting that there may have been a northward migration via the Ryukyu Islands. In contrast, studies of ancient mitochondrial DNA demonstrate genetic continuity among Holocene hunter-gatherer populations in the Paleo-Sakhalin-Hokkaido-Kurile Peninsula, whereas the Pleistocene genetic history is little explored. Although it is largely supported, the assumed population continuity from the Pleistocene to the Holocene inside the Japanese Archipelago is also challenged by an examination of the Paleolithic record and a comparison of the short- and long-term chronologies of the Japanese Paleolithic, implying that the Japanese Paleolithic record was created by hunter-gatherer population migrations from the north and south with substantial time lag and endemic technological invention and transformation during the Late Pleistocene.

Since the beginning of paleoanthropology, human population history in East Asia has been critical in assessing the evolution of human lineages. Although the Pleistocene human fossil records are still limited in this large and diverse geographic area, advances in human fossil and genetic studies have revealed that various species and populations in the genus *Homo* (e.g., *Homo erectus*, archaic *Homo sapiens*, modern *H. sapiens*, *Homo floresiensis*, and Denisovans) were present during the Pleistocene in eastern Asia (C. Bae 2010; Etler 1996; Reich et al. 2010; Xiao et al. 2014). The geographic location of the Japanese Archipelago, characterized by the eastern end of Eurasia between the extensive Chinese mainland, Siberia, and the northern Pacific Ocean, makes Japan a unique feature in human evolution. In terms of the human migratory record out of Africa, the Japanese Archipelago is, in addition to Australia and the Americas, one of the farthest points along the Eurasian trail. In addition, it is a cul-de-sac in the sense that no more explorations into new terrestrial habitats were achieved until more extensive explorations were conducted of the smaller islands in the surrounding oceans of the northern Pacific.

Unlike in China, where fossil evidence of *H. erectus*, archaic *H. sapiens*, and modern *H. sapiens* is present (C. Bae 2010; Dennell 2010, 2015; Etler 1996; Liu et al. 2010; Xiao et al. 2014), the fossil record in Japan is attributed solely to modern *H. sapiens* and dated to late marine isotope stage (MIS) 3 and MIS 2 (Kaifu and Fujita 2012; Nakagawa et al. 2010). On the other hand, there

is an abundant Upper Paleolithic archaeological record in Japan, mainly due to the intensive excavation projects carried out by various organizations that include local government offices and cultural resource management firms (Barnes 1990; Nakazawa 2010). Despite the accumulation of a rich Paleolithic archaeological record, there is still limited evidence of human occupation before late MIS 3 (>40,000–38,000 BP), unlike in China, where affirmative cultural evidence has been accumulated since at least the late Early Pleistocene (Dennell 2009; Gao 2013; Gao and Norton 2002; Norton et al. 2010*a*; Wang 2005). Here, I will provide an overview of the current understanding of the Paleolithic archaeological and Late Pleistocene paleoanthropological records in this particular geographic region and propose how they may contribute to future directions in human evolutionary studies in Asia. Given my background, the discussion will be biased toward the archaeological evidence, but recent discussions and contributions about human migration history and genetic studies are incorporated where applicable.

Paleogeography and Human Migrations

The arc-trench system of the Japanese Archipelago was created by complex tectonic activities involving five plates: Eurasia, Amur, Okhotsk, Pacific, and the Philippine Sea (Taira 2001). The topographic characteristics of the islands were formed by the interactions of these plates. This resulted in the formation of four larger islands: Hokkaido, Honshu, Shikoku, and Kyushu from the north to south. There are also thousands of smaller islands in and around the Pacific and the Sea of Japan. The Ryukyu Islands are the long chain of islands situated in the south-

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west between Kyushu and Taiwan. Because of continuous tectonic forces, volcanism and earthquakes often happened even during the Pleistocene. The current position of this long chain of the four major islands, stretching between 45°N and 31°N, was eventually established by the onset of the Holocene, when the global sea level rose to its current level (Yonekura et al. 2001). During the Pleistocene, numerous islands, including the four larger islands, were connected to form part of the larger island or peninsula (Iwase et al. 2012; Ota and Yonekura 1987). For instance, between MIS 4 and MIS 2, Honshu, Shikoku, and Kyushu were connected to form a single island, commonly referred to as "Paleo-Honshu," while Hokkaido formed the southern end of a peninsula in northeastern Siberia, commonly called the "Paleo-Sakhalin/Hokkaido/Kurile Peninsula" (Paleo-SHK; Ono 1990).

The palynological record in Japan allows us to reconstruct vegetation changes and spatial variation across the entire archipelago during the Late Pleistocene. A recent study by Takahara et al. (2015) provides a synthetic picture of MIS 3 vegetation in and around the Japanese Archipelago (i.e., Sakhalin, Paleo-SHK, Paleo-Honshu, Ryukyu, and Taiwan) using 47 locational pollen samples. Species in temperate to cool forests vary according to the latitudes and altitudes in Japan, resulting in a vegetation map that is a mosaic of cold and temperate forests, whereas relatively high occurrences of deciduous broad-leaf forests are observed regardless of vegetation zones. During the Last Glacial Maximum (LGM), on the other hand, the area of deciduous broad-leaf forest shifted to the southwestern coastal margin of the Paleo-Honshu, and cool and temperate forests mostly covered Japan (Iwase et al. 2012, fig. 2).

Given the unique geographic features of the Japanese Archipelago, several different migration routes to the islands are viable. Saitou (2005) proposes six possible routes of human entry (fig. 1). The first route is a migration from the Korean Peninsula to northern Kyushu via the Tsushima Strait (route 1). The second is a route of migration from the Russian Far East in the north to Hokkaido via Sakhalin Island (route 2). The third possible track is also a southward migratory route, from the Kamchatka Peninsula in western Beringia to eastern Hokkaido via the Kurile Islands (route 3). The fourth is a northward route that originates in southern China, extends to Taiwan Island and to the Ryukyu Islands, and crosses over the southern Pacific Ocean, eventually reaching southern Kyushu (route 4). The fifth route goes east from eastern China to Kyushu and crosses the East China Sea (route 5). The sixth route is from the coastal Russian Far East (Primorskii) to Honshu and crosses the Sea of Japan (route 6). All of these routes are viable if humans have advanced seafaring skills and the ability to navigate oceans over long distances even when landmarks are no longer visible. Even during the LGM, when sea levels may have dropped by as much as 100 m, Paleo-Honshu Island was not connected to either the Korean Peninsula (Tada 1999) or southern China; small strips of open ocean would have remained between these different landmasses (Li et al. 2014). Although Hokkaido was connected to Sakhalin and eastern Siberia to form the Paleo-SHK,

there is no evidence that Hokkaido was connected to Paleo-Honshu at this time (Ono 1990). Given these possible land connections, terrestrial human migrations are only achievable through route 2, the northern entry route from Far Eastern Russia to Hokkaido. The other five routes all require a certain level of seafaring navigation capability, which was clearly present in the region by the advent of the Late Paleolithic, as evidenced by obsidian transportation from the Pacific island of Kozu to Paleo-Honshu (Ikeya 2015; Shimada et al. 2017; Tsutsumi 2010).

Compatibility, Inconsistency, and Biases in the Study of Prehistoric Human Migrations: Human Paleontology, Genetic Studies, and Archaeology

In evaluating the routes and timing of the earliest human migrations into the Japanese Archipelago, employing multiple lines of evidence is a useful approach to reach a synthetic picture. Currently available data are from human paleontology, genetics, and archaeology, which should be combined with our understanding of the geography and paleoenvironment of Pleistocene Japan. The most ubiquitous record comes from archaeology, whereas there are limited human fossil remains. Although studies of DNA have provided a picture of how different human populations contributed to the formation of modern Japanese, sources of data, particularly ancient DNA, are still small in number. Below, I discuss the Japanese records of human fossils, genetic studies, and archaeology to build a more synthetic picture of what the peopling of the Japanese Archipelago likely resembled.

Human Fossil Record

In 1931, the first discovery of a possible Pleistocene human fossil, known as the "Akashi Genjin" (Akashi hominin), from the Nishiyagi Coast in western Japan was made by archaeologist Nobuo Naora (Harunari 1994). Although the original specimen of the Akashi hominin was lost during World War II, a later reexamination of the cast of the innominate bone indicated that the specimen was likely from a Holocene modern *Homo sapiens* (Endo and Baba 1982). Since the discovery of the Akashi hominin, a number of Pleistocene human fossils have been reported in Japan, with the majority of them found on the Ryukyu Islands in the southern part of the archipelago (table 1). To date, no Pleistocene human remains have been identified in Hokkaido and northern Honshu.

All of the ages established for these Pleistocene human fossils fall in the second half of MIS 3 or MIS 2. The dates for these fossils are usually obtained from analysis of associated charcoal, but the age of the human fossils from the newly discovered Shiraho-Saonetabaru Cave was determined with direct radiocarbon dating (Nakagawa et al. 2010). Despite the scarcity of Pleistocene human remains, paleoanthropologists have discussed the routes of these Late Pleistocene humans on the basis
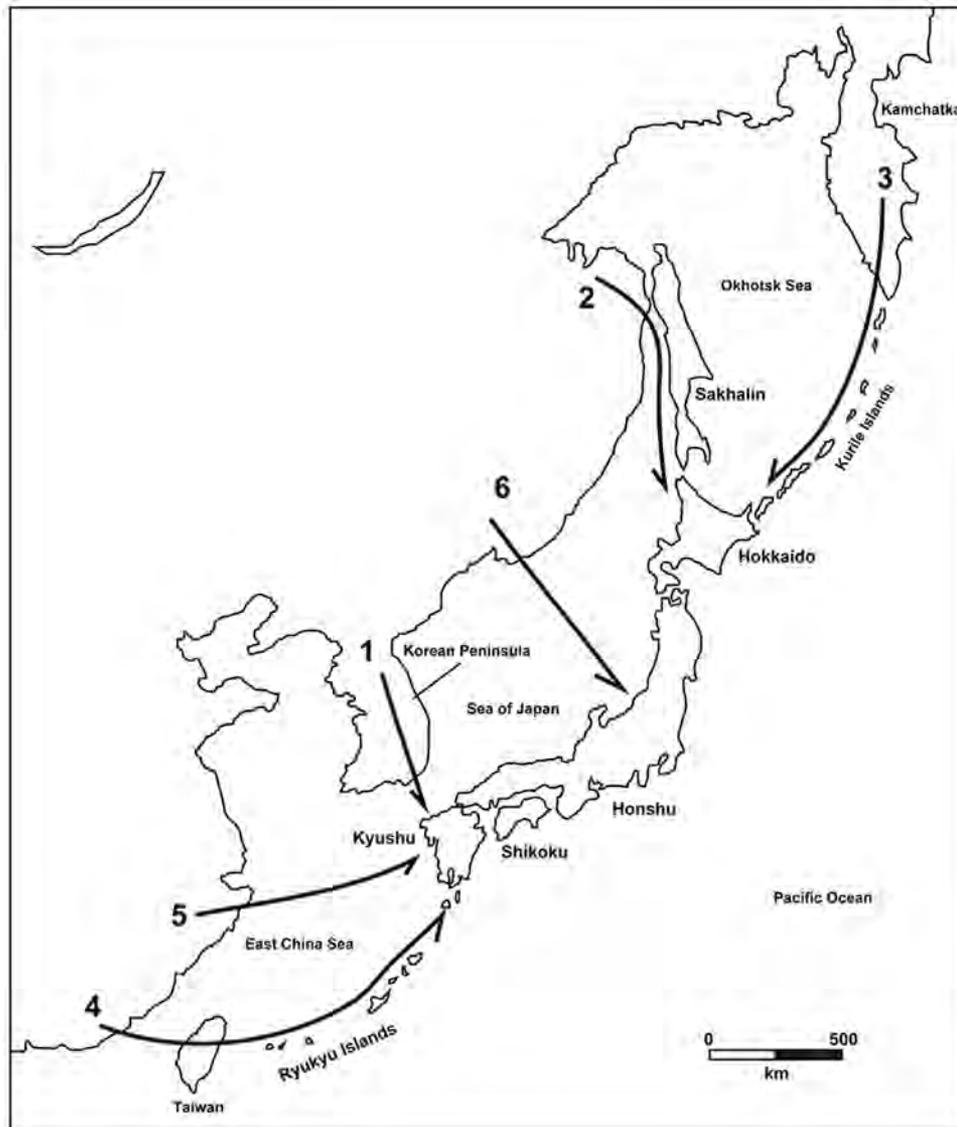
Figure 1. Expected migratory routes from neighboring regions to the Japanese Archipelago. Routes on the map are redrawn from Saito (2005:79).

of their morphology. For example, it was suggested that the Minatogawa individuals were morphologically different from the Holocene Jomon (Neolithic) population in Japan and may be more closely linked with populations from Southeast Asia (Baba, Narasaki, and Ohyama 1998). Human fossils from the collapsed karstic cave site of Nekata in Hamakita City present a more complicated picture. The human remains from the upper layer of Nekata, known as the Hamakita upper specimen, are morphologically close to Jomon, while the specimen (tibia) from the lower level was not assigned to Jomon (Kondo and Matsu'ura 2005; Suzuki 1966; Suzuki and Endo 1966). Because the associated date is from the Late Pleistocene, the tibia fossil was simply referred to as a "Palaeolithic hominid," with no specific assignment (Kondo and Matsu'ura 2005:155).

As opposed to the limited number of Pleistocene human remains, there are more Holocene human remains from prehistoric sites in Japan that date to the Jomon (hunter-fisher-gatherers) and Yayoi (agriculturalists; Barnes 2015; Habu 2004; Imamura 1996; Mizoguchi 2013). A number of metric and morphometric studies of the human skeletal remains from Jomon and Yayoi sites indicate that they represent different populations (e.g., Dodo and Ishida 1990; Kaifu 1995, 1997; Nakahashi 1993). The physical difference between the Jomon and Yayoi led to the proposal of the admixture model for explaining the formation of "Japanese." This is referred to as the "dual-structure model" and was proposed by Kazuo Hanihara (1991:25). The dual-structure model proposes that humans first entered the Japanese Archipelago from Southeast Asia with a continual

Table 1. A list of Pleistocene human remains from the Japanese Archipelago

Region, site	Anatomical parts	Context	Radiocarbon dates (BP)	Dated specimens	Reference(s)
Honshu:					
Hamakita (Upper)	Cranial fragments, clavicle, humerus, ulna, innominate	Sediments inside fissure	14,050 ± 50 (Beta-160571), 14,200 ± 50 (Beta-160572), 13860 ± 50 (Beta-160570)	Human remains (parietal, occipital, humerus)	Kondo and Matsu'ura 2005; Suzuki 1966
Hamakita (Lower)	Tibia	Sediments inside fissure	17,910 ± 70 (Beta-94983)	Faunal remains (leopard or tiger)	Kondo and Matsu'ura 2005; Suzuki 1966
Ryukyu:					
Yamashita-cho Cave 1	Femur, tibia	Upper layer of the cave	32,100 ± 1000	Charcoal fragments	Suzuki 1983
Minatogawa Fissure (Minatogawa Man series)	Skeletons (5 individuals)	Clay layer in the lower fissure fillings	18,250 ± 650 (TK-99), 16,600 ± 300 (TK-142)	…	Baba et al. 1998; Matsu'ura and Kondo 2011; Suzuki and Hanihara 1982
Minatogawa Fissure (Upper Minatogawa series)	Nine postcranial (>3 individuals)	Likely from the upper fissure fillings	…	…	Matsu'ura and Kondo 2011
Shimojibaru	Talus, metatarsal, infant skeleton, mandible	Clay layer below travertine	15,200 ± 100	Crab shell	Matsu'ura and Kondo 2000
Pinza-abu	Right humerus, right femur, parietal, occipital, lumbar vertebra, hand bones, isolated teeth	Clay layer below flowstone	25,800 ± 900 (TK-535), 26,800 ± 1300 (TK-605)	Charcoal fragments	Hamada 1985; Sakura 1985
Shiraho-Saonetabaru Cave	Right parietal, second metatarsal, right fibula	Unconsolidated muddy sediments likely secondary deposition in a chamber	20,416 ± 113, 18,752 ± 100, 15,751 ± 421	Gelatin from bone collagen	Nakagawa et al. 2010

Note. Dates for the Minatogawa Fissure (Minatogawa Man series) are listed for references, because these dates were obtained from charcoals sampled from the clay layer with little certain association with the human remains (Kondo and Matsu'ura 2005).

influx from the Jomon but were later assimilated by the Yayoi peoples, who originated from mainland Northeast Asia some 3,000 years ago. According to this model, populations in the southern lands of Japan (i.e., Honshu, Shikoku, and Kyushu) were the result of admixture between Jomon and Yayoi, whereas Ainu, an indigenous population in Hokkaido, and Ryukuans, an indigenous people living in the Ryukyu Islands, were not assimilated and retained Jomon morphology. The dual-structure model proposes that gene flow occurred from both Southeast and Northeast Asia. Human genetic studies largely support the admixture model for the Ryukuan and Ainu populations and their relations to Jomon populations (e.g., Dodo and Ishida 1990; Hammer et al. 2006; Horai et al. 1996; Omoto and Saitou 1997; Shigematsu et al. 2004; Tanaka et al. 2004). However, the genetic relationship between Southeast Asia and Jomon is less supported (e.g., Jinam, Kanzawa-Kiriyama, and Saito 2015; Omoto and Saitou 1997), suggesting that Late Pleistocene and Holocene hunter-gatherer population history in Japan is more complex than a simple migration from Southeast Asia. In contrast, Paleolithic migrations from Southeast Asia, as proposed in the original admixture model, have not been explicitly tested through comparative analyses of the Paleolithic archaeological records of Japan and adjoining regions.

How Do the DNA Studies Tell Us about the Routes of Human Entry into Japan?

The Holocene human fossil record supports an admixture model in which the Paleolithic population originated from both southeastern and northeastern Asia (e.g., Hanihara 1991). The mitochondrial DNA (mtDNA) analyses of modern Japanese revealed that non-African superhaplogroups M and N originally derived from modern *H. sapiens* dispersing out of Africa (Forster 2004) that eventually came to be the Japanese indigenous populations of Ainu and Ryukuan (e.g., Tanaka et al. 2004; cf. Maca-Meyer et al. 2001). Because Ainu and Ryukuan are descendants of the original Jomon populations (Hanihara 1991; Horai et al. 1996; Omoto and Saitou 1997) and M and N superhaplogroups represent southern and northern routes of human migrations, respectively (Tanaka et al. 2004), the Holocene Jomon population was founded by both northward and southward gene flows.

Studies of ancient mtDNA from the Jomon skeletal remains of Hokkaido show genetic relations between Jomon and Ainu, because both populations retain high frequencies of the haplogroup N9b (Adachi et al. 2011), whereas N9b is scarce among East Asian populations other than Japanese (Tanaka et al. 2004:1842) and is likely skewed to northern regions in Japan (Shinoda 2007). Because the coalescent time of N9b is estimated to be approximately 22,000 year ago (Adachi et al. 2011:355), populations that have this haplogroup emerged around the LGM. In Hokkaido, Epi-Jomon human remains in Hokkaido also have N9b (Adachi et al. 2011), which suggests some degree of gene flow during the LGM to the late Holocene in Hokkaido (22,000–2000 years ago).

As discussed above, both genetic studies based on ancient Jomon mtDNA and those based on modern mtDNA more or less support the "dual-structure model" (Hanihara 1991). This also suggests a complex population history even during the Holocene. Nevertheless, what do these genetic implications tell us about Pleistocene population migrations into Japan? In other words, what does the genetic affinity of the Jomon peoples tell us about Paleolithic population dynamics? In general, because the descendants of Jomon and Yayoi both contributed to the formation of the current Japanese population, Paleolithic foragers should be regarded as the founding population of the Jomon (Hanihara 1991). However, the extent to which Pleistocene Paleolithic populations contributed to modern Japanese is largely unidentified, mainly because there are few genetic and human fossil records, with the exception of some good fossil specimens, notably Minatogawa Man (Baba, Narasaki, and Ohyama 1998; Suzuki 1982). The remaining question is how we understand the complexity in Japanese Paleolithic population history. A question that will not be addressed here is whether there is clear evidence that the Jomon were the direct descendents of the Japanese Paleolithic foragers and whether both hunter-gatherer populations were genetically continuous for the past 30,000 years in Japan.

What Does Archaeology Tell Us about Human Entry into Japan?

The Paleolithic archaeological record provides a basic picture of Pleistocene human population history in Japan. Although the number of Paleolithic sites during the 1960s was only slightly more than 300 (Ohyi 1968:52), the number of registered sites is now greater than 15,000 (Japan Palaeolithic Research Association 2010). Some clarification is necessary, however, regarding this latter number. The "sites" in the recent database include assemblages and collections of artifacts recorded in various contexts, ranging from extensively excavated sites to a few specimens collected on the surface. Because a single cultural level in a deeply excavated multilayered Paleolithic open-air site is counted as a single site, a single location was sometimes counted multiple times, and site size and artifact density from a single site are not standardized among the recorded sites. Although some bias is present in the record, the database is still useful to explore to understand general macro- and microregional patterns of human occupation across the entire Japanese Archipelago.

Considering the regional geographic features and Paleolithic culture history, I divided the 47 prefectures into 7 broader regions (fig. 2). From north to south, they are labeled as north (N), northeast (NE), southeast (SE), central (C), southwest (SW), south (S), and far south (FS). N, S, and FS are isolated islands corresponding to Hokkaido, Kyushu, and Ryukyu islands. NE, SE, C, and SW are the divisions of Honshu Island, the main island in the archipelago along with adjacent Shikoku. Divisions of NE, SE, C, and SW are based on the presence of mountain chains, plains, and the Pleistocene paleogeography. For example, C is
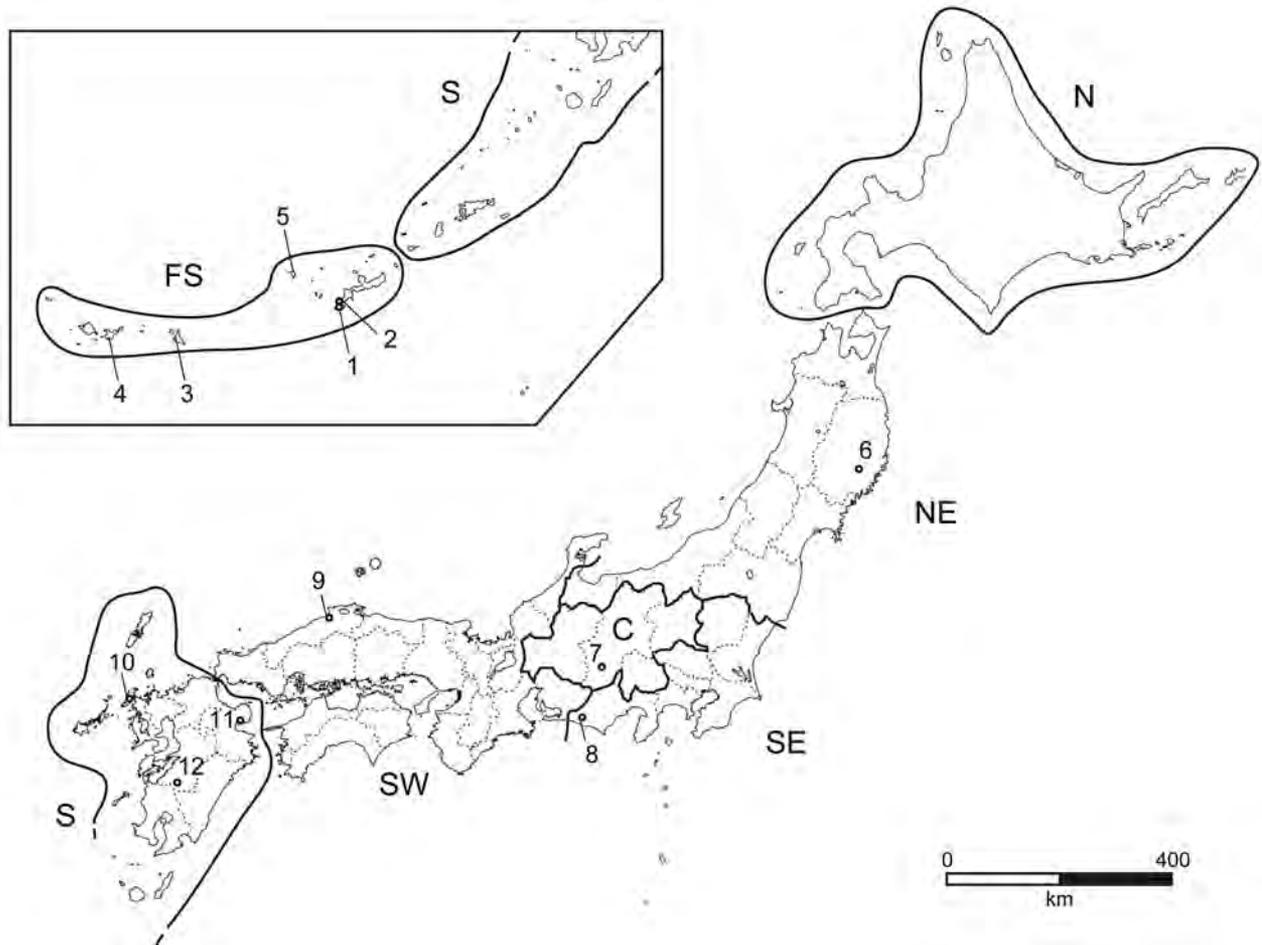
Figure 2. Microregions in the Japanese Archipelago. Bold lines represent the boundaries of microregions. Dotted lines within the islands define the current 47 administrative prefectures. Locations with numbers show the human paleontological and/or pre–Upper Paleolithic archaeological sites mentioned in the text. The sites are Minatogawa (1), Yamashita-cho (2), Pinza-abu (3), Shiraho-Saonetabaru (4), Shimojibaru (5), Kanedori (6), Takesa-Nakahara (7), Hamakita (8), Sunabara (9), Iriguchi (10), Sozudai (11), and Ōno (12). C = central; FS = far south; N = north; NE = northeast; S = south; SE = southeast; SW = southwest.

the region characterized by high-altitude mountains and plains mostly above 600–1,000 m asl. SW is the region in the middle of the Pleistocene Paleo-Honshu Island. Using the site location data recorded in the database, the number of archaeological sites is counted according to the microregions (table 2). The microregions are then sorted by site density using the areal extent data announced by the Geospatial Information Authority of Japan (2015). SE is the microregion with the highest density, followed by S, C, SW, NE, N, and FS. The highest density in SE is probably explained by sampling bias, due to the high population density in the Tokyo area. It is also because the deeply excavated sites yielded multiple levels of human occupation on the Musashino and Sagamino Uplands in the southern part of SE (e.g., Yajima and Suzuki 1976; Yamaoka 2010). Except for the microregions with the highest density (SE) and lowest density (FS), the site density shows a south to north inclination. High site density in SE, followed by a gradual increase from C to SW, NE, and N, is observed. The sites are all

attributed to the Pleistocene, whereas the chronological affiliations of these sites vary depending on the region, especially between N (the southern part of Paleo-SHK) and the rest of the microregions (i.e., Paleo-Honshu and Ryukyuan islands). The

Table 2. Counts, areal extent, and density of Late Pleistocene sites in Japan

Microregion	No. sites	Areal extent of microregion (km²)	Site density per 100 km²
Southeast	7,484	27,436.64	27.3
South	2,855	42,232.7	6.8
Central	1,537	35,010.4	4.4
Southwest	2,413	89,023.22	2.7
Northeast	1,612	98,563.63	1.6
North	862	83,424.22	1.0
Far south	8	2,281	.4
Total	16,771	377,971.81	4.4

Paleolithic in the Paleo-Honshu record started at the beginning of the Upper Paleolithic, around 40,000–37,000 years ago, and ended around 11,500 years ago (Yamaoka 2010; Yoshikawa 2014), whereas the beginning of the Paleolithic record in Hokkaido is not earlier than 30,000 years ago (Izuho et al. 2012; Naoe and Kudo 2014). Thus, the time depth of the Paleo-Honshu Paleolithic record is approximately 27,000 years, as opposed to 18,500 years for Paleo-SHK, because the reliable dates obtained from the hearths in the Agonki-5 site in Sakhalin are 23,500 years ago (Kuzmin et al. 2004; Vasilevski 2003). Because of the difference in time depths, the south to north inclination of site density implies that the earlier Paleolithic sites are more abundant in southern Japan than in northern Japan. High site density in the S microregion (Kyushu) next to the SE of the southern Kanto region in Honshu suggests that waves of the earlier hunter-gatherers would have migrated into Kyushu and spread to the north along Paleo-Honshu Island. Conversely, the likelihood of earlier human population migrations in the early Upper Paleolithic (EUP) from eastern Siberia via Paleo-SHK is not supported. On the one hand, site density patterns alone do not answer the question of timing and size of northerly migratory populations from Paleo-Honshu to Paleo-SHK. The lowest density of the FS microregion of the Ryukyu Islands suggests that human arrivals into the Ryukyu Islands were relatively low and that occupations were not necessarily continuous, unlike the situation in the microregions in Paleo-Honshu. Relatively high site density in C (the central region in Paleo-Honshu) suggests that humans occupied high-elevation regions during the Upper Paleolithic. Good examples are represented by the open-air sites located on the Nobeyama Plateau, where Paleolithic hunter-gatherers could have followed seasonal movements between the central highlands and southern Kanto regions in SE (e.g., Tsutsumi 2011), similar to pastoral transhumance (e.g., Chang and Tourtellotte 1993), and where groups of hunter-gatherers seasonally aggregating to kill large herbivores around lakes would have sometimes succeeded (e.g., Norton et al. 2010*b*). Given the population entry routes (fig. 1), the observed south to north inclination of site density in the Paleo-Honshu suggests that the majority of Paleolithic migratory groups were from the Korean Peninsula and southern China. If so, routes 1 and 5 are the best-supported routes for early hunter-gatherers' dispersals into the Japanese Archipelago.

Paleolithic Chronologies in Japan: Short- versus Long-Term Chronologies

In the study of population history, an establishment of cultural chronology is one of the major debated areas of research among the other topics in Paleolithic studies in Japan. Below, I give an overview of the long-term and short-term chronologies and discuss how both chronological models are relevant to global models of human population migrations and dispersals in Eurasia.

Clear evidence of the Japanese Paleolithic appears beginning around 40 ka, and blade technology was incorporated since the

earliest lithic assemblages appeared in the southern Kanto region in the SE microregion (Yamaoka 2010; but see Nakamura 2012). The gradual but consistent increase in the number of blade tools (e.g., endscrapers, burins, and perforators) and various blade-production technologies, including prismatic blade technology, which certainly spread across Japan during the Upper Paleolithic, suggests that the technology of the Japanese Upper Paleolithic is not dissimilar to that of the Upper Paleolithic in Europe. On the contrary, unique stone tools characterized in the Japanese EUP are principally represented by three classes of stone tools (fig. 3): trapezoids defined as abruptly and/or minimally retouched small flakes (Sato 1988), backed blades (Ono 1988) characterized by abrupt retouches and truncations on elongated flakes and/or blades traditionally described as knife-shaped tools (Serizawa 1960; Sugihara 1965; Tozawa 1990), and edge-ground axes (Tsutsumi 2012). The combination of trapezoids, knife-shaped tools, and edge-ground axes in EUP is unique to the Japanese Paleolithic industry, and they have not been recovered together in neighboring regions, such as South Korea (K. Bae 2010; Lee, Bae, and Lee 2016), which suggests that they were newly innovated in Japan at the beginning of the Upper Paleolithic; however, edge-ground stone axes attributed to MIS 3 have recently been identified at the Galsanri and Yonghodong sites in Korea (Lee, Bae, and Lee 2016). Indeed, knife-shaped tools long persisted as the formal stone tool class in the Japanese lithic industries, and the "knife-shaped tool culture" is the technocomplex that is extensively distributed from Kyushu to southern Hokkaido (e.g., Ambiru 1986; Morisaki 2012; Naganuma 2010; Ono 1988; Yoshikawa 2010). In the Korean Peninsula, the Upper Paleolithic industry has tanged points (Seumbe Chireugae) from its initial stage with the emergence of blade technology (C. Bae 2017, in this issue; K. Bae 2010; Lee 2015, 2016; Seong 2008, 2009; Seong and Bae 2016). Tanged points also appeared in Japan in the late Upper Paleolithic, around 30,000 years ago, mainly in the Kyushu region; however, they occur rather briefly, perhaps in response to small-scale human migrations from Korea or cultural transmission after the collapse of the regional environment in Kyushu, caused by the large explosive event of the Aira Volcano, which occurred some 30,000 years ago (Matsufuji 1987; Morisaki 2015). The traits shared between the retouch technologies used in the Japanese knife-shaped tools and the Korean tanged points make archaeologists hypothesize that an immediate technological transmission of tanged points from Korea to Japan at the beginning of the Upper Paleolithic stimulated the invention of knife-shaped tools (Ambiru 2010), which could be evidence of foraging groups migrating to Kyushu from the Korean peninsula (C. Bae 2017, in this issue; Matsufuji 1987).

Chronometric dates, mostly radiocarbon dates based on associated charcoal, demonstrate that the lithic industry characterized by a composite of trapezoids, knife-shaped tools, and edge-ground axes appeared in Japan at 40,000 to 38,000 years ago (Izuho and Kaifu 2015; Tsutsumi 2012; Yamaoka 2010). A substantial number of EUP assemblages (~500) dated to 38,000 to 30,000 years ago further indicate that modern *H. sapiens* mi-
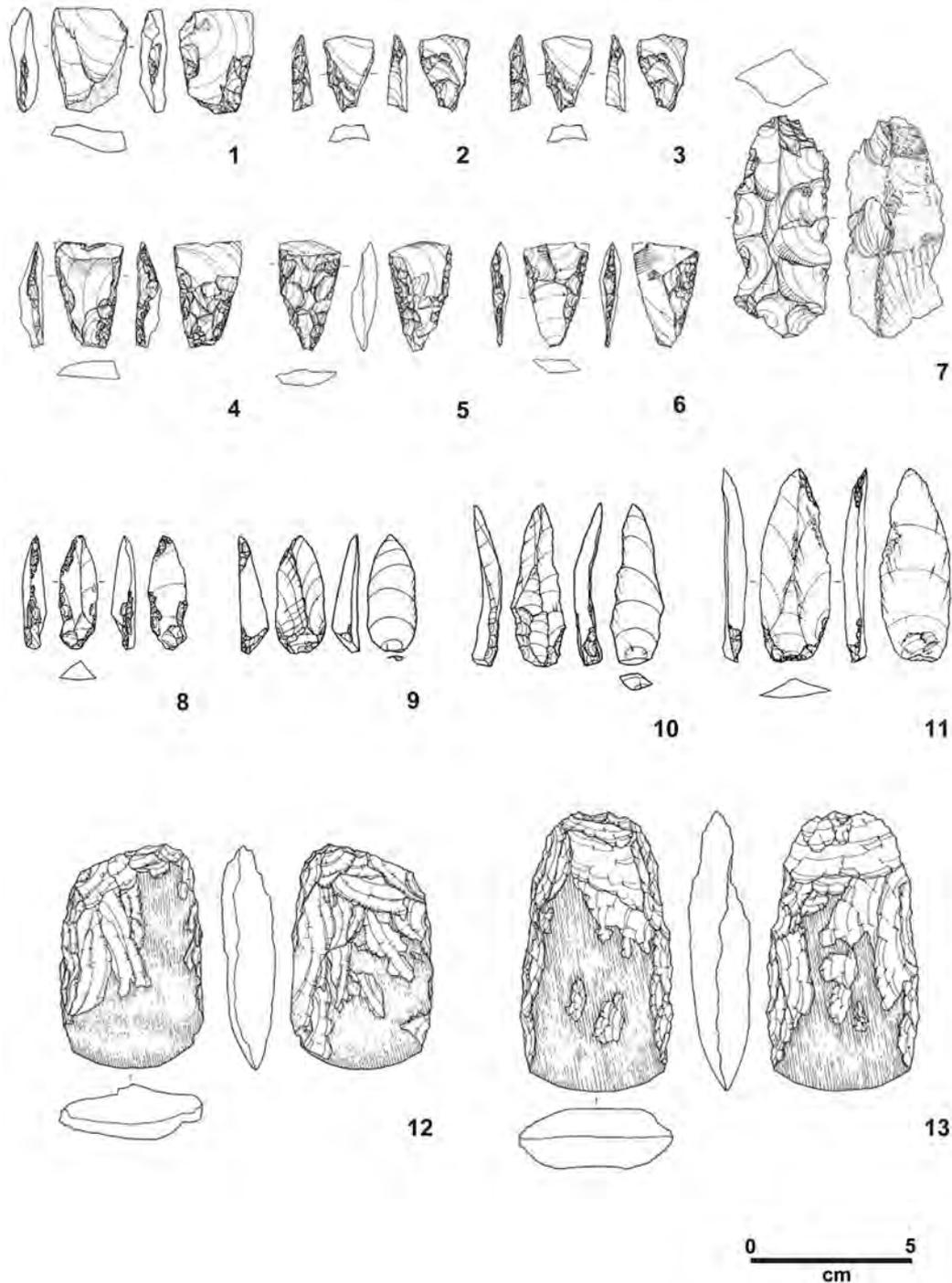
Figure 3. Examples of the major stone tools from the early Upper Paleolithic assemblages. 1–6 = trapezoids; 7 = a flake core with small flake scars served for blanks of trapezoids; 8–11 = knife-shaped tools (backed blades); 12–13 = edge-ground axes. Tools 1–3 and 8 are from Jizoden (Kanda 2011). Tools 4–7, 12, and 13 are from Hinatabayashi B (Tani 2000). Tools 9 and 10 are from Happusan (Suto 1999). Tool 11 is from Nawateshita (Yoshikawa 2006).

grated into the Japanese Archipelago around 40,000 years ago, bringing the new lithic technological complex (Izuho and Kaifu 2015). Culture-chronological division between the Early and Late Paleolithic to characterize lithic industries in East Asia

(Gao and Norton 2002; Ikawa-Smith 1978; Seong and Bae 2016) may also be validly applicable to the current Japanese Paleolithic record, although it is necessary to address the question of whether there was Paleolithic human occupation before 40 ka

and, if there was, how the earlier Paleolithic record is related to other East Asian Paleolithic records, notably those in China and Korea.

The possibility of an archaeological record before 40 ka was largely dismissed when the Early Paleolithic hoax was exposed in 2000. At that time, it was shown conclusively that the Early and Middle Paleolithic stone tool industries from Miyagi Prefecture were all faked by an amateur archaeologist beginning in the 1980s (Nakazawa 2010; Yamada 2001). Before the fakes were produced, however, the reality of an Early Paleolithic in Japan had been seriously discussed for several sites, such as Sozudai in northern Kyushu and Hoshino in Honshu (Serizawa 1971; Yanagida and Ono 2007). The debate regarding the reality of the Early Paleolithic industry was largely over the issue of whether the fractured flakes were man-made artifacts or not (i.e., geofact). Quaternary geologists suggested that the geological layers of "archaeological artifacts" were derived from alluvial/colluvial sediments that could have created naturally fractured cobbles to make flake-like geofacts (Arai 1971). In contrast, a systematic examination of the angle between the striking platform and the ventral surface of flakes from the pre-40 ka level in the Sozudai site suggested that they were man-made (Bleed 1977), which was largely supported by the proponents of the long-term chronology in the Japanese Paleolithic (Serizawa 1982). Although debate over these sites was shelved while the sensational finds were being "discovered" in Miyagi Prefecture, since the hoax was exposed, many of these sites have subsequently been revisited (e.g., Hagiwara 2006; Ikawa-Smith 2016; Matsufuji 2010; Naruse 2010; Sato 2016; Wada 2016). The candidate assemblages for occupation of the archipelago before the Upper Paleolithic are Kanedori (Tohoku region, NE), Takesa-Nakahara (central Japan, C), Sunabara (southwestern Honshu, SW), and Iriguchi (northern Kyushu, SW; see fig. 2). Multiple criteria have been employed to assign them to before the Upper Paleolithic. First, flaking and retouch technologies have been used. Besides mechanical criteria to distinguish flakes from geofacts (Barnes 1939; Bleed 1977), a peculiar flaking technology called "obtuse angle technology" (Nagai 2011) that is often found in spheroids in the "Lower/Middle Paleolithic" industry in South Korea (Lee 2015) is chosen. The second criterion is whether these stone tools are really different from or similar to the earliest Upper Paleolithic assemblages (i.e., edge-ground axes, knifeshaped tools, and trapezoids) with respect to patterns in tool morphology, reductive technology, and raw material use (e.g., Matsufuji 2010; Suto 2006). For example, Matsufuji (2010:196) suggests that crude and large tools with two small flakes recovered from the Kanedori IV layer are different from the EUP industry, and therefore it is attributed to the "broader East Asian core and flake tool tradition." The third criterion is the chronological age of the assemblage. Instead of using chronometric dates associated with tool assemblages from before the Upper Paleolithic, Japanese Paleolithic archaeologists have usually employed tephras to develop culture-stratigraphic sequences.

Based on the above multiple criteria, most of the Japanese assemblages from before the Upper Paleolithic cannot support the arrival of humans before 40 ka. However, some recently excavated sites, notably Sunabara, have been investigated through examination of site integrity (Matsufuji and Uemine 2013; Uemine, Matsufuji, and Shibata 2016) and microscopic analysis of fracture mechanics in rhyolite (a coarse-grained material recovered from the site) to identify the man-made nature of lithic artifacts (Uemine 2014). These efforts may eventually stand up to further scientific scrutiny to support an MIS 5e human arrival in the archipelago, as some researchers propose. However, in a case like Sunabara, researchers will be further required to explain how man-made "artifacts," naturally fractured debris, and naturally transported pebbles were all recovered together in the same alluvial sediments (i.e., layer VIa; Uemine 2014). Only a thorough analysis of the site formation processes may really answer this question.

Among the other artifacts, the lithic assemblages from Kanedori layers IV and III are the most promising lithic artifacts attributable to before the Upper Paleolithic in Japan (Kuroda et al. 2005, 2016; Matsufuji 2010). The lower level of Kanedori layer IVb, where the lower assemblage was recovered, has multiple tephras that were secondarily deposited, suggesting that the age of layer IVb is in the time range of 50,000 to 90,000 years ago (Soda 2005; Yagi 2005). Despite the seeming credibility of stratigraphy, lithic artifacts, and tephra-assisted chronometric dates in the Kanedori assemblages from before the Upper Paleolithic, the number of candidates for Japanese lithic assemblages from before the Upper Paleolithic is still small. Even among the 16 so-called assemblages, there are surface collections (e.g., Kaseizawa) that are undateable (Sato 2016:31, table 1). More detailed evaluation of the characteristics and variability in those assemblages requires further systematic comparison through technological and morphological studies (e.g., Bleed 1977; Nagai 2011). Given the sporadic and sparse occurrence of those candidates for sites from before the Upper Paleolithic, categorizing them into the notion of the "Early Paleolithic" and the extent to which they are comparable to the archaeological record in the East Asian mainland (e.g., Gao 2013; Gao and Norton 2002; Wang 2005) will be an important future research avenue.

Discussion

How much do we know about the Pleistocene human population history in Japan, and how much do we not know? With respect to human migratory routes into the Japanese Archipelago, of the six hypothesized routes of human entry (fig. 1), the routes from the Korean Peninsula and southern China to Kyushu (i.e., routes 1 and 5), a southern part of Paleo-Honshu Island, are the most parsimonious based on the Paleolithic site density and technological and morphological comparisons of formal stone tools between Japan and Korea during the EUP. This route was likely, given that hunter-gatherer population density in the adjacent regions would have been higher than Paleo-Honshu at the time of the earliest population entry. For example, researchers have identified an increasing number of

Middle and Late Pleistocene sites in southern China (e.g., Pei et al. 2013; Shen and Keates 2003; Wang 2003, 2005; Wei et al. 2017), suggesting that the Late Pleistocene hunter-gatherer population density in southern China was higher than that in Paleo-Honshu.

In contrast with the extensive Paleolithic record in Japan, the Pleistocene human fossil record is primarily concentrated in the Ryukyus. This implies that Upper Paleolithic hunter-gatherers had already migrated into the far southern Japanese islands by seafaring, although the migratory route to get to the Ryukyus is still not clear. It is possible that the initial foragers to arrive in the Ryukyus came from Taiwan in the south (Kaifu et al. 2015) or from southern Kyushu in the north. The latter route was present at least during the Holocene (Obata, Morimoto, and Kakubuchi 2010; Yamazaki 2012). To further complicate the various migration models, ancient DNA data largely support gene flow from eastern Siberia to Hokkaido, possibly since the LGM. If this were the case, Pleistocene population dynamics were more complex than the admixture model, which assumes population continuity from the Paleolithic to Jomon, followed by the admixture of late Holocene Yayoi peoples, as outlined in the dual-structure model (Hanihara 1991).

A more complex picture of Pleistocene hunter-gatherer migrations into the Japanese Archipelago is legitimately implied from the long- and short-term chronologies of the Japanese Paleolithic record. In the framework of the long-term chronology, the question is the extent to which human populations before the Upper Paleolithic (>40 ka) contributed to the establishment of subsequent hunter-gatherer populations since 40 ka. Regardless of the relationship between populations, given the scarce evidence of credible human occupations before 40 ka, which has so far only been provided from a small number of archaeological sites (e.g., lithic industry from the Kanedori before 50 ka), the human population size before 40 ka in Japan was smaller than that of the Upper Paleolithic. In stone tool technology, although it could be an effect of small sample size ($n = 40$), there seems to have been a change from the unstandardized retouched tools and heavy-duty tools in the industry before 40 ka, as represented by the Kanedori III assemblage, to the formal and standardized stone tool inventory consisting of trapezoids, knife-shaped tools, and edge-ground hand axes in the EUP. This change further suggests that the EUP tool inventory and technology were independently invented among hunter-gatherers before the Upper Paleolithic. In contrast, the currently dominant short-term Paleolithic chronology may pose a different explanation for technological change. In the short-term chronology, the EUP hunter-gatherers were the first population to enter into the Japanese Archipelago. In this context, the EUP tool inventory and blade technology were all brought into Japan, and the subsequent proliferation was the result of relatively rapid population expansion across the archipelago (i.e., demic expansion; Cavalli-Sforza, Menozzi, and Piazza 1993). The Upper Paleolithic demic expansion in Japan syncs well with the modern *Homo sapiens* single-dispersal model out of Africa and rapid dispersal into South Asia (e.g., Forster and Matsumura 2006; Mellars 2006*a*,

2006*b*). However, Upper Paleolithic lithic industries that appear after the end of the EUP (~30,000 years ago) exhibit extensive regional variation, particularly in the technological, morphological, and stylistic characteristics of the complexes represented by the knife-shaped tools (e.g., Morisaki 2012; Ohyi 1968; Yoshikawa 2010), bifacial points (e.g., Hashizume 2015), and microblade cores (e.g., Sato and Tsutsumi 2007). The observed variation might have been created by a combination of human migrations from the East Asian mainland and endemic technological invention and transformation among Upper Paleolithic hunter-gatherers between the different microregions in the Japanese Archipelago. The interactions and foraging across the boundaries of microregions are often perceived in archaeological patterns, including the long-distance transportation of obsidian (e.g., Tsutsumi 2010) and isolated occurrences of regionally stylistic weapons outside of their core areas, such as the Kou-type knife-shaped tools (e.g., Kato 1975; Morisaki 2012). Moving forward, it will be critical to evaluate the extent to which indigenous hunter-gatherer population density at the microregional scale and the size of populations dispersing from the East Asian mainland covaried and influenced cultural change and variation on the archipelago. Given the complex nature of the Paleolithic archaeological record, human occupation history in Japan is likely compatible with a multiple-dispersal model of *H. sapiens* (e.g., Bae and Bae 2012; Boivin et al. 2013; Lahr and Foley 1994; Petraglia et al. 2010).

What makes the population history in Japan complicated is that the migration from the north via Paleo-SHK was significantly later than for Paleo-Honshu. While a small number of trapezoids that are morphologically comparable to those of the EUP in Paleo-Honshu have been identified in some assemblages in eastern Hokkaido, allowing some archaeologists to place them in late MIS 3 (e.g., Izuho and Takahashi 2005; Oda and Morisaki 2016), archaeological assemblages from the sites having secure associations of chronometric dates and stratigraphy in Hokkaido only appear at the onset of the LGM, 25,000 years ago (Izuho et al. 2012). Flake technology, blade, and microblade technologies were incorporated into the LGM technocomplex in Hokkaido (Izuho et al. 2012; Nakazawa and Izuho 2006, Nakazawa et al. 2005), which later converged into the microblade technocomplexes (Nakazawa and Yamada 2015). This development likely resulted from a combination of independent innovation, cultural transmission, and demic expansion from eastern Siberia and Paleo-Honshu in and after the LGM (e.g., Buvit et al. 2016; Graf 2009; Nakazawa et al. 2005; Nakazawa and Yamada 2015). Why the initial occupation of Paleo-SHK lagged behind that of Paleo-Honshu by some 15,000 years is another area that needs to be further investigated.

Although the number of migratory events is difficult to tease out from the current archaeology, human paleontology, and human genetic records, it is likely that it was the result of the admixture of two opposite large migratory events, similar to the Korean Upper Paleolithic (K. Bae 2010; Bae and Bae 2012). This population admixture likely occurred during MIS 2 (30,000 to 11,500 years ago) and involved an influx of hunter-gatherers

from the north and south. Evident increases in the number of sites and stone tool technological variability during MIS 2 in both Paleo-Honshu and Paleo-SHK (e.g., Nakazawa and Yamada 2015; Ono et al. 2002; Suto 2006) could be explained by demographic increase and an associated cumulative adaptive culture model (e.g., Henrich 2004; Shennan 2001; Powell, Shennan, and Thomas 2009, 2010).

An examination of current evidence in Paleolithic archaeology, human paleontology, and human genetics in Japan necessarily provides a complex picture of Late Pleistocene demographic history. In the vast region of Asia, describing the Pleistocene population history in the Japanese Archipelago will doubtlessly be important in understanding human colonization and evolutionary history. Moreover, the accumulated Paleolithic record in Japan has the potential for improving understanding of the complexity of Pleistocene hunter-gatherer cultural and biological evolution.

Acknowledgments

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The Timing and Nature of Human Colonization of Southeast Asia in the Late Pleistocene

A Rock Art Perspective

by Maxime Aubert, Adam Brumm, and Paul S. C. Taçon

Recent technological developments in scientific dating methods and their applications to a broad range of materials have transformed our ability to accurately date rock art. These novel breakthroughs in turn are challenging and, in some instances, dramatically changing our perceptions of the timing and the nature of the development of rock art and other forms of symbolic expression in various parts of the late Pleistocene world. Here we discuss the application of these methods to the dating of rock art in Southeast Asia, with key implications for understanding the pattern of recent human evolution and dispersal outside Africa.

Rock art is the world's most widespread and long-lasting form of visual heritage and an archive of deep-time human experience. Rock art consists of paintings, drawings, stencils, prints, engravings, bas relief, and beeswax designs placed in caves and rock shelters, on boulders and rock platforms. Rock art sites are special, often spectacular places that reflect ancient human experience, identity, history, change, conflict, political viewpoints, spirituality, and relationships to land. As modern humans colonized the globe, they transformed natural landscapes into culturally meaningful places, and the worldwide distribution of rock art attests to its potency as a form of symbolic storage. This is because the creation of rock art within enduring rocky landscapes allowed ancient humans to transmit complex thought between different groups and across generations. Stories, experiences, and important events could be conveyed in new ways not solely reliant on oral history, enhancing memories and generating new interpretations in the process.

The roots of the modern human capacity to communicate using symbols likely have a long development (McBrearty and Brooks 2000; Taçon 2006; and see various references in Mellars et al. 2007) rather than resulting from a sudden, dramatic, and relatively recent evolutionary change in human cognition, as has often been argued (e.g., Klein 1989, 1992; Pfeiffer 1982; Wadley 2001). Meandering lines engraved on the surface of a bivalve shell from Trinil on the Indonesian island of Java at ~500 ka (Joordens et al. 2015), presumably the handiwork of *Homo erectus*, suggest that a capacity for complex abstract reasoning and symbolic thought may have existed among certain archaic and now extinct forms of humans. Concerning the latter, the apparent use of mineral pigments as colorants dates to at least 300–200 ka in both Africa (Barham 2002) and Europe (Roebroeks et al. 2012) and thus precedes the evolution of our species. Some authorities also contend that at least one now-extinct *Homo* lineage—Neanderthals—engaged in distinctly modern human-like patterns of symbolic activity, including the use of ochre and other pigments as colorants (e.g., Roebroeks et al. 2012); use of perforated shells (Zilhão et al. 2010), bird feathers, claws (Finlayson et al. 2012; Peresani et al. 2011), and other objects as bodily ornaments; engraving of abstract patterns on immobile rock surfaces (Rodríguez-Vidal et al. 2014); and the production of elaborate stone structures inside dark caves (Jaubert et al. 2016). Scientists are divided over the meaning of this behavior, however; indeed, the notion that even late-surviving Neanderthals had acquired elements of cognitive "modernity," either independently or through direct cultural (or genetic) contact with *Homo sapiens*, remains the subject of protracted debate (e.g., Langley 2013; Taçon 2010).

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Current evidence suggests that the capacity for modern human cognition and symbolic behavior emerged during the Middle Stone Age (MSA) of sub-Saharan Africa (e.g., Henshilwood, d'Errico, and Watts 2009; Henshilwood et al. 2011; Lombard 2011, 2012) and, most likely, prior to the radiation of our species from out of this continent. Ochre pieces engraved with nonfigurative imagery (mostly simple geometric patterns) have been recovered from Klasies River (d'Errico, García Moreno, and Rifkin 2012), Blombos Cave (Henshilwood, d'Errico, and Watts 2009; Henshilwood et al. 2002), and Klein Kliphuis (Mackay and Welz 2008) in deposits thought to date to ~100 ka, ~100–72 ka, and ~50 ka, respectively. A paint-making "workshop" was also recovered from stratified deposits at Blombos Cave dating to ~100 ka (Henshilwood et al. 2011). Engraved ostrich eggshell fragments from Diepkloof (Texier et al. 2010, 2013), Klipdrift Shelter (Henshilwood et al. 2014), and Apollo 11 (Vogelsang et al. 2010) have been dated to ~60 ka, ~70–55 ka, and ~50 ka. The earliest example of representational or "complex" art from Africa consists of stone plaques adorned with figurative depictions of animals, among other visual imagery. These objects were recovered from excavations at Apollo 11 Cave in Namibia in archaeological levels dated to ~30 ka (Jacobs et al. 2008; Vogelsang et al. 2010; Wendt 1972, 1974, 1976). With regard to other material expressions of symbolic thought—personal ornaments—shell beads from Blombos date to as early as 75 ka, while the oldest known examples of objects unmistakably modified into jewelery by modern humans (marine shell ornaments dated to ~100 ka) were recovered from Skhul Cave and Qafzeh Cave in Israel (Bar-Yosef Mayer 2005; Bar-Yosef Mayer et al. 2009; Vanhaeren et al. 2006).

It has long been argued or tacitly assumed by many scholars that the origin of representational or complex art, especially rock art, lay outside of Africa in the deep, dark caves of Upper Paleolithic Europe (e.g., Clottes and Lewis-Williams 1998; Hodgson 2012, 2017; Lewis-Williams 2002). Research into the beginnings of art has traditionally been influenced by the idea of a creative explosion that is said to have occurred around 40 ka among the first modern human inhabitants of Europe. For many authorities, this was a key period in human evolution during which the minds of our ancestors underwent rapid and profound changes, and a panoply of new and sophisticated forms of symbolic behavior emerged (Clottes and Lewis-Williams 1998; Hodgson 2012, 2017; Klein 1989, 1992; Pfeiffer 1982). In particular, the masterful creations of the Aurignacian artists of Western Europe, such as the stunning paintings of lions, horses, and other animals in France's Chauvet Cave (37–33.5 ka; Quiles et al. 2016) and the exquisitely crafted ivory figurines (~40–30 ka; Conard 2003) from the Swabian Alps of Germany, are viewed as pivotal milestones in the emergence of modern culture (e.g., Hodgson 2017).

As recently announced, however, new dating evidence has emerged for equally early rock art in Southeast Asia (Aubert et al. 2014; Taçon et al. 2014), challenging long-held assumptions about the emergence of the first rock art traditions. The purpose of this paper, in light of this discovery, is to consider the ways in which new forms of rock art dating are altering conventional ideas about the origin of art and symbolic expression and first appearances of the "modern" mind outside Africa. The paper consists of two parts. First, we present a detailed overview of rock art dating and how it works, providing the necessary background for our subsequent discussion of recent breakthroughs in the dating of Pleistocene art in tropical Southeast Asia, with a focus on the Sulawesi artworks. Second, we consider the implications of these findings for our understanding of the dispersal of *H. sapiens* into this region.

Dating Rock Art

There are two main groups of radiometric dating methods that can be applied to rock art: direct and indirect methods. The former implies that the archaeological item itself (the art) is directly dated. Indirect dating, however, relies on the dating of associated materials. It is therefore imperative that the relationship (i.e., the context) between the dated sample and the art is unambiguous. In some rock art studies, direct dating often involves the radiometric dating of associated materials such as secondary mineral accretions (i.e., speleothem) in direct association with the art (e.g., Aubert et al. 2014) or the sediments in which it occurs (e.g., Huyge et al. 2011). The term "direct dating" is often used to distinguish radiometric rock art dating methods from nonradiometric methods, such as the use of "diagnostic" subject matter (e.g., Akerman 1998) and superimposition of rock art styles (Walsh and Morwood 1999). This paper only refers to radiometric dating methods, and, as such, the direct dating of rock art requires that the archaeological item itself (i.e., the art) is directly dated. The dating of associated materials such as secondary mineral accretion in association with the art is known as indirect dating.

Direct Dating of Rock Art

Radiocarbon dating can in principle be applied to determine the age of organic materials present as part of the paint composition. For example, the radiocarbon dating of charcoal pigment has been used to provide age estimates for various cave paintings and drawings, with famous examples from sites across Europe such as Chauvet Cave in southern France (e.g., Quiles et al. 2016). It is always possible that charcoal pigment used by prehistoric image-makers was significantly older than the marking event that created the artwork. Hence, and despite implicit assumptions to the contrary, radiocarbon dating of charcoal pigment can only provide a maximum age for the art. There is also the added difficulty of potential contamination by other sources of carbon. These contaminating materials can, in principle, be removed by chemical pretreatments (Douka and Higham 2017). The potential mixing of charcoal of different ages, which cannot be removed by pretreatment, can also be an issue.

Similarly, rock art images created using beeswax—well-known motif types in some parts of northern Australia, in particular—can be directly dated with radiocarbon. These images are predominantly composed of bee-collected plant resin and a small amount of wax (Morwood, Walsh, and Watchman 2010; Taçon et al. 2004, 2010). A light pretreatment (Nelson 2000) is usually applied in order to remove nonorganic contaminants, but no pretreatment for organic contaminants can be used. The results therefore represent the total organic carbon content of the material used to create the imagery. The dating of beeswax motifs can also provide minimum and maximum ages for overlying and underlying artwork.

Organic binders or other intrusions of organic materials such as blood, fats, semen, saliva, urine, and plant juices and fibers could have been mixed with inorganic components in paints (e.g., Gillespie 1997; Loy et al. 1990; Prinsloo et al. 2013). These can potentially be radiocarbon dated, but the nature and source of the organic components must be identified. Consequently, the selected organics chosen to represent the painting event need to be separated from unrelated organic fractions. The positive identification of these organic components is quite difficult and often a matter of debate (Gillespie 1997; Loy et al. 1990; Matheson and Veall 2014; Prinsloo et al. 2013). It is sometimes possible to visually identify and physically extract organic materials such as plant fibers from paint (e.g., Watchman and Cole 1993). Organism-specific organic compounds (biomarkers) can be, in principle, identified, isolated, purified, and radiocarbon dated (e.g., Eglinton et al. 1996). Compound-specific radiocarbon analysis is a promising avenue for rock art dating. Challenges include the difficulty of obtaining adequate quantities of samples from selected fractions.

In brief, pigment layers (and associated mineral accretions; see below) are likely to contain a mixture of organic substances, each with a different radiocarbon signature. These may potentially include unrelated younger and older organic materials that could have been incorporated at or after the marking event. Furthermore, certain living organisms, such as predatory invertebrates, are known to incorporate carbon from several sources (e.g., Hågvar and Ohlson 2013; Teuten, Xu, and Reddy 2005). These sources might be older than the marking event (Hågvar and Ohlson 2013). Total radiocarbon analysis can therefore lead to misleading age estimates for marking events. It is essential that the nature and source of these organic substances be positively identified and separated from other unrelated sources. This allows the radiocarbon age of the sample to be tied directly to its provenance, which could then be related to the marking event.

In the vast region encompassing mainland and island Southeast Asia, where the number of dated rock art sites is extremely small, direct dating of motifs has, to our knowledge, never been applied. Radiocarbon dating could potentially be applied to the numerous charcoal paintings and drawings attributed to the Austronesian expansion in the region in the Holocene (O'Connor et al. 2015).

Indirect Dating of Rock Art

The indirect dating of rock art, as described here, requires that the art be radiometrically dated by association. This can occur in the form of excavated pieces of decorated rock surfaces that have detached from overhead art panels and subsequently become incorporated into the burial matrix (e.g., David et al. 2013; Wendt 1976) or, indeed, portable artworks (*art mobilier*) recovered from securely dated stratigraphic contexts. Similarly, decorated rock surfaces that have been covered or partly covered over by sediments in situ can potentially be dated by association with the sedimentary deposit (e.g., Huyge et al. 2011; Rosenfeld, Horton, and Winter 1981). In the first instance, analyzing datable materials present in the sedimentary units in which the artwork was found, or immediately above, can provide a minimum age for the art. In the second instance, datable materials present at the same depth or above the artwork provide the minimum age. Datable materials include any material usually used for dating archaeological deposits, such as organic material (radiocarbon), grains of quartz and feldspars (luminescence), fossil bones and teeth (electron spin resonance and uranium series), and speleothem (uranium series). Providing accurate and reliable dates for art using these techniques relies on establishing whether the association between the datable materials and the art is genuine (e.g., ruling out the possibility of movement of older or younger sediment, vertical displacement or intrusion of art objects, and so on).

Rock surface coatings are often found in association with rock art. Some of these features may be datable or may contain datable materials. If an age estimate is obtained for mineral accretions overlying a painting or an engraving, it can provide a minimum age for the art. Similarly, an age estimate for a rock surface coating underlying a painting can provide a maximum age for the art. Examples of datable rock surface coatings often found in association with rock art include amorphous silica skins (e.g., Morwood, Walsh, and Watchman 2010), rock "desert" varnishes (e.g., Watchman 2000), oxalate-rich crusts (e.g., Morwood, Walsh, and Watchman 2010), and calcium carbonate accretions (e.g., Aubert et al. 2007, 2014; Pike et al. 2012).

Radiocarbon dating has been used to date organic materials in rock surface coatings overlying and underlying rock art. In most cases, the analyses are performed on the total organic content and, as such, face similar issues as those mentioned above for the direct dating of pigment layers (e.g., possible contamination from carbon from various sources unrelated temporally to the marking event). Moreover, the modes of formation of certain rock surface coatings such as rock desert varnishes and oxalate-rich crusts are not fully understood, making any dating attempt with radiocarbon or other methods dubious. Compound-specific carbon analysis (stable isotopes and radiocarbon) could potentially resolve questions about their modes of formation as well as providing a valuable dating method.

There are other indirect rock art dating methods available, such as optically stimulated luminescence dating (OSL), which has been applied to mud-wasp nests associated with rock art (Roberts et al. 1997; Ross et al. 2016). However, these have never been applied in Southeast Asia and are not described here.

Southeast Asia's Dated Rock Art

Southeast Asia harbors a significant collection of prehistoric rock art, possibly spanning many tens of thousands of years of human cognitive and cultural evolution (Taçon et al. 2014). The region encompassing mainland and island Southeast Asia includes some 400,000 km² of karst, including some of the largest limestone karst ecosystems on earth (Clements et al. 2006). Rock art is often found within these landscapes and is sometimes partly covered over by secondary calcium carbonate deposits. Rock art is also sometimes found over layers of calcium carbonate accretions or even sandwiched between them, in the latter instance providing the potential opportunity to acquire both minimum and maximum ages for associated art. Two dating methods, radiocarbon dating and uranium-series dating, have been applied to date these calcium carbonate accretions in association with what has now been revealed as some of the most ancient surviving examples of rock art on the planet.

Calcium carbonate accretions such as flowstone (e.g., Aubert et al. 2007; Pike et al. 2012; Taçon et al. 2012) and coralloid speleothem (Aubert et al. 2014) have been found in association with rock art and can provide minimum and maximum age estimates for the art. Radiocarbon dating can be applied to calcium carbonate accretions (Plagnes et al. 2003; Taçon et al. 2012) but is considered problematic principally because of possible contamination from a range of sources of carbon (similar to the issues mentioned above) and unknown contribution from geologically "dead" carbon (Harmon and Wicks 2006). The dead carbon content in speleothem can be up to at least 38% (Genty et al. 2001), and its contribution will result in an overestimated radiocarbon age. Therefore, obtaining reliable calendar ages with speleothem radiocarbon dating requires estimation of the fraction of dead carbon incorporated in the sample. This is usually achieved by using both uranium-series and radiocarbon chronologies simultaneously (e.g., Genty et al. 2001). When possible, active calcium carbonate accretions can also be employed to estimate the dead carbon fraction, assuming a constant input through time. The issues related to contamination from unknown sources of carbon could also potentially be addressed by compound-specific carbon analysis.

Uranium-series disequilibrium dating is the method of choice for dating calcium carbonate accretions in association with rock art (e.g., Aubert et al. 2007, 2014; Pike et al. 2012; Plagnes et al. 2003; Taçon et al. 2012). Similar to the method mentioned above, uranium-series disequilibrium dating can provide minimum and maximum ages for individual motifs. When precipitated from saturated solutions, calcium carbonate usually contains small amounts of soluble uranium (^{238}U and ^{234}U)

that eventually decay to ^{230}Th. The latter is essentially insoluble in cave waters and will not precipitate with the calcium carbonate. This produces disequilibrium in the decay chain, whereby all isotopes in the series are no longer decaying at the same rate. Subsequently, all the isotopes in the decay chain will decay until secular equilibrium, the rate at which the thorium decays will equal the rate at which it is being produced by the decay of uranium, is reached. Because the decay rates are known, the precise measurement of these isotopes allows calculation of the age of the carbonate formation. The dating range of the uranium-series approach depends on the ability to measure isotopic ratios that are different from, but close to, equilibrium. This is based on the size of the errors, which is a function of the uranium concentrations in the sample and the detection system. Multicollector inductively coupled plasma mass spectrometry (MC-ICP-MS) measurements can be used to estimate closed system $^{230}Th/^{234}U/^{238}U$ ages ranging from just a couple of years up to about 600,000 years. For more information on this dating method and its applications, see Bourdon et al. (2003).

Recent improvements in uranium-series analysis enable the measurement of minute calcium carbonate samples at very high precision. These improvements now allow the measurements of minute samples in direct association with rock art. However, in order to accurately date rock art with such a technique, certain principles must be met:

1. *The marking event that is being dated must be unambiguous.* This principle applies to any rock art dating method whereby the art was intentionally made rather than a by-product of some other activities. A pigment layer found sandwiched between layers of rock surface coatings with no identifiable motif is not diagnostic evidence for rock art production (e.g., Aubert et al. 2007; Watchman 1993). Similarly, a pigment layer with no identifiable motif found on a slab recovered from an excavation cannot be directly linked to rock art production (e.g., O'Connor and Fankhauser 2001). Ocherous materials occur naturally in caves and rock shelters (Aubert et al. 2007; Huntley et al. 2015; Taçon et al. 2012). Moreover, ochre was not exclusively used for creating rock art (e.g., d'Errico, García Moreno, and Rifkin 2012; Rifkin et al. 2015; Rosso, d'Errico, and Zilhão 2014; Zipkin et al. 2014).

2. *The stratigraphic relationship between the dated sample and the pigment layer must be unambiguous.* This principle also applies to any indirect rock art dating method. Calcium carbonate accretions are usually composed of multiple layers that have been deposited at different times. These layers can also be undulating, with their complex topography complicating attempts to precisely define their stratigraphic position in relation to the pigment layer. In Sulawesi (see below and Aubert et al. 2014), samples of coralloid speleothems overlying rock art motifs were sawn in situ so as to produce a continuous microstratigraphic profile extending from the outer surface of the coralloid through the pigment layer and into the underlying rock face or coralloid (Aubert et al. 2014; fig. 1). This sampling strategy was employed because at some locations
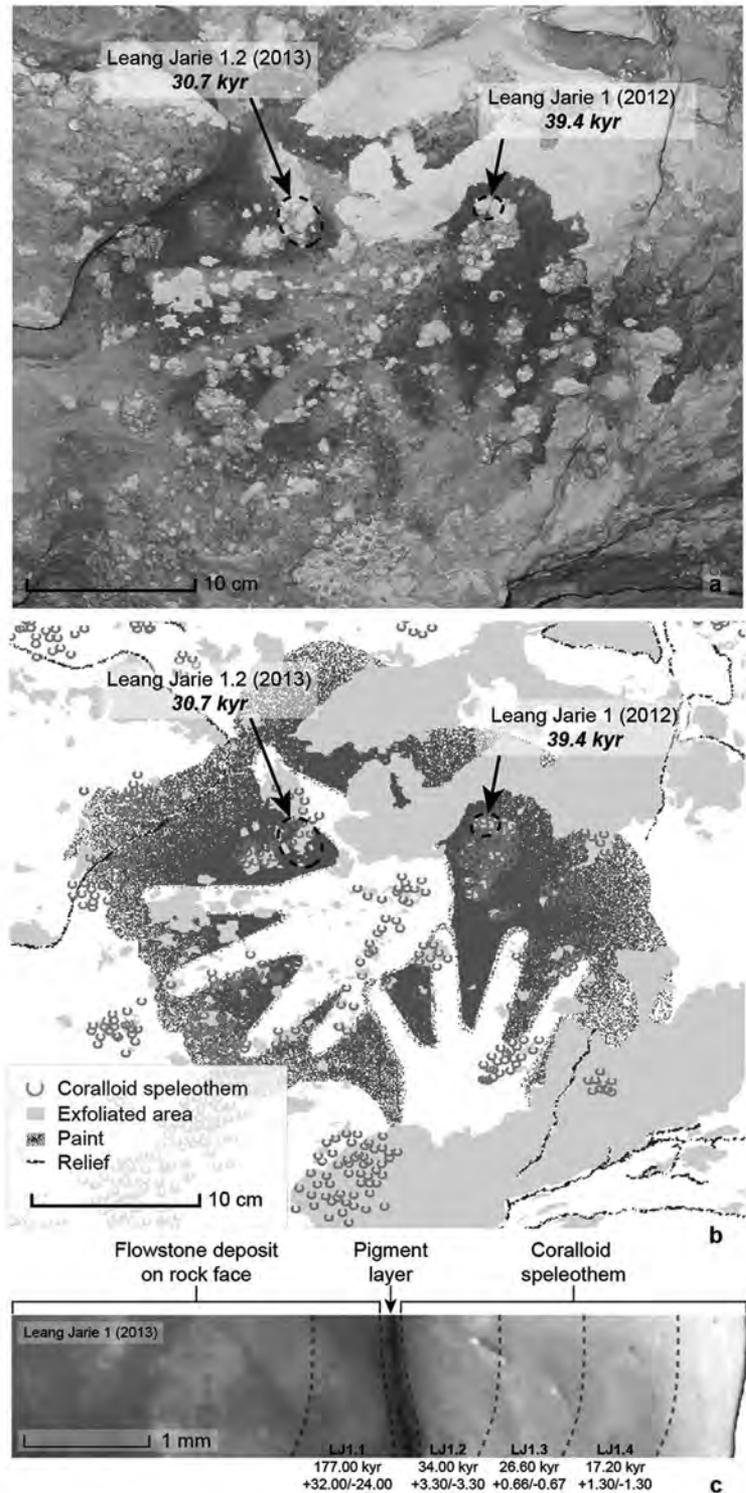
Figure 1. Dated rock art from Leang Jarie, Sulawesi, Indonesia. *a*, *b*, Photograph (*a*) and tracing (*b*) showing the locations of the dated coralloid speleothems and associated hand stencils. *c*, Profile of the coralloid speleothem Leang Jarie 1 (2013) showing the microexcavated subsamples bracketing the age of the paintings. The Leang Jarie 1 (2012) sample is from above the pigment layer and so only provides a minimum age for the underlying hand stencils. Source: *Nature* (Aubert et al. 2014). A color version of this figure is available online.

pigment layers directly overlying coralloid speleothems were observed with no additional calcium carbonate accretions covering them. Coralloid speleothems were also observed where the surface had completely weathered away, making it impossible to determine from visual inspection alone if the pigment layer associated with the identifiable motif had also weathered away or if portions of it were still preserved within the microstratigraphic deposit. Therefore, analyses were carried out only on samples for which there was a directly observable continuity between the pigment layer within the accretions and an identifiable rock art motif rather than an assumed correlation. In the laboratory, these samples were subsequently microexcavated in arbitrary "spits" over the entire surface of the coralloids. The pigment layer was visible across the entire length of the sample; therefore, the calcium carbonate accretions sampled for dating could be directly related to the art. The added benefit of this sampling methodology is that it can yield minimum and maximum ages for the art.

With samples such as these, each microexcavated sample comprises an average of several calcium carbonate depositional events. As such, the calculated age will represent an average age for those events. Further, it is important to note that while the radiocarbon and uranium-series dating methods may be used on the same calcium carbonate sample, in most cases the former method cannot be used as a control for the latter (see Pike et al. 2016).

3. *The dated sample must be "pure."* It is common for calcium carbonate to be contaminated by detrital materials such as windblown or waterborne sediments, and this can lead to uranium-series ages that are erroneously older than the true age of the sample. This is because the detrital fraction will contribute to the overall amount of uranium-series nuclides so that the sample does not reflect a radioactive disequilibrium related to the time of carbonate formation. The effects of detrital contamination can be identified and often corrected for by measuring the activity of ^{232}Th that is solely present in the detrital fraction but which plays no part in the decay chain of uranium. The degree of detrital contamination is expressed as ^{230}Th/^{232}Th activity. High ^{230}Th/^{232}Th values (>20) indicate little or no effect on the calculated age, while low values (<20) indicate that a significant correction will be required (Bourdon et al. 2003). Since it is difficult to determine the exact ^{230}Th/^{232}Th value of the detrital component, corrections for initial ^{230}Th are usually made on the basis of the ^{230}Th/^{232}Th ratio for bulk Earth at secular equilibrium (.825 ± 50%). This is usually acceptable for samples with low- to midlevel detrital contamination (^{230}Th/^{232}Th >5). For samples with a high level of detrital contamination (^{230}Th/^{232}Th <5), the calculated age is highly dependent on the values used to correct for the detrital component.

Isochron techniques can also be used to correct for the effect of detrital contamination. Cogenetic subsamples having different amounts of contamination are analyzed, and the activity ratio of the different isotopes in each of the subsamples are plotted against each other. This enables the determination of the ^{232}Th-free end-member activity ratios of ^{230}Th/^{238}U$_{carbonate}$ and ^{234}U/^{238}U$_{carbonate}$ (Ludwig and Titterington 1994). This strategy is difficult to apply to rock art dating, however, owing to the significant number of cogenetic subsamples required.

4. *There must be a demonstration that the calcite has not undergone remobilization of uranium.* A conceivable problem with the uranium-series dating method is that calcium carbonate accretions can behave as an open system for uranium, whereby the element can be leached out of the accretions or remobilized (e.g., Plagnes et al. 2003). In such instances, the calculated ages will be too old because the dating method relies on the accurate measurement of uranium versus its decay product ^{230}Th. In Sulawesi, this problem was tackled by avoiding porous samples and by measuring a series of subsamples (at least three and up to six per sample; fig. 1). The ages of these subsamples were all in chronological order, confirming the integrity of the dated coralloids. If uranium had leached out of the samples, a reverse age profile would have been evident, meaning the ages would have gotten older toward the surface, where they should be younger. This strategy also provides the opportunity to apply Bayesian statistics to calculate statistical age estimates for a marking event (Douka and Higham 2017; Wood 2015).

Laser Ablation Uranium-Series Dating

It is technically possible to use laser ablation uranium-series dating (Eggins et al. 2005) to date calcium carbonate accretions in association with rock art. The method has been successfully used to date similar calcium carbonate accretions in geological contexts (e.g., Gliganic et al. 2014; fig. 2). The method has also been used to provide minimum age estimates for human remains and other osseous materials (e.g., Aubert at al. 2012; Duval et al. 2012; Grün et al. 2010).

The method can also be used to quickly access the closed system assumption required for dating calcium carbonate accretions in association with rock art. The small spot size of the laser ablation system (typically 100–200 μm spot diameters) offers several advantages over solution-based methods. Apart from the ability to demonstrate that the calcite has not undergone remobilization of uranium, it is also possible to obtain a series of cogenetic subsamples that can potentially be used to correct for the effect of detrital contamination. However, the larger analytical errors usually associated with such measurements could further complicate these corrections. Nonetheless, the spatial resolution obtained with this method allows the determination of age estimates physically closer to the pigment layer.

South Sulawesi, Indonesia

The "tower" karst region of Maros-Pangkep in southern Sulawesi contains a record of prehistoric rock art that was first reported in the scientific literature in the 1950s (van Heekeren 1952). Previously, Indonesian archaeologists had identified
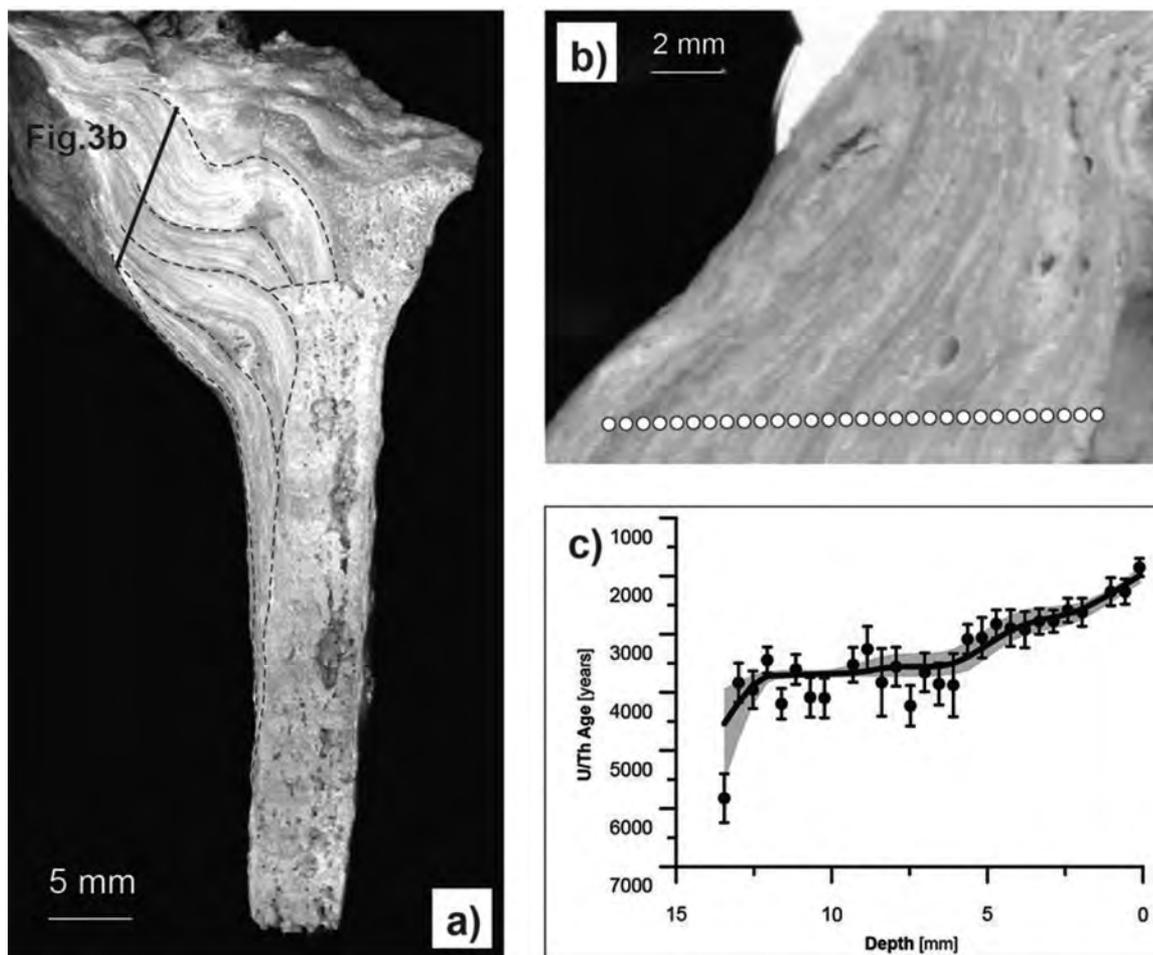
Figure 2. Mt. Chambers Gorge speleothem: (*a*) section of speleothem showing laminae. (*b*) Positions of 30 LA-ICP-MS U/Th measurements along a transect of speleothem, the position of which is shown as the black line in *a*. (*c*) U/Th ages (black circles) plotted against depth with the growth model (StalAge1.0) shown as black line and shading. Note that the orientation of *b* and *c* are the same. Dashed lines demarcate four intervals of fine laminae separated by more continuous and darker laminae. This methodology could be applied to the dating of rock art. Source: Gliganic et al. 2014. A color version of this figure is available online.

two temporally distinct phases of parietal art production based on patterns of superimposition (Eriawati 2003): the initial phase is characterized by red blown-pigment hand stencils and rare, naturalistic paintings of large mammals (predominately endemic wild boars), while the later, younger phase is dominated by black drawings of human and animal figures and a wide array of geometric signs. Until recently, it was presumed that the first phase of rock art was produced by the so-named Toaleans (Bulbeck 2004:150–151), early- to mid-Holocene hunter-gatherer communities of supposedly Mesolithic character (Bulbeck 2004; Bulbeck et al. 2000; van Heekeren 1952). None of the rock art was thought to be Pleistocene in age (but see O'Connor and Bulbeck 2013).

In an effort to establish a chronology for the extensive body of imagery known from the first phase of rock art production in Maros-Pangkep, uranium-series dating of calcium carbonate accretions overlying and underlying rock art images was recently applied to date a sample of 14 parietal motifs (12 hand

stencils and two figurative animal paintings) from seven sites in the region (Aubert et al. 2014). The most ancient examples, a hand stencil from Leang Timpuseng, with a minimum age of 39,860 years (40,700 +870/−840), and another hand stencil from Leang Jarie with a minimum age of 39,350 years (39,670 +320/−320), are now the world's earliest known hand stencils. In addition, on the same rock art panel on the ceiling at Leang Timpuseng, a figurative depiction of a wild pig endemic to Sulawesi, the babirusa (*Babyrousa* sp.), or "pig-deer," is at least 35,400 years old (36,900 +1,600/−1,500), while an incomplete and indeterminate animal figure (probably a pig) on the wall of a nearby site is at least 35,700 years old (44,000 +9,100/−8,300). This is equivalent in age to what was previously considered to be the earliest two-dimensional portrayals of the animal world from France's Chauvet Cave, which are attributed to the time interval between 37,000 and 33,500 cal BP years ago (Quiles et al. 2016). The minimum and maximum age estimates obtained from Maros suggest that stenciled depictions of human hands

were produced in this karst region, and possibly elsewhere on Sulawesi (Oktaviana et al. 2016), apparently as part of a continuous artistic tradition, for a period of at least 13,000 years (Aubert et al. 2014).

East Kalimantan, Indonesia

In the early 2000s, a French-Indonesian team reported the dating of two hand stencils from a remote karst area in northeastern Kalimantan, the Indonesian portion of Borneo (Plagnes et al. 2003). At a high-level cave site, Gua Saleh, the authors removed a large cave drapery (~50 cm long, ~15 cm wide, by ~1 cm thick) found overlaying two red-colored stencil motifs. The sample was broken into pieces, which were then analyzed for uranium-series and radiocarbon dating. Except for subsample BOR5, the results showed a discrepancy between the uranium-series and radiocarbon age estimates whereby the uranium-series ages estimates are older than the radiocarbon results. Moreover, the uranium-series age estimates are in reverse chronological order, suggesting that the cave drapery in this instance behaved as an open system for uranium. Nonetheless, sample BOR5 was located at the base of the cave drapery, and the uranium-series and radiocarbon analysis returned an age estimate of ~10 ka. Cave draperies, or "curtains," are distinct and notoriously porous forms of secondary calcium carbonate deposition and are thus not ideal for uranium-series dating. Nevertheless, owing to the particular way in which these speleothems form, the base of the drapery is generally less porous and may therefore be suitable for uranium-series dating. The results from Plagnes et al.'s (2003) pioneering study suggest that red-colored hand stencils from Borneo are Pleistocene in age and are possibly older than around 10,000 years in age.

Lene Hara, East Timor

For the Gua Saleh rock art dating study, Plagnes et al. (2003) used thermal ionization mass spectrometry (TIMS) to measure the uranium-series isotopes. Because of the relatively low uranium concentrations in the samples (.057–.180 ppm) and the technology employed, large masses of samples were required (2–4 g). In the research design of the project, the decision to employ this approach may have justified the use of a large cave drapery for uranium-series dating.

Aubert et al. (2007) used, for the first time, MC-ICP-MS to date small calcium carbonate deposits in association with rock art in Timor. MC-ICP-MS requires far less uranium than TIMS, opening up new possibilities and avenues for rock art dating. Aubert et al. (2007) showed that MC-ICP-MS can be used to demonstrate a closed system for uranium for small samples of calcium carbonate deposits in direct association with rock art. The data showed that at Lene Hara Austronesian-like paintings at the surface of the flowstone were younger than $6.3 \pm .55$ ka, consistent with the hypothesis that these artworks were created by early Austronesian people—the first

known farmers in the Southeast Asian region. Furthermore, a red pigment lamination was identified within the calcium carbonate deposit. Although not forming a visible image, this line of red colorant in the speleothem sample was arguably part of a rock art motif. Aubert et al. (2007) bracketed the age of the red line to between 24 ± 1.5 and 29.3 ± 1.2 ka, suggesting—but not demonstrating, for the reasons outlined above—an earlier phase of cave painting may have occurred at the site prior to the onset of the last glacial maximum at ~22 ka.

In 2010, O'Connor and team reported the dating of newly discovered petroglyphs at Lene Hara (O'Connor et al. 2010). The petroglyphs were found on two speleothem columns (cols. A and B). As these authors observed:

> A loose piece from the margin of the exfoliating layer into which the petroglyphs are carved; LH09-1-1, a powder sample drilled from the left periphery of the speleothem mass; and LH09-1-2, a sample drilled from the truncated top of the column . . . were expected to yield maximum ages for the petroglyphs on column A. (665)

The samples returned uranium-series age estimates of 36.76 ± 1.3, $29.4 \pm .53$, and 39.62 ± 1.2 ka. For column B, "two samples were taken in proximity" to one of the petroglyphs and were "expected to produce a maximum age for petroglyph B1 and for the weathering of the surface." These two samples returned uranium-series age estimates of $13.72 \pm .16$ ka and $12.63 \pm .22$ ka (O'Connor et al. 2010:665). Three other samples were "taken from the edge of a relatively unweathered calcite sheet that forms the outermost layer of the column to the immediate left of petroglyph B1. As such, the calcite sheet is expected to provide a minimum age for the petroglyph" (O'Connor et al. 2010:665). These samples returned uranium-series age estimates of $10.10 \pm .35$ ka, $10.17 \pm .19$ ka, and $10.18 \pm .20$ ka. Consequently, the authors argue that engravings were produced during the time interval between ~12.5 and ~10.2 ka. If so, these images would represent the most ancient petroglyphs discovered thus far in Southeast Asia.

The petroglyph dates from Lene Hara warrant a note of caution, however. It is important to point out that the three samples taken as minimum age estimates do not directly overlay the petroglyph under study. Instead, the investigators argue that the calcite surface underlying this more recent calcite sheet showed "an equivalent degree of weathering to that affecting both the carved surface and the petroglyph itself," suggesting that deposition of the younger sampled calcite sheet "appears to have taken place after the petroglyph was carved and subsequently weathered" (O'Connor et al. 2010:656). The argument for minimum age therefore depends on a range of assumptions related to how one assesses rates or degrees of weathering in the flowstone surface (i.e., the rock art "panel"). O'Connor et al. note that the more recent calcite sheet, at apparently ~10.2 ka, "shows minimal pitting," implying that most of the weathering on the carved surface and the petroglyph must have occurred rapidly (i.e., over a maximum of ~2.3 millennia) after the engraving was produced. However,

such evaluations are invariably subjective, and there are no widely accepted criteria for quantitatively assessing the rate of weathering of engraved markings on rock surfaces, regardless of the particular substrate used.

Cognitive Evolution and Early Human Migration

As noted above, debate about the origin of modern human symbolic behavior has traditionally focused on the intensively studied record from Upper Paleolithic Europe (Belfer-Cohen and Hovers 2010; Shea 2011). Recent critiques of this Eurocentric bias, in our view, have essentially replaced it with an Africanist one (Belfer-Cohen and Hovers 2010; McBrearty 2007; McBrearty and Brooks 2000). Despite this, it is increasingly recognized that Southeast Asia is of fundamental importance to this debate in terms of the potential of the region to yield insight into the dispersal and behavioral variability of early modern human colonists (e.g., Belfer-Cohen and Hovers 2010; Brumm et al. 2017; Klein 2000; Shea 2011).

Rock art that has been directly dated using robust and reproducible scientific methods provides a potentially invaluable medium for studying cognitive evolution and Pleistocene human migration. Rock art is a form of visual expression almost exclusively associated with the presence of modern humans (despite some claims for Neanderthal rock art such as by Rodríguez-Vidal et al. 2014), and, as reviewed above, when associated with calcium carbonate accretions it can be reliably dated past the radiocarbon barrier using the uranium-series method. At present, the world's oldest surviving rock art, a red "disk" with a minimum age estimate of 40,800 years, is from El Castillo in Upper Paleolithic Spain (Pike et al. 2012) and dates to shortly after the initial arrival of our species in Western Europe (~41,500 years ago; Higham et al. 2011). The recent rock art dates from southern Sulawesi include the hand stencil from Leang Timpuseng, which is compatible in age with the dated red disk from El Castillo. Elsewhere in Southeast Asia, we now have securely dated Pleistocene rock art at a total of seven sites on Sulawesi, where a longstanding tradition of stencil art may date back at least 40,000 years, dated Pleistocene rock art at a single cave site on the large landmass of Borneo, and possible evidence for pre-LGM rock art production in a cave on the island of Timor. So what can the oldest surviving rock art recorded in Southeast Asia, and the world, tell us about the pattern and timing of the dispersal of modern humans outside Africa?

Despite the early presence of rock art at El Castillo and the controversially old chronology inferred for the figurative animal paintings from Chauvet, prevailing wisdom holds that rock art was not significant to the colonization of Europe by Aurignacian peoples. The famous animal paintings found in decorated caves of Upper Paleolithic Europe are thought to be a predominately, though not exclusively, Magdalenian phenomenon, one that was mostly concentrated in specific parts of Western Europe (Bahn and Vertut 1997). The vast majority of known European cave art sites occur in a series of karst valleys in southwestern France and northeastern Spain—the Franco-Cantabrian region (Mellars 2009). Rock art sites of known or presumed Late Pleistocene age have been documented outside this region, such as in Italy and Britain, but these are typically isolated and separated by long distances, and in some instances the art has not been authenticated (Bahn and Vertut 1997:45). The restricted distribution of Pleistocene rock art in Europe has long puzzled archaeologists. It is sometimes proposed that rock art was concentrated in the Franco-Cantabrian region owing to the large number of limestone caves in these areas of France and Spain (Bahn and Vertut 1997:200). However, other parts of Europe have extensive karstic landscapes but no dated Upper Paleolithic rock art. For instance, limestone caves in Germany's Swabian district have yielded carved animal and human figurines from Aurignacian layers (e.g., Conard 2003), but there is no parietal art of proven Pleistocene age from this region or anywhere in Germany or surrounding parts of central Europe (but see Welker 2016).

The pattern of rock art distribution in Southeast Asia appears to be broadly similar: in the island archipelago of Indonesia, for example, rock art of definite or probable Pleistocene age seems to be concentrated in specific karst regions where it is unusually abundant, such as northeastern Kalimantan (Fage and Chazine 2009; Setiawan 2014), southern Sulawesi (Aubert et al. 2014; Oktaviana et al. 2016), and the western coast of New Guinea (Arifin and Delanghe 2004; Aubert et al. 2014; Taçon et al. 2014). The quantity of rock art documented thus far in these areas, which have been only partially explored by scientists, is impressive. In the Maros karsts, for example, and the adjoining Pangkep district to the north, local cultural heritage managers have recorded at least 120 rock art sites in a tiny portion of this ~450 km² karst area. The majority of documented sites are located in the karst border plains close to modern roads and infrastructure rather than in the more remote and difficult to access areas of mountainous terrain, which, owing to their ruggedness, are yet to be systematically surveyed. Even in the most intensively studied areas close to urban settlements, new rock art sites are discovered each year. In sites with dated Pleistocene art, moreover, surviving images are often very heavily weathered; the original limestone surfaces containing rock art panels are extensively exfoliated, and in many instances only isolated patches of red paint or fragments of a hand stencil or animal painting are visible. It appears that an immense body of Pleistocene cave paintings once existed in the Maros-Pangkep landscape but is now lost, while some individual sites would have harbored extensive rock art galleries. In other parts of Indonesia, on the other hand, rock art is extremely scarce or absent in karst areas that would have offered the same geological potential for the creation of parietal art, namely, plentiful limestone rock face "canvases" in sheltered environments that were eminently suited to human habitation. Consider two of the largest islands in Indonesia, Java and Sumatra. Both are emergent landmasses on the Sunda Shelf and harbor extensive karst terrains; however, no rock art has ever been documented in the many limestone caves and shelters on Java, despite intensive searching (e.g., in the Gunung

Sewu karsts) and despite fossil evidence for modern humans on the island by at least 37.4–28.5 ka (Storm et al. 2013). Sumatra, roughly the same size in total land area as Spain, is larger and less densely populated than Java and has been much less comprehensively explored. However, there is still only one Sumatran site with published rock art, Gua Harimau, and the oldest motifs in this cave are more than likely of Austronesian origin (Oktaviana, Setiawan, and Saptomo 2015).

Was Pleistocene rock art formerly more uniformly distributed across the oceanic islands and continental landmasses of tropical Southeast Asia but has now survived only in isolated areas with optimal preservation conditions, or could the restricted distribution of rock art in the region constitute a real historical pattern? Were parts of Southeast Asia analogous to the Franco-Cantabrian region of Europe—special places where Pleistocene rock art cultures flourished?

Concerning the former, the Sulawesi rock art dates seem to dispel the implicit notion that faster limestone erosion rates in the humid tropics would have erased any visible evidence for rock art after only a few millennia. With regard to the latter possibility, therefore, the apparent proliferation of rock art sites in certain parts of Southeast Asia may be a reflection of other factors, such as the specific migration pathways followed by the first modern humans to enter the region as part of the colonization of Australia at 60–50 ka. It may be noteworthy, for instance, that the only sites in this region that contain rock art of known or presumed Pleistocene age fall along one of the two most likely dispersal routes from Sunda to Sahul—Birdsell's (1977) northern route from the easternmost edge of Sunda (Kalimantan) to Sulawesi and then to the northwestern margin of Sahul (West Papua). Following on from this, it is also conceivable that Pleistocene Southeast Asia harbored specific regions of artistic innovation that gave rise to distinct rock art traditions, centers of cultural innovation that were perhaps analogous to the Franco-Cantabrian region.

With the above points in mind, two hypotheses can be proposed to explain the presence of securely dated evidence for rock art by ~40 ka in Western Europe and Sulawesi, but thus far nowhere in between: (1) the human capacity to conceive and create rock art arose independently at roughly the same time among modern human populations in these two widely separated parts of the Pleistocene Old World; (2) rock art emerged in Africa prior to our species' dispersal from this continent and was subsequently exported throughout Pleistocene Eurasia as part of a coherent suite of modern cultural complexity, a repertoire that also included personal bodily ornaments and other material manifestations of symbolically mediated behavior. We think that of these two hypotheses the majority of scholars would regard the second as the most inherently plausible. Two further implications of this scenario can therefore be envisioned. The first is that rock art as a cultural trait was integral to the dispersal of modern humans from out of Africa—perhaps, as these colonizers spread out rapidly across Eurasia, painting or otherwise decorating caves and shelters was their way of socializing new and exotic landscapes and demarcating group territories (Taçon 1994; Taçon and Brady 2016; Taçon et al. 2014). It follows that an essentially continuous trail of Pleistocene rock art may have connected Southeast Asia to both Europe and Africa—a vast record of early human symbolic expression that either has not survived along most parts of the early human migration routes or is yet to be revealed owing to a lack of intensive rock art survey in Asia and/or the difficulties of directly dating rock art. If true, this would imply that at least some parietal motifs in Western Europe currently interpreted on stylistic grounds to postdate the settlement of this region by *Homo sapiens* may, in future, be shown to date from the initial period of modern human colonization. The second implication is that rock art, although distinctly African in origin and extremely ancient, was not a ubiquitous component of the first modern human cultures to expand outside Africa, especially as part of the main dispersal waves that led to the colonization of Europe by ~41.5 ka and Australia by 60–50 ka; instead, Pleistocene rock art traditions arose in different places and times owing to the particular needs and histories of specific *H. sapiens* groups, including the possibility of localized increases in population density that may have driven the development and spread of complex rock art traditions (Powell, Shennan, and Thomas 2009).

Unfortunately, we presently lack the empirical evidence required to test these and other scenarios. However, following the Sulawesi rock art dating results, research is now underway (led by the first author, Aubert, with Indonesian colleagues) to determine the age of hand stencils, animal art, and other early parietal art in northeastern Kalimantan, West Papua, and adjacent areas using uranium-series dating. The wide-ranging karstic zones of eastern Borneo, Sulawesi, and western New Guinea, in particular, with their positions along likely colonization routes and abundance of prehistoric rock art, offer major potential to broaden our knowledge of a crucial period in early human prehistory.

Conclusions

Rock art is of global scientific importance, and its accurate dating is among the most challenging areas of geochronology and archaeology. As reviewed in this paper, recent technological breakthroughs now enable the accurate dating of such assemblages, advancing our knowledge of human cognitive and cultural evolution. In Southeast Asia, where the total number of Late Pleistocene archaeological sites is limited, rock art now provides a key proxy for tracing the pattern and timing of the initial peopling of the region by modern humans. It seems plausible to argue that modern humans had the capacity to make complicated rock art since they evolved in Africa, but that rock art was made at different places and times to reflect the needs of specific groups of early hunter-gatherers. For Southeast Asia, this seems to have occurred at least 40,000 years ago, based on evidence from Sulawesi, but as this is a minimum age from a single locality, it may have

Figure 3. Large animal painting from South Sulawesi, Indonesia. The style is similar to other animal paintings from this region. Source: Kinez Riza. A color version of this figure is available online.

begun much earlier. It is also possible to speculate that a distinct rock art tradition, which perhaps arose in a specific area akin to a rock art center, moved quickly throughout the region, possibly through the northern island chain of Indonesia to Australia. A future research question to explore when new rock art dates are available is whether there was a single, continuous artistic culture rapidly moving through the island chains of Southeast Asia all the way to Pleistocene Sahul, with human hand stencils and large naturalistic paintings of animals constituting the main designs (fig. 3), or whether similar types of hunter-gatherer groups independently invented comparable forms of rock art as they colonized this region. If the former was the case, then the presence of strikingly similar kinds of rock art along a rough transect running from the easternmost edge of Asia (Kalimantan) to Sulawesi and the northern tip of Sahul (from where it stretches westward from New Guinea to the Kimberley and Arnhem Land) hints at the fundamental role that rock art played in the colonization of this region by *Homo sapiens*, as well as the existence of what may have been the most widespread and enduring tradition of visual culture in the history of humankind.

Acknowledgments

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Hominin Dispersal and Settlement East of Huxley's Line

The Role of Sea Level Changes, Island Size, and Subsistence Behavior

by Sue O'Connor, Julien Louys, Shimona Kealy, and Sofía C. Samper Carro

The thousands of islands east of Huxley's Line have never formed a single land mass or been connected to Sunda or Sahul. The earliest records of hominins in this area are stone tools recovered from Pleistocene deposits on Flores and Sulawesi. Subsistence by these hominins as well as the later subsistence patterns exhibited by *Homo floresiensis* suggest that exploitation of marine resources was, at best, rare and opportunistic. Likewise, the fragmentary hominin remains recovered from Late Pleistocene deposits from Callao Cave in the Philippines exploited large game at the expense of marine resources. In contrast, the earliest zooarchaeological records of modern humans are dominated by marine fish and shellfish and include the earliest evidence of pelagic fishing using shell tools, implying complex fish-capture technology. Pleistocene lithic assemblages on these islands are unspecialized, indicating reduction of predominantly locally available stone to produce flakes and irregularly retouched pieces. By the terminal Pleistocene, records of human subsistence on very small islands indicate almost total reliance on marine foods for protein. We propose that strong links exist between subsistence strategies and dispersal throughout Wallacea, with subsistence strategies available to pre-*sapiens* hominins in the region being a major limiting factor in their dispersal.

The movement of hominins through island Southeast Asia and into Australia is the last leg of several migration events that began in Africa thousands of years before. Debate over the route(s) taken by these hominins is ongoing, with various hypotheses supporting an inland or coastal route (Erlandson and Braje 2015; Groucutt et al. 2015; Reyes-Centeno et al. 2014 and other papers in this volume). Regardless of route choice, however, once hominins arrived at Huxley's Line (see

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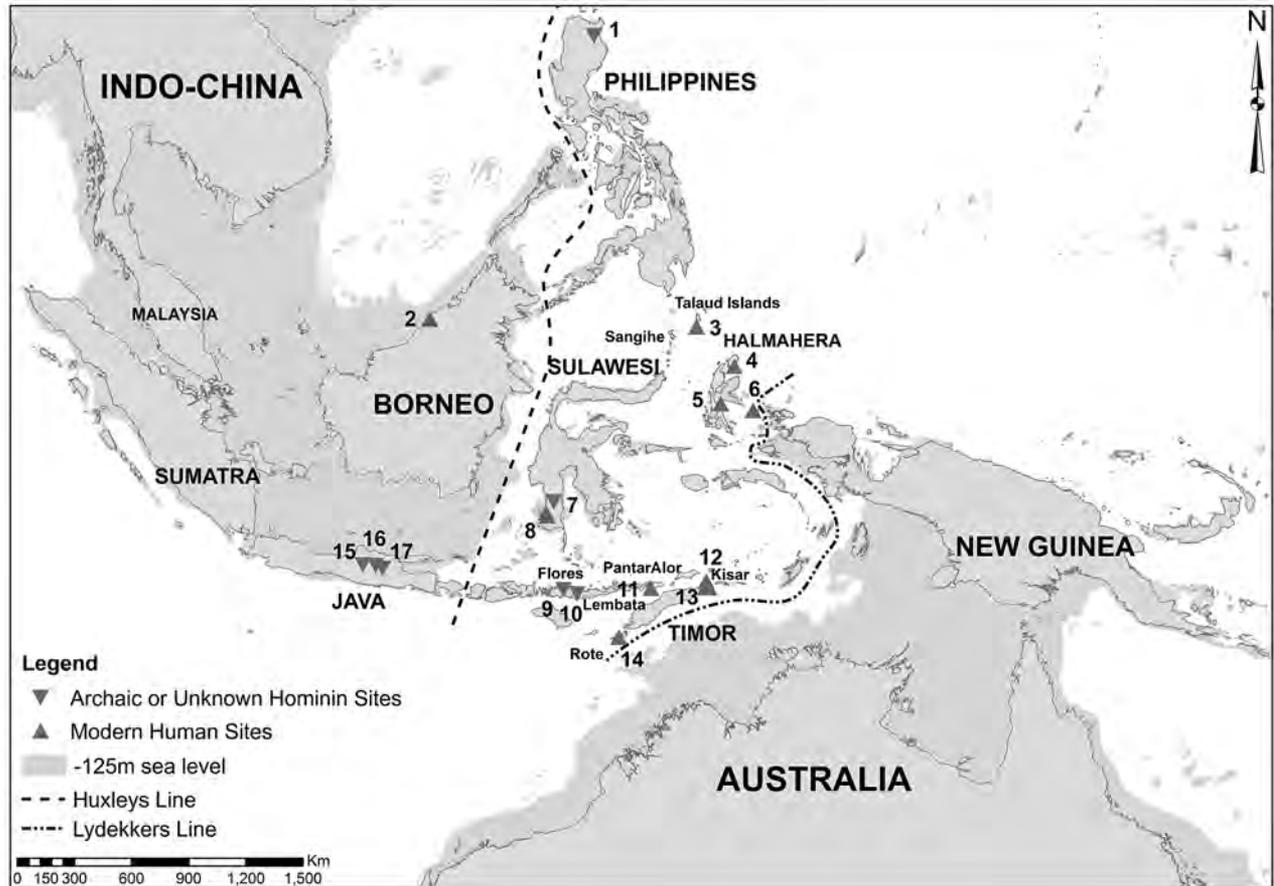
fig. 1), earlier Pleistocene hominins would have had to undertake sea journeys to reach Sulawesi and Flores, and late Pleistocene *Homo sapiens* would have had to undertake even longer sea crossings to arrive on Sahul.

Dispersals by the earliest hominins in the region are likely to have been incidental and possibly enabled by natural rafts carried by oceanic currents and perhaps tsunamis (Dennell et al. 2014). Irrespective of dispersal mechanism, successful colonization of an island requires that subsistence needs are met, although this aspect does not appear to have been given as much consideration in the migration of pre-*sapiens* east of Huxley's Line as in the migration of *H. sapiens*. For example, Allen and O'Connell (2003, 2008) and O'Connell and Allen (2007, 2012) applied the tenets of optimal foraging to predict the pattern of human dispersal to Australia, arguing that the movement of humans through Wallacea was driven by a negative change in resource availability, which was driven, in turn, by fluctuations in sea level that encouraged relocation to more optimal areas (i.e., new islands). However, hypotheses such as these have yet to be convincingly tested due to limited archaeological records in the region (Anderson 2017; Kealy, Louys, and O'Connor 2016).

Sea level changes also affect island size and intervisibility between islands. The lower sea levels produced during glacials are generally thought to have been optimal for migration in the Wallacean archipelago, because the shorter distances between

Figure 1. Map of island Southeast Asia showing sites mentioned in text. Downward-pointing triangles indicate sites associated with archaic or "unknown" hominin localities, and upward-pointing triangles indicate sites associated with modern humans. A color version of this figure is available online.

islands would presumably have made sea crossings easier (Birdsell 1977; Kealy, Louys, and O'Connor 2016, 2017). However, some researchers (Chappell 1993; O'Connell, Allen, and Hawkes 2010; O'Connor and Chappell 2003) have argued that rising sea levels after 55 ka might have encouraged and even facilitated colonization. The small number of Pleistocene archaeological sites in the region makes it hard to test competing migration hypotheses as they relate to timing and sea level changes (Anderson 2017; Kealy, Louys, and O'Connor 2016).

Although Pleistocene archaeological records are rare in Wallacea, the situation is beginning to improve, with new sites recorded and sequences analyzed in the past few years (O'Connor 2007; O'Connor et al. 2010; Pawlik et al. 2015; Robles et al. 2015; Samper Carro et al. 2016; Szabó, Brumm, and Bellwood 2007). In particular, the zooarchaeological records produced on several Wallacean islands allow for the examination of some of the factors that may have been influential in facilitating dispersals in the region. Here, we review these records, paying particular attention to the environmental limitations of small oceanic islands for successful colonization. We examine the probable subsistence behavior and distribution of the first hominins

in the region and contrast these with *H. sapiens* in the later Pleistocene in the context of sea level changes and island size during the likely periods of movement.

Bathymetry and Sea Level Changes at the Regional Scale

The Pleistocene saw enormous changes in the spatial environment of the Wallacean Archipelago (Kealy, Louys, and O'Connor 2017). Driven largely by dramatic changes in climate, with secondary tectonic influences, the islands of Wallacea have experienced a combination of emerging and subsiding phenomena, enlargements and shrinkages, and joining and separation that have affected the dynamics of this area. Such changes had a major impact on the island ecosystems as well as the most parsimonious pathways for human movement between islands (Kealy, Louys, and O'Connor 2016).

To date, archaeological investigations in the Wallacean Archipelago have been patchy, with most research focused on the larger islands of Sulawesi, Flores, and Timor. Logically, the larger Wallacean islands would have presented more diverse

and reliable habitats for sustaining genetically viable populations. In the past 100,000 years, sea levels in Wallacea have fluctuated below present-day heights, with drops of up to 135 m during the last glacial maximum (LGM; Lambeck and Chappell 2001). Studies in Timor and other islands also suggest the region has experienced a significant degree of tectonic uplift during this time, although neither the geographic extent nor the results of the research are consistent throughout Wallacea (Chappell and Veeh 1978; Cox 2009; Hantoro et al. 1994; Jouannic et al. 1988; Major et al. 2013; Nexer et al. 2015; Pirazzoli et al. 1993; Sumosusastro et al. 1989). A summary of these studies and the uplift rates recorded therein indicates a dearth of uplift research in regions such as the Halmahera Archipelago (Kealy, Louys, and O'Connor 2017, their table 1); in contrast, Timor-Leste has had numerous studies producing uplift rates that range from 0.1 to 0.6 m/kyr.

The consideration of an uplift variable in paleogeographic reconstructions is important for avoiding overestimations of island size and connectivity at times of lower sea levels. The lack of comprehensive uplift measurements throughout Wallacea means an accurate model of island uplift is currently unavailable; however, an average rate, calculated from islands with known uplift data, provides one alternative (Kealy, Louys, and O'Connor 2017). We acknowledge that this is an average calculated from data with significant variability; however, we consider a conservative estimate on past island extent prefer-

able to ignoring uplift entirely. Thus, we adjusted the Lambeck and Chappell (2001) sea level curve to account for an average uplift rate of 0.5 m/kyr (Kealy, Louys, and O'Connor 2017) for the past 100,000 years (fig. 2). As the majority of the uplift rates are from Quaternary (and largely Holocene) limestone (Chappell and Veeh 1978; Cox 2009; Hantoro et al. 1994; Major et al. 2013; Sumosusastro et al. 1989), any minor changes in uplift rate over this time will also be averaged out across the 100-kyr sea level curve. When sea level fluctuations are adjusted for this uplift rate, the sea level trend remains the same; however, the relative drop in sea level as measured from the shoreline decreases over time (fig. 2). This is an important consideration for paleo-shoreline reconstructions, particularly those concerning the periods hypothesized for initial human colonization of Wallacea and Sahul (fig. 3). The reconstructions presented here are based on the most recent bathymetric chart of Wallacea (obtained from the General Bathymetric Chart of the Oceans data set, downloaded from http://www.gebco.net; Smith and Sandwell 1997) and the adjusted sea levels from figure 2. The reconstruction does not take sedimentation and erosion processes into account because of the unavailability of such data. Hindcasting these changes in sea level and uplift to the period of earliest hominin movements at ~1 Ma is not realistic. Nevertheless, while lowered sea levels created larger landmasses and allowed for some Wallacean islands to be connected, many of the volcanic islands in this region—for example, Pantar—were

Table 1. Archaeological sites pertaining to hominin dispersal and settlement east of Huxley's Line

Site	Published date[a]	Reference(s)
Callao Cave	66.7 ± 1 ka to Late Holocene	Mijares et al. 2010
Niah Cave	~50 ka (47,170–50,000 ka) to Late Holocene	Higham et al. 2016
Liang Sarru	35,034–33,864, 22,628–21,941 and Holocene	Ono, Soegondho, and Yoneda 2009
Daeo 2	16,767–15,889 to Late Holocene	Bellwood et al. 1998
Siti Nafisah	5,572–5,296 to Late Holocene	Bellwood et al. 1998
Golo Cave	36,350–35,001 to Late Holocene	Bellwood et al. 1998
Talepu	194–118 ka to after 103 ± 9 ka	van den Bergh et al. 2016b
Leang Timpuseng and Maros region	40.70 +0.87/–0.84 ka to Late Holocene	Aubert et al. 2014
Liang Bua	193 ± 33 ka (initial hominin occupation), 49.6 ± 0.5 ka (*Homo floresiensis* terminal date), 19.2 ka to Late Holocene (modern humans)	Sutikna et al. 2016; Westaway et al. 2007
Liang Bawah	238–181 ka to Late Holocene	Gagan et al. 2015
Mata Menge	810 ± 40 ka to 650 ± 20 ka	Brumm et al. 2016
Tangi Talo	No in situ artifacts; fauna dated to 900 ± 70 ka	Aziz et al. 2009; Morwood et al. 1998
Tron Bon Lei	21,000–20,560 to 3,195–3,010	O'Connor et al., forthcoming b; Samper Carro, Louys, and O'Connor 2017
Here Sorot Entapa	15,338–15,091 to Late Holocene	New data, this article
Jerimalai	43,002–41,313 to Late Holocene	O'Connor 2007
Lene Hara	42,454 ± 450 to Late Holocene	O'Connor, Allen, and Hawkes 2010
Matja Kuru 2	36,307–35,031 to Late Holocene	O'Connor, Robertson, and Aplin 2014
Lua Meko	28,603–27,676 to Late Holocene	Mahirta 2009
Sangiran Dome	1.66 ± 0.04 Ma to Middle Pleistocene	Bouteaux et al. 2007; Sémah, Saleki, and Falguéres 2000
Ngebung	800 ka	Bouteaux and Moigne 2010
Trinil	540 ± 100 ka to 430 ± 50 ka	Joordens et al. 2015
Kedung Brubus	700–800 ka	Storm 2012; van den Bergh et al. 1996

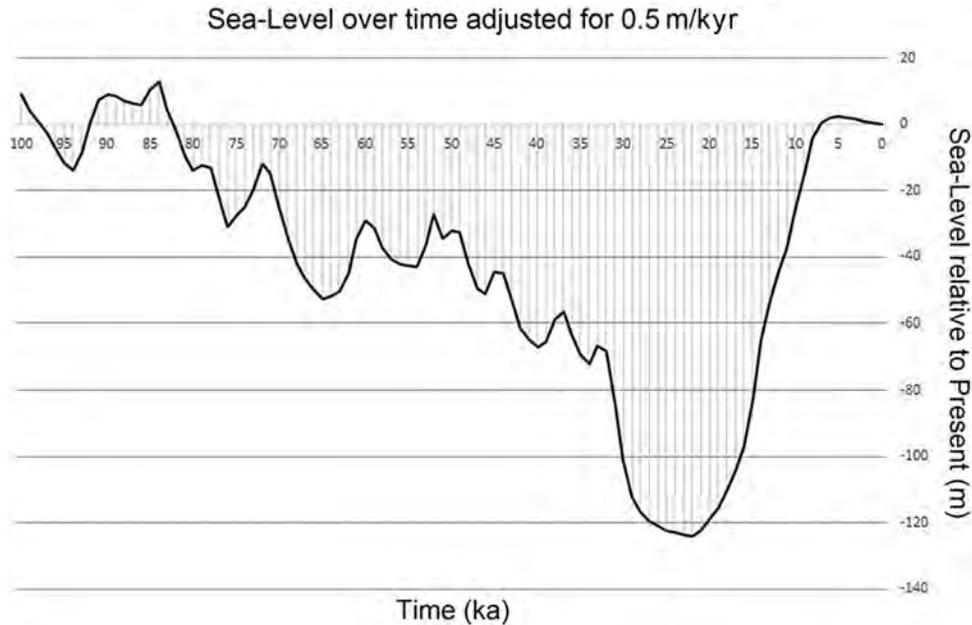[a] Ages are the published calibrated ^{14}C, electron spin resonance, and U-series dates.

Figure 2. Sea level for the past 100 kyr (Lambeck and Chappell 2001) adjusted for 0.5 m/kyr uplift as calculated in Kealy, Louys, and O'Connor (2017, their table 1).

smaller than today, because they have been undergoing active formation since that time.

Subsistence and Dispersal of Early Hominins in Asia

When hominins began to introduce large amounts of animal protein into their diets through access and processing of carcasses is not known; however, by at least 2 Ma, hominins (likely *Homo erectus*) were practicing persistent carnivory in East Africa (Ferraro et al. 2013; Lemorini et al. 2014; Parkinson 2013; Plummer 2004), and in the Early Pleistocene, primary access of fleshed carcasses by hominins is recorded at several sites (Domínguez-Rodrigo, Bunn, and Yravedra 2014; Organista et al. 2016). Organista et al. (2016:620–621) suggest that the hominin group responsible for the dense concentration of megafauna at Bell Korongo, Olduvai Gorge, exhibited "a degree of cooperative behaviour that required a capacity for strategy, organization, communication, and physical effort." Such traits were no doubt useful in the initial dispersal of hominins outside of Africa and into Asia, although, as many other mammalian families attest, such traits are not absolutely essential for widespread migrations between Asia and Africa (e.g., O'Regan et al. 2011).

In Asia, subsistence behavior of Early to Middle Pleistocene hominins is poorly known, due in large part to a dearth of zooarchaeological evidence (Dennell 2015). Whether this dearth represents a genuine lack of evidence or reflects the much smaller volume of zooarchaeological studies in the region is unknown, but certainly taphonomic studies of faunal remains associated with hominins in the region are rare. Boaz et al. (2004) has

suggested that Chinese *H. erectus* scavenged remains from a hyena den in Locality 1 of Zhoukoudian. A more recent taphonomic analysis of cervid remains from layer 3 of Zhoukoudian found no evidence of anthropogenic modifications (Zhang et al. 2015). Likewise, visual examination of a subset of faunal remains from Gongwangling found no evidence of cut marks on bones (Louys et al. 2009). Hominins likely had a role in the accumulation of large-bodied mammal remains in Panxian Dadong; however, whether this was primarily from scavenging or from hunting activities remains unresolved (Schepartz, Stoutamire, and Bekken 2005; Schepartz et al. 2003). Findings from Ubeidiya tentatively suggest some evidence for butchery and hunting of medium-size game (Gaudzinski 2004).

In Java, Storm (2012) has suggested that *H. erectus* occupied a largely carnivorous niche on the basis of the number of identified specimens and minimum number of individuals from Dubois legacy collections (specifically, Kedung Brubus and Trinil; see table 1). Storm (2012) was understandably cautious in his conclusions; a visual examination of these collections by one of the authors (J. Louys) in 2006 revealed no marks that could be unambiguously attributed to Pleistocene hominins. Likewise, Bouteaux et al. (2007) found no evidence of anthropogenic modifications on remains from several Sangiran Dome localities (Tanjung, Sendang Busik, Ngrejeng Plupuh, Grogol Plupuh, and Bukuran; table 1). The lack of obvious marks on these bones does not necessarily mean that Early and Middle Pleistocene hominins did not have access to or consume large and medium-size game. They may instead be a result of processing with tools made of materials other than stone that leave less obvious signatures on the bone, such as bamboo (West and
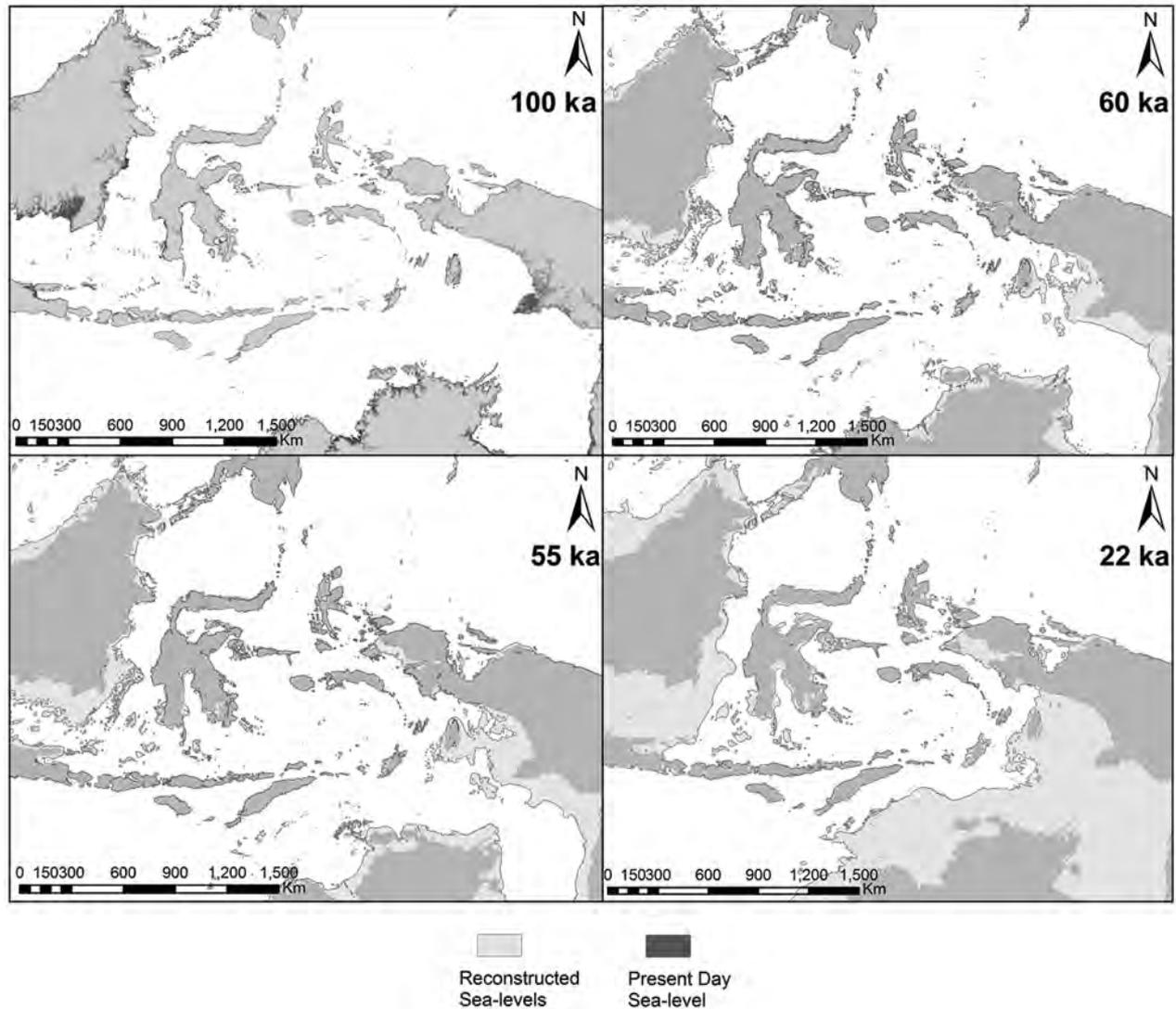
Figure 3. Palaeo-shoreline reconstructions for Wallacea and neighbors for 100 ka, 60 ka, 55 ka, and 22 ka. Modeled using the General Bathymetric Chart of the Oceans 30 arc-second bathometry chart (Smith and Sandwell 1997). Sea levels are based on the adjusted curve in figure 2. A color version of this figure is available online.

Louys 2007) or shells (Choi and Driwantoro 2007), as well as the depositional setting of the assemblages in question, minimizing the potential for hominin actions on faunal remains. For example, Zhoukoudian is primarily interpreted as a hyena den, and the aforementioned Sangiran Dome deposits represent natural fluvial accumulations (Bouteaux et al. 2007), neither of which might attract hominin attention.

Although rare, direct evidence of processing of animal carcasses by Asian *H. erectus* does exist. Choi and Driwantoro (2007) report likely shell tool cut marks on bovid (*Bos* species) remains from Bukuran and Sangiran, and Bouteaux and Moigne (2010) reported cut marks and percussion damage on long bones belonging to *Axis* species and *Duboisia* species recovered from Ngebung 2 (table 1). Despite limited direct evidence, the use and processing of large and medium-size game by Pleistocene Asian

hominins is inferred by most researchers through extension of the realized niche that *H. erectus* occupied in Africa (e.g., Bouteaux et al. 2007; Dennell 2014; Larick and Ciochon 2015). This represents a reasonable inference.

Evidence of the use of marine resources for subsistence by *H. erectus*, however, is even more circumstantial. Freshwater shellfish were known to *H. erectus* populations, and the shells were used as tools and perhaps even for decorative art (Choi and Driwantoro 2007; Joordens et al. 2015). Evidence of coastal, lacustrine, swamp forest, lagoon, and marshy environments present during the deposition of the Trinil HK assemblage demonstrates that aquatic resources were present at the same time as *H. erectus* in Middle Pleistocene Java (Joordens et al. 2009). Likewise, the presence of crocodile and fish remains in Ngebung is suggestive of exploitation of aquatic resources

(Moigne et al. 2004). However, direct evidence of the exploitation of marine resources by Early and Middle Pleistocene hominins has yet to be shown. No doubt Pleistocene hominins were opportunistic omnivores and would not have refrained from using any resources available to them. Nevertheless, on the basis of the environmental contexts in which they have been recovered, it is probable that pre-*sapiens* hominin populations were constrained to environments where fresh water, animals, and plants were plentiful (Dennell 2014), and it appears that aquatic resources constituted only a minor element of protein intake.

East of Huxley's Line, Early Pleistocene hominins are restricted to the islands of Flores. There, the Early Pleistocene vertebrate fauna population was clearly impoverished (Dennell et al. 2014; Meijer et al. 2010), particularly in comparison with the faunal records of similar periods on Java and China. Only a dwarf stegodon (*Stegodon sondaari*), the Komodo dragon (*Varanus komodoensis*), and a giant tortoise (*Geochelone* species) are known from the site of Tangi Talo (Brumm et al. 2010; Meijer et al. 2010), dated to approximately 0.9 Ma (Aziz et al. 2009; Morwood et al. 1998). After the deposition of Tangi Talo, a turnover was recorded at Mata Menge and similarly aged sites, and a new, larger species of stegodon (*Stegodon florensis*), a rat (*Hooijeromys nusatenggara*), the Komodo dragon, and a tool-making hominin are recorded (Brumm et al. 2010, 2016; Meijer et al. 2010; van den Bergh et al. 2016*a*; see table 1). The habitat at Mata Menge has been reconstructed as one composed of open, savannah-like grasslands with a wetland component (Brumm et al. 2016). The specific identity of the small-bodied hominin responsible for the stone tools on Mata Menge is not known (van den Bergh et al. 2016*a*); however, recent analyses have suggested *H. erectus* was the likely ancestor of this hominin (as well as the later *Homo floresiensis*; Kaifu et al. 2015; van den Bergh et al. 2016*a*; van Heteren 2012; van Heteren and de Vos 2007; van Heteren and Sankhyan 2009), and its dispersal from Java in the Early Pleistocene is not contradicted by paleobiogeographical data (Dennell et al. 2014). In addition to the terrestrial fauna and associated archaeology, crocodiles, ducks, swans, and abundant freshwater mollusc species were recovered from Mata Menge (Brumm et al. 2016; van den Bergh et al. 2009*a*). Whether these were natural or anthropogenic is not known, although the age profile of the stegodon assemblage is consistent with a natural mass death event (Brumm et al. 2016). This age profile contrasts with both the later Liang Bua and the Middle Pleistocene Panxian Dadong stegodon assemblages, which are dominated by young individuals and thought to have been, at least in part, accumulated by hominins (table 1; Brumm et al. 2016; Schepartz, Stoutamire, and Bekken 2005).

A much more nuanced and detailed record of faunal-hominin associations is present in the *H. floresiensis*–bearing Liang Bua deposits. There, a long sequence of faunal and archaeological records are dated to earlier than ca. 50 ka (Sutikna et al. 2016), suggesting that the dominant animal resources used by *H. floresiensis* were potentially stegodons, Komodo dragons,

monitor lizards, and a variety of birds and rats (van den Bergh et al. 2009*b*). Most significantly, although small amounts of terrestrial gastropods were recovered in the excavations, molluscs and other aquatic fauna are completely absent from deposits dating to earlier than 11 ka; deposits from 11 ka and after are accepted to have been accumulated by *Homo sapiens*, which suggests that such resources played no part in the subsistence strategies of *H. floresiensis* (Szabó and Amesbury 2011). This is consistent with the (admittedly sparse) evidence of subsistence strategies of hominins across Asia. Overall, these records suggest that *H. floresiensis* and its ancestor, probably *H. erectus*, made no use of aquatic resources on Flores and required access to large- and medium-bodied vertebrate remains for survival.

Sulawesi has often been cited as the origin of *H. floresiensis* populations (e.g., Morwood and Oosterzee 2007), and recent lithic finds from Talepu in the Walanae Valley on this island are consistent with early hominin colonization of Wallacea (van den Bergh et al. 2016*a*; table 1). Although the stone tools from Talepu in Sulawesi cannot be tied to any particular hominin species, van den Bergh et al. (2016*b*) make a case that they could have been made by archaic *Homo*. As on Flores, the fauna recovered in association with the tools are medium- to large-bodied terrestrial species, namely buffalo, stegodon, and a large extinct endemic pig (*Bubalus*, *Stegodon*, and *Celebochoerus*), and could thus have been used by hominins for subsistence. In addition to these species, Sulawesi also hosts seven extant species of macaque, the Sulawesi babirusa (*Babyrousa celebensis*), the Sulawesi warty pig (*Sus celebensis*), and two species of anoa (*Bubalus depressicornis* and *Bubalus quarlesi*) that would have potentially been available to early hominin scavengers or hunters, although these species have thus far not been recovered from Early to Middle Pleistocene archaeological excavations.

In the Philippines, a hominin fossil from Callao Cave in Luzon has not yet been identified to species. It was referred to *Homo* species (Mijares et al. 2010) and favorably compared with small-bodied *Homo* species, such as *Homo habilis* and *H. floresiensis* (Larick and Ciochon 2015), although provisionally attributed to *H. sapiens* by Mijares et al. (2010). It has a minimum age of around 50 kyr (Grün et al. 2014) and is found in association with several large taxa: the native brown deer (*Cervus mariannus*), the Philippine warty pig (*Sus philippensis*), and an extinct bovid (Piper and Mijares 2007). The brown deer dominates the assemblage, with more than 90% of the identifiable bone fragments assigned to cervid. Interestingly, although no stone tools have been recovered from this level at Callao Cave, cut marks are present on deer remains, implying the use of perishable tools by this hominin (Mijares et al. 2010). Only miniscule aquatic remains have been recovered from the cave (Piper and Mijares 2007), which suggests that these did not constitute a part of subsistence behavior at this site (see table 1).

With so few Early to Middle Pleistocene hominin sites east of Huxley's Line, it is difficult to be confident about the realized niche of pre-*sapiens* hominins on Wallacean islands. The African record gives every reason to expect that *H. erectus* was a resourceful and opportunistic species, making use of whatever

resources were on hand. This is reflected, albeit less clearly, in the Asian record. Regardless, however, it would appear that this species had a reliance on sources of large- or medium-bodied carcasses to survive, and we argue that these requirements help explain the restricted distribution of hominins in Wallacea. *Homo floresiensis* and the new records from Sulawesi (van den Bergh et al. 2016b) demonstrate that water crossings were not a barrier to hominin dispersals, even if such dispersals were unintentional and subject to prevailing oceanic conditions (Dennell et al. 2014). However, successful colonization of islands requires not only travel but that the subsistence requirements of the colonizing species are met. We argue that, for early hominins, this would have required access to adequate terrestrial faunal resources and that complete or near-complete reliance on aquatic resources required technological and behavioral innovations that were beyond the reach of pre-*sapiens* hominins in Wallacea.

Zooarchaeological Records and Subsistence Strategies of *Homo sapiens* in Wallacea

There are few sites in Sunda that inform on the subsistence of *H. sapiens* at the time of first modern human maritime dispersal. Niah Cave in Sarawak, with a record spanning at least 50,000 years (Higham et al. 2016), perhaps gives us the clearest picture of the eclectic and flexible nature of modern human economic activities in Sunda before their arrival in Wallacea. At the time of the earliest recorded occupation, Niah was about 30 km from the Pleistocene coastline, and the people living there pursued diverse subsistence strategies, exploiting resources from the forests surrounding the caves and a range of freshwater environments. Pig seems to have been a major prey (*Sus barbatus*), but a wide range of species were exploited, including langurs, macaques, porcupines, monitors and smaller lizards, snakes, birds, and bats as well as molluscs and fish (Piper and Rabett 2017). Niah continued to be used during the LGM when lowered temperatures and a downward migration of the montane forest are indicated by the presence of the lesser gymnure (*Hylomys suillus*) and the ferret badger (*Helictis orientalis*), species that are today restricted to the highlands of Mount Kinabalu (Cranbrook 2000). As sea level rose after the LGM and coastal estuaries began to establish, there is evidence for an increasing focus on estuarine resources. The Niah fish assemblage includes large individuals from freshwater streams and estuaries, which indicates the use of nets or spears in their capture (Barker et al. 2007). Niah is also unique in preserving evidence of Pleistocene plant exploitation and includes fragments of fruits, nuts, and parenchyma (Barton, Paz, and Carlos 2017; Paz 2005), showing that "rainforest tuberous plants such as aroids, taro, yam, and sago palm" (Barker 2005:97; Barton 2005) were collected. Interestingly, many of the tubers required multistage processing to render them safely edible, demonstrating that early modern humans west of Huxley's Line possessed an advanced knowledge of plants, at least some of which would be familiar east of Huxley's Line.

Sulawesi, the largest of the Wallacean islands, was first occupied by modern humans by at least ~40 ka (Aubert et al. 2014). The earliest archaeological records on this island thought to be definitely attributable to *H. sapiens* are in South Sulawesi in the limestone karst near the modern city of Maros (table 1). Simons and Bulbeck (2004) show that, in the earliest period of modern human occupation, hunting focused on the endemic suids *Sus celebensis* and *Babyrusa* but included *Anoa* species as well as an extensive range of medium-size to small mammals (Simons and Bulbeck 2004). Interestingly, the South Sulawesi sites have no evidence for maritime resources use, but this may be due to transport distance, because at the time of earliest settlement, the Pleistocene shore would have been approximately 60–80 km away.

The Talaud-Sangihe Archipelago, lying between Mindanao and North Sulawesi, is of particular interest because it comprises 77 tiny and remote islands with little in the way of terrestrial faunal resources. Despite intensive coastal survey of a number of islands in this group, the only Pleistocene-aged site discovered in the Talauds to date is Liang Sarru shelter on Salibabu, which today is only ~100 km². Liang Sarru has evidence of episodic use in the Pleistocene between ~35 and 32 ka and again between 22 and 17 ka, after which it appears to have remained unoccupied until the Holocene (table 1; Ono, Soegondho, and Yoneda 2009; Tanudirjo 2001). There is currently no archaeological evidence that the Talaud group acted as a stepping stone for colonization from the Philippines to Sulawesi, because the Liang Sarru sequence postdates initial modern human settlement in Sulawesi (Aubert 2014; Ono, Soegondho, and Yoneda 2009), and commensal rodent genetics suggest colonization of Talaud by agriculturalists from the south (Louys et al., forthcoming). While fossils of *Stegodon* are known from the Sangihe group, and bats, rats, birds, and marine vertebrates occur in the extant fauna, the Pleistocene occupation levels of Liang Sarru consist entirely of marine shellfish and a few urchin remains. The complete lack of Pleistocene vertebrate fossils from the Talaud Islands is puzzling. Poor preservation is unlikely to be the explanation, because marine shells are abundant and would have assisted the preservation of bone if it was deposited. While the lack of vertebrate fauna may be an effect of small sample size, exploration and excavation has been more intensive here than in many islands of the other Wallacean groups. It seems possible that the initial phase of settlement of the Sangihe-Talaud Islands comprised fleeting opportunistic visits by small, highly mobile groups of mariners coming to exploit seasonal island resources. Alternatively, perhaps the Liang Sarru sequence records an early "Robinson Crusoe" settlement that was ultimately unsuccessful (Leppard 2015; Leppard and Runnels 2017), and thereafter the islands remained unoccupied until about 22 ka when, due to the lowered sea levels of the LGM, individual islands of the Talaud group were connected to form a single mega-island incorporating the current islands of Karakelong, Salibabu, Kabaruan, and Sara. The Talaud mega-island reached between 1654.4 km² (calculated with average Wallacan uplift of

0.5 m/kyr) and 1693.9 km² (excluding uplift; fig. 4). Occupation of Liang Sarru during this phase appears to have been intensive but again short lived, lasting only until the end of the LGM ~17 ka. The subsistence record during this phase is also solely shellfish, but stone artefacts are significantly more abundant, perhaps indicating a larger population or more regular use of the cave. Except in terms of total numbers, the stone artefact assemblage has been characterized as changing little through time. The earliest and LGM assemblages include low numbers of retouched flakes, some of which are classified as concave and convex scrapers with steep working edges suitable for wood working (Ono, Soegondho, and Yoneda 2009; Tanudirjo 2001:239–247).

Golo Cave on Gebe Island in northern Maluku has parallels with Liang Sarru. Golo was occupied by ~36 ka (table 1; Bellwood et al. 1998). At this time, Gebe Island was merged with neighbouring Yu, Fau, and Uta islands, forming a single landmass of between 644.30 km² (using average 0.5 m/kyr uplift) and 724.09 km² (excluding uplift; fig. 5). Golo contains no subsistence evidence in the Pleistocene levels aside from marine shellfish (Bellwood et al. 1998:239). These comprise predominantly upper intertidal species dominated by a variety of limpets and small gastropods (*Nerita* species and *Thais* species) as well as barnacles (arthropods), some oysters, and carnivorous gastropods from Muricidae, which Szabó and Amesbury (2011:12) believe indicate foraging at local oyster beds. The Pleistocene horizons at Golo Cave contain few stone artefacts. The lithic assemblage includes a mere 51 stone artefacts made on a variety of metavolcanic rocks and comprises flake shatter, simple unretouched flakes, undiagnostic fragments, three cores, and a hammerstone. No retouched pieces were identified. However,

flaked *Turbo marmoratus* opercula occur, and flakes of this dense shell may have substituted for flaked stone (Szabó, Brumm, and Bellwood 2007).

At ~8 ka, Golo sees the first appearance of vertebrate fauna: bones of a now extinct *Dorcopsis* wallaby (Bellwood et al. 1998: 251–253; Flannery et al. 1998), a cuscus (*Phalanger alexandrae*) that still occurs on the island today (Flannery and Boeadi 1995), and a small quantity of reptile, bird, and fish bone (Bellwood et al. 1998). Because there are "no good taphonomic reasons" (Szabó and Amesbury 2011:12) for the absence of bone below the 8-ka level, the wallaby and phalanger have been argued to be human introductions to Gebe in the Holocene. However, the cuscus is apparently endemic to Gebe, and the absence of any bone whatsoever in the Pleistocene levels makes it difficult to test whether the wallaby is indeed a translocation (P. Piper, personal communication, February 2015). If preservation were not an issue, it would be expected that some bones of endemic species would occur in the Pleistocene deposit, and perhaps changes in site function provide a better explanation for the absence of bone in the Pleistocene layers at Golo. The terminal Pleistocene horizon, just below the first appearance of vertebrate fauna, is said to contain circular and semicircular coral stone arrangements containing volcanic pebbles, the latter transported to the cave from the southern part of the island, which suggests a ritual use of the cave at this time (Bellwood et al. 1998:252). Golo also contains large numbers of coral cooking stones, and the marine shell is reportedly heavily burnt (Bellwood et al. 1998:252). It is possible that this area of the site had a specialized function for cooking vegetable foods. This could perhaps be resolved by micromorphological work on the sed-
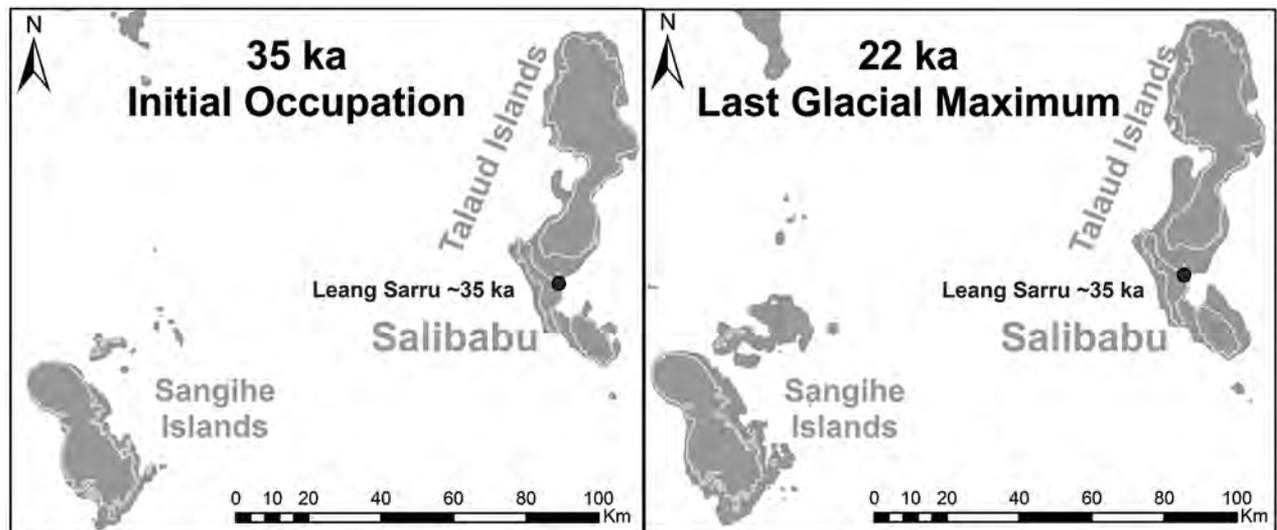

Figure 4. Reconstructions of the Talaud and Sangihe island archipelagos at the time of the first known occupation (~35 ka at Leang Sarru) and during the peak of the last glacial maximum (~22 ka). Reconstructed using the uplift-adjusted sea level curve from figure 2 and the General Bathymetric Chart of the Oceans bathometry chart (Smith and Sandwell 1997). A color version of this figure is available online.
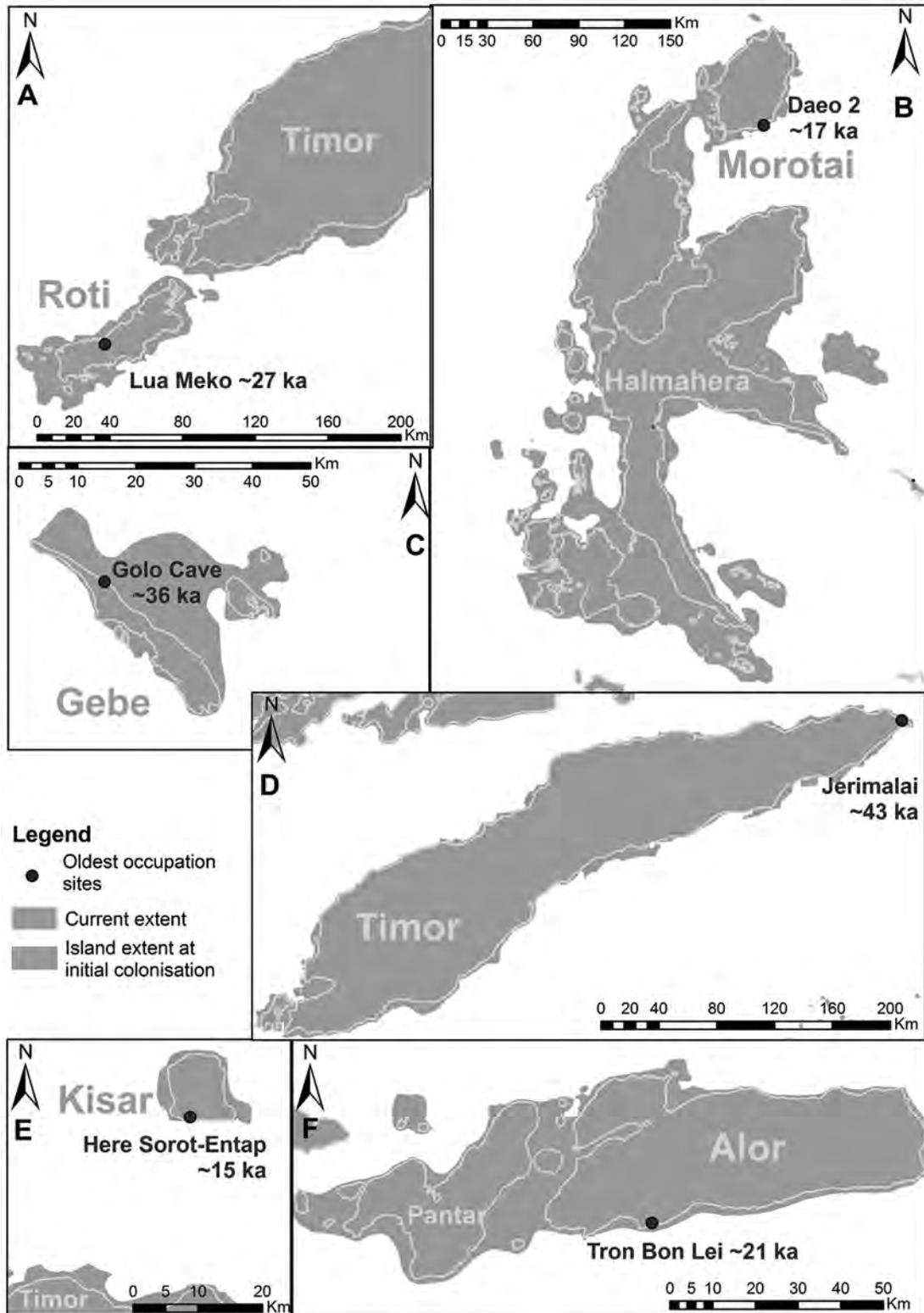
Figure 5. Reconstructions of island size at the time of first known occupation for Roti (*A*), Morotai (*B*), Gebe (*C*), Timor (*D*), Kisar (*E*), and Alor (*F*) islands. Reconstructed using the uplift-adjusted sea level curve from figure 2 and the General Bathymetric Chart of the Oceans bathometry chart (Smith and Sandwell 1997). A color version of this figure is available online.

iments. Siti Nafisah Cave in Halmahera also has *Dorcopis*, along with an unknown bandicoot species, in layers dating to the mid-Holocene, but by the Late Holocene, both had become extinct (table 1; Bellwood et al. 1998:253).

Daeo 2 Cave in Morotai to the north in Halmahera was first occupied ∼17 ka (table 1; Bellwood et al. 1998) and, at this time, was connected to Halmahera, Bacan, and other smaller surrounding islands (fig. 5). This combined land area would have been approximately 39,422 km² (using an average 0.5 m/kyr uplift) to 40,161 km² (without uplift). Interestingly, despite relatively good faunal preservation down to the Pleistocene units, Daeo 2 has no evidence of the extinct *Dorcopsis* or bandicoots found in Gebe and Halmahera, but it does have a cuscus, murids (including one large species), and quantities of fish bone, the latter being most abundant in the Holocene units (Bellwood et al. 1998:246). Bellwood et al. conclude that, because Morotai is visible from and close to Halmahera, and these marsupials are absent, it would seem that initial colonization was followed by a long period of relative isolation (Bellwood et al. 1998:246–247). The absence of *Dorcopsis* and bandicoot on Morotai at the time when Morotai and Halmahera were joined suggests that the marsupials were translocated to Halmahera, but they must have been introduced after the two islands were separated, perhaps in the mid-Holocene. Simple unretouched flakes made on locally available beach pebbles occur at Daeo 2, but the authors are not specific about technology or distribution within the site.

Timor, the largest island on the southern dispersal route (as defined by Birdsell 1977), has produced some of the earliest dates for modern human use of the Wallacean Archipelago. Jerimalai Shelter and Lena Hara Cave have sequences dating back to ∼42 ka (see table 1; O'Connor 2007; O'Connor, Allen, and Hawkes 2010). These sites are formed in uplifted coralline terraces and are within a kilometer of today's coastline. Due to the steep bathymetric drop off in this region, the sites would always have been proximal to the coast. Rocky shore shellfish, fish, and marine turtle dominate the earliest Pleistocene levels of both sites. The Pleistocene levels of Jerimalai contain a large quantity of fish bone, and pelagic species form a significant component of the assemblage (O'Connor, Ono, and Clarkson 2011). In contrast, Matja Kuru 2 of comparable antiquity (O'Connor, Robertson, and Aplin 2014), but located about 6 km from the coast today, has a Pleistocene assemblage dominated by giant rats; reptiles, such as pythons, lizards, and freshwater turtle; and some bat and small murid that may not be of anthropogenic origin. Marine shell was recovered in the Pleistocene and Holocene levels, but quantities are small in comparison with Lene Hara and Jerimalai, and marine fish and sea turtle are poorly represented, no doubt due to the greater transport distance from the coastline to this site. The Timor lithic assemblages evidence the predominant use of good-quality chert to produce flakes from a range of cores that include multiplatform, single-platform, bidirectional, bipolar, and radial cores. At Jerimalai, the only assemblage yet studied in detail, retouched pieces occur in low numbers, and overall the assemblage shows remarkable conservatism over time (Marwick et al.

2016). Small numbers of very tiny obsidian flakes from an as-yet-unknown source—but one thought likely to be external to Timor—were also identified in deposits dating predominantly to after ∼14 ka (Reepmeyer, O'Connor, and Brockwell 2011). The Timor-Leste sites also contain a range of shell items, including fish hooks by at least ∼16 ka (O'Connor, Ono, and Clarkson 2011) and decorative items that begin to be made immediately after first occupation; like the lithics, these change little through time (Langley and O'Connor 2016; Langley, O'Connor, and Piotto 2016).

The archaeological assemblage from an area on the southern coast of Alor Island, Tron Bon Lei, provides insights about human subsistence strategies north of Timor. Settlement as recorded by the deposit in this shelter first occurred at ∼21 ka (table 1; Hawkins et al. 2017), at a time when sea levels were low and Alor Island was merged with neighboring Pantar, Pura, Marisa, Rusa, Ternate, and Treweng islands, forming a single island of between 3,862 km² (estimated with an average 0.5 m/kyr uplift; fig. 2) and 3,910 km² (without uplift).

In one Tron Bon Lei shelter that is within a few hundred meters of the current coastline, a 1 × 1-m test pit yielded abundant marine shellfish and fish bone accumulations dated from 21 to 3 ka, along with stone artefacts manufactured from basalt, obsidian, and chert, which suggests a human population almost solely dependent on marine resources before the Neolithic (Hawkins et al. 2017; Samper Carro, Louys, and O'Connor 2017; Samper Carro et al. 2016). The faunal assemblage from the Late Pleistocene–early Holocene occupation levels contained over 40,000 fish bones, with differences observed in the quantity of remains, taxonomic representation, and prey size between the Late Pleistocene and early Holocene layers. The Pleistocene assemblages (dated from 21 ka to 10 ka) had a larger number of faunal remains compared with more recent accumulations, which suggests resource depression or alternatively a decrease in occupation intensity of the shelter during the early Holocene (S. C. Samper Carro, personal observation). This is surprising in view of the fact that coastal resources would have been more accessible in the Holocene after the rise in sea level and stabilization of near-shore coastal environments, and this contrasts with the abundance of Holocene-aged archaeological evidence documented in other Southeast Asia island environments more generally (e.g., Mahirta 2009:50, 61). The Tron Bon Lei Pleistocene assemblage contains a larger percentage of carnivorous fish families relative to herbivores as well as a larger number of remains from families of pelagic species. Prey size is larger in the Pleistocene levels, reflecting the larger quantity of pelagic fishes compared with reef environment fishes (O'Connor et al., forthcoming *b*; Samper Carro et al. 2016). This likely represents changes in fishing practices and/or technology, whereby hook and lure fishing during the Pleistocene declined in importance relative to other capture methods, such as netting. The fish assemblage from Alor has strong similarities with the assemblage composition at both Jerimalai and Lene Hara in Timor-Leste, except turtle bone is not common in the Alor deposits. In terms of nonvertebrate fauna, the

Tron Bon Lei pit B assemblage has a dense and well-preserved shell midden throughout the Pleistocene and early- to mid-Holocene levels. Interestingly, the Pleistocene levels are dominated by an arthropod: a large barnacle; there are kilograms of this barnacle in some of the Pleistocene excavation units. In terms of molluscs, rocky substrate marine species predominate and include limpets and false limpets (Fissurellidae; *Cellana* and *Patella* species), abalone (*Haliotis* species), Chitonidae, and Neritidae. *Turbo* species, *Tectus* species, *Soccostrea*, *Tridacna* species, *Hippopus* species, Thiaridae, Muricidae, and *Stombus* species are also represented, and there are very small contributions from freshwater taxa. Crabs and urchins were recovered from all excavation units in variable quantities (O'Connor, personal observation).

Analysis of the stone artefacts from this site is in progress, but like Jerimalai, the assemblage comprises cores, flakes, and low numbers of flake tools with no formal patterning. The obsidian artefacts have been identified as having distinct geochemical signatures indicating three separate source locations (Reepmeyer et al. 2016). One of the obsidians is a geochemical match for the high-silicate obsidian in the Timor-Leste sites and, interestingly, appears in Tron Bon Lei at about the same time, ~14 ka. While the source for this obsidian is not yet known, the small size of the artefacts made on it, the absence of artefacts with cortex, and the late appearance of this obsidian in the sequence combine to suggest that the source is not in Alor and instead suggest its maritime transport from elsewhere in the Sunda arc to Timor and Alor (Reepmeyer et al. 2016).

The tiny island of Kisar to the northeast of Timor is only approximately 10 km × 8.7 km with a total area of 81.15 km². It has a narrow coastal platform owing to its rapid rate of uplift and deep offshore profile. While it would have been slightly larger during periods of low sea level, it would never have been much larger than it is today. Our recent excavation at a shelter on the south coast, Here Sorot Entapa, demonstrates that the island was occupied by at least 15 ka. Based on a small testing in 2015 of two 1 × 1-m excavations (pits A and B), the site was first occupied at 13,176 ± 30 WK-43325 (15,091–15,338 cal BP; marine shell). The occupation horizon at 15 ka is directly underlain by sterile coralline sands that are dated to 45,840 ± 2,687 (WK-46537) on coral from a culturally sterile deposit. The coral date corresponds well with the estimated age for the uplift of the terrace in which the shelter is formed, demonstrating that it would have been available for habitation before 15 ka. The archaeological fauna in both test pits is overwhelmingly dominated by fish, shellfish, urchin, and crab. Aside from marine resources, these shelters contain only occasional bones of endemic small rodents, shrews, bats, small lizards, and snakes. Analysis of the lithics has not yet begun; however, as in the other Wallacean sites, the assemblage appears to be composed of cores, flakes, and low numbers of irregularly retouched flakes.

Roti Island immediately east of Timor was also occupied in the Pleistocene. Lua Meko Cave, near the north coast, has a lower nonbasal age of ~28 ka cal BP (24,420 ± 250 ANU-10908) associated with sparse stone artefacts and marine shell (table 1; Mahirta 2009:52). Roti was not connected to Timor at this time; however, the water crossing separating the two islands at this time would have been between 3.04 km (without uplift) and 3.52 km (with use of an average 0.5 m/kyr uplift). Vertebrate faunal remains occur in the older Pleistocene units of Lua Meko but are fragmentary, heavily encrusted in carbonate, and not identifiable to taxon, so discussing subsistence is challenging. Based on the internal structure, most of the bone fragments in this lower unit are probably marine turtle. Marine shell in the lower Pleistocene levels included species from the families Chitonidae, Turbinidae, and Cypraeidae, which can be collected on rocky substrate or intertidal areas of the reef. The Holocene units see the appearance of mangrove mudflat– and sandy substrate–associated shellfish as well as an overall increase in taxa from a broader range of habitats as sea levels rise and stabilize. Low numbers of stone artefacts occur in the earliest levels of Lua Meko and appear remarkably similar to those from Timor-Leste in that they evidence generalized reduction of chert to produce simple flakes but no specialized artefact forms (Mahirta 2009).

Discussion

On the basis of current data, it appears that *Homo erectus, Homo floresiensis*, and other non-*sapiens* hominins in the region made use of available terrestrial resources, particularly medium- to large-bodied fauna. No similar evidence of significant marine resource exploitation by these hominins exists. A scarcity of terrestrial faunal resources on the small islands east of Flores and Sulawesi, combined with an inability to develop and employ sophisticated fishing technologies, may have precluded successful dispersal by these hominins any farther east. Although unsuccessful dispersals to small islands (i.e., dispersals that did not produce a genetically viable population) are certainly possible or even likely, being unsuccessful, they would necessarily have been archaeologically short-lived, such that the chances of their discovery remain slim to nonexistent (e.g., Leppard and Runnells 2017).

Outside Flores, Luzon, and Sulawesi, conditions favorable for successful hominin colonization, based on island size and geological history, might have been present on the islands of Sumba and Timor. Sumba hosts at least one species of stegodon (*Stegodon sumbaensis*); however, its record is too poorly known, both archaeologically and palaeontologically, to speculate on further. Timor, on the other hand, has been explored extensively for archaeological deposits (e.g., Glover 1986; O'Connor 2007; O'Connor, Allen, and Hawkes 2010), and during the Pleistocene, it hosted two species of pygmy stegodons, a giant land turtle, and a Komodo dragon–sized lizard in the Late Pleistocene (Hooijer 1971). Although early claims were made for the association between stone tools and stegodon remains in Timor (e.g., Glover and Glover 1970; Maringer and Verhoeven 1975; Maringer and Verschuuren 1981), the idea that Pleistocene hominins other than *Homo sapiens* made it east of Flores is now discounted (Allen 1991; Jones and Spriggs 2002; O'Con-

nor 2002). The subsistence constraints of pre-*sapiens* hominins may well explain this distribution. Certainly, direct movement of early hominins from Flores to Timor is possible; however, migration eastward through the islands of Lembata, Pantar, and Alor is more likely, because sea crossing distances are smaller (some of these islands were connected during glacial periods). Other than a giant (~2-kg) rat species, Alor Island hosts only small-bodied terrestrial endemics (Hawkins et al. 2017; Samper Carro et al. 2016). Lembata and Pantar have no Pleistocene prehistoric records, but Pantar's faunal history is likely to be similar to Alor's. Subsistence strategies of Pleistocene *H. sapiens* on the smaller Wallacean islands, such as Alor, appear to have required the exploitation of almost exclusively maritime resources (Samper Carro et al. 2016), strategies seemingly not employed by earlier hominins. The likely route to Timor would therefore have precluded hominins, which would explain their apparent absence from this large island.

Thus, independent of seafaring abilities, we suggest that the distribution of modern humans in Wallacea was dictated by the flexibility of subsistence strategies, without which continuous and successful survival on small islands with depauperate faunas was not possible. The suggestion that the dispersal of pre-*sapiens* Asian hominins was limited by subsistence strategy is clearly one that requires additional testing, and future research in the area should aim to fill the dearth of detailed zooarchaeological studies of Early and Middle Pleistocene hominin assemblages. Furthermore, with so few islands in the region that boast any kind of Pleistocene archaeological record, further exploration and fieldwork in the region may dramatically alter this model. As aptly demonstrated with the announcement of the discovery of *H. floresiensis* over a decade ago, the potential for unexpected discoveries in the region should not be underestimated.

All records indicate that *H. sapiens* that moved through the islands east of Huxley's Line were able to do so as a result of ecological flexibility and innovation, which allowed them to successfully subsist on the most depauperate of islands through the exploitation of almost purely marine resources. Whether the direct ancestors of the first modern human colonizers of Wallacea were already exploiting such resources, or whether such innovations in subsistence behavior occurred as a result of the unique environments present in Wallacea, is not answered by the archaeological records west or east of Huxley's Line. Nevertheless, on the basis of current records from the region, it appears that extensive and systematic marine exploitation was the purview of only *H. sapiens* and that this shift in subsistence strategy occurred concurrent with first arrival on all island groups.

Detailed zooarchaeological examinations of Late Pleistocene archaeological assemblages consistently indicate that *H. sapiens* relied almost exclusively on marine resources on small islands and coastal sites. Away from the coast, modern humans on the larger Wallacean islands took advantage of a range of small and medium-size murids, reptiles, bats, and birds. As sea levels rose and fell over the past 50,000 years, the Wallacean islands changed size. In some cases, islands that are adjacent today were joined together, creating larger land masses that were perhaps better suited to sustaining permanent human populations. Conversely, when sea levels were high, these islands were separate, as they are today, and they may have been used in a more transient fashion with groups making their livelihood by moving between small island groups to take advantage of shifting or seasonal resources (Ono, Soegondho, and Yoneda 2009; Tanudirjo 2001).

Most of the Wallacean sites lack skeletal remains in the earliest layers, and the stone artefact assemblages lack patterned, specialized, and curated tool production, such as retouched blades and backed artefact technologies that are typically associated with behaviorally modern humans in other regions of the world. However, the Pleistocene levels of Jerimalai, with its emphasis on pelagic fishing and shell artefact production, and the stone structures in Golo convincingly demonstrate modern humans to have been the occupants of these sites. It is likely that the development of specialized and curated technologies may have occurred in the face of specific or changing environmental conditions (Petraglia et al. 2009) and were simply not required in the islands of Wallacea, which did not experience major climatic oscillations during the human occupation timespan, and where maritime resources seem to have formed the mainstay of the diet before the Late Holocene ~3.5 ka (see also Szabó, Brumm, and Bellwood 2007). This hypothesis receives some support from the personal ornament repertoire made on marine shell in the Timor-Leste assemblages. These ornaments appear immediately after first settlement, perhaps indicating an early phase of experimentation and innovation following immediately on modern human entry into a new and unfamiliar environment. Once invented, however, these artefacts show remarkable conservatism over time in terms of form, raw material selection, manufacturing, and use wear (Langley and O'Connor 2016; Langley, O'Connor, and Piotto 2016).

Despite their maritime capabilities, there is no evidence for return voyaging after initial migration into Wallacea. Return voyaging might be seen in the human-assisted movement of animals or other resources, found to be absent in the islands after settlement, from the Asian mainland, from New Guinea, or from larger islands, such as Sulawesi. Human-assisted movement of faunal species would be one way of increasing available protein on the small islands with limited fauna. However, evidence that this strategy was pursued in the Pleistocene is scarce. The earliest-claimed translocation is from Laing Bawah, the cave adjoining Liang Bua in Flores, where a fragment of pig skull coated in carbonate was dated by U-Th to between 33 and 23 ka. Gagan et al. (2015:533) suggest that this indicates that *Sus* species "may have dispersed into Island Southeast Asia earlier than previously recognized." In the adjacent cave, Liang Bua, despite a well-stratified excavation spanning a period of ~20 ka, van den Berg report the presence of Sulawesi warty pig, *Sus celebensis*, at only 7 ka (van der Bergh et al. 2009b). All other introduced species at Liang Bua are associated with the Neolithic

and the appearance of pottery. The potential translocation of *Sus* species in Flores at such an early date is very surprising in view of the fact that *Sus* species have not been reported elsewhere in the Wallacean islands until the Neolithic or more recently. There are no other records of Pleistocene faunal translocations into the Wallacean Archipelago.

Java is home to at least one species of endemic pig, *Sus verrucosus*, and Sulawesi hosts two endemic porcines (Corbet and Hill 1992). If the early occurrence for the pig in Flores is substantiated, it more likely represents an unusual (although by no means unique) colonization for a medium- to large-bodied placental east of Wallace's Line rather than a deliberate translocation by people. The *Dorcopsis* in Golo Cave on Gebe Island and at Siti Nafisah in Halmahera is likely to be a mid- to Late Holocene translocation, at least in Halmahera, in view of its absence in Daeo 2 Cave in Morotai (which was connected to Halmahera until the early Holocene). In Timor-Leste, the cuscus *Phalanger orientalis* was originally reported from ~9.5 ka on the basis of associated radiocarbon ages obtained on shellfish (O'Connor 2006). This specimen has now been directly dated to ~3 ka (O'Connor 2015). Our recent investigation of some of the smaller Wallacean islands has also found no evidence for species introductions until the Late Holocene. Alor and Kisar have no translocated fauna before the Neolithic (J. Louys, personal observation). If the introduction of exotic species stood to benefit human settlement anywhere, Kisar would seem to be a prime candidate. The evidence would suggest that modern humans did not need to take animal protein sources with them to successfully settle even the smallest islands east of Huxley's Line.

The earliest evidence for interisland transport of materials is the high-silicate obsidian artefacts found in the Timor-Leste coastal assemblages and in Tron Bon Lei in Alor after ~14 ka (Reepmeyer 2016). Although the source of this obsidian is currently unknown, it is likely to be on one of the volcanic islands of the Sunda arc to the east of Timor and Alor. The presence of this geochemically distinct obsidian demonstrates that regular interisland voyaging was occurring from this time, at least from the source island to Timor and Alor. In view of this, it is all the more surprising that no attempt was made to transport terrestrial fauna from the mainland or from the more faunally diverse islands in the archipelago.

Rather, it would seem that the maritime subsistence strategies honed in the Wallacean archipelago >40 ka were sufficient for the population sizes for tens of millennia after initial settlement. Resources such as plants must have been a mainstay of the diet, and a better understanding of their role should be a priority for future work. Perhaps most surprising of all is that, despite the unbalanced and depauperate terrestrial faunas on the islands of Wallacea, none of the Pleistocene faunal assemblages currently indicate that modern humans moving through the archipelago impacted ecosystems significantly as a result of clearance, firing, or direct predation. On the basis of current evidence, a human role in the extinction of stegodon on Timor has been argued as unlikely (Louys, O'Connor, and

Price 2016). Of the four genera of giant rats on Timor, all of which are extinct today, all survived from the time of human arrival until a few thousand years ago (Louys, Aplin, and O'Connor 2015). Similarly, *Babyrusa* and the *Anoa* species in Sulawesi are today under threat of extinction but are found throughout Pleistocene archaeological sites and through to the Late Holocene in some sites in Southeast Sulawesi (O'Connor et al., forthcoming *a*). The *Dorcopsis* wallaby on Gebe and Halmahera and the Halmahera bandicoot are also Late Holocene extinctions, perhaps casualties of Neolithic land clearance (Bellwood et al. 1998). Although few Pleistocene sequences have been studied in depth, those currently available show no firm evidence of over hunting or extinctions. Contrasting the history of Pleistocene and Holocene extinctions on oceanic islands should be made a priority for future research.

Acknowledgments

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Human Dispersal from Siberia to Beringia

Assessing a Beringian Standstill in Light of the Archaeological Evidence

by Kelly E. Graf and Ian Buvit

With genetic studies showing unquestionable Asian origins of the first Americans, the Siberian and Beringian archaeological records are absolutely critical for understanding the initial dispersal of modern humans in the Western Hemisphere. The genetics-based Beringian Standstill Model posits a three-stage dispersal process and necessitates several expectations of the archaeological record of northeastern Asia. Here we present an overview of the Siberian and Beringian Upper Paleolithic records and discuss them in the context of a Beringian Standstill. We report that not every expectation of the model is met with archaeological data at hand.

The paleoanthropology of northeastern Asia and Alaska is paramount to understanding initial human dispersal in the Western Hemisphere because of their Late Pleistocene connection by the Bering Land Bridge, the now submerged continental shelf below the Bering Strait between far northeastern Russia and western Alaska. The biogeographical region, called Beringia, extends from the Verkhoiansk Range in eastern Siberia east to the Mackenzie River in northwestern Canada and includes Kamchatka, Chukotka, and the Bering Sea area (Hoffecker and Elias 2007; Hopkins et al. 1982; fig. 1). DNA of ancient human skeletons and living populations indicates direct links between far northeastern Asia and America. This high-latitude migration began after 50 ka and continued through the late glacial, a nearly 40 kyr odyssey through previously uninhabited landscapes characterized by starts and stops (Buvit et al. 2015; Graf 2009, 2010; Hamilton and Buchanan 2010) and involving noticeable responses to extreme conditions, especially 26–20 ka at the last glacial maximum (LGM; see Dennell 2017 for discussion of the ecology of initial dispersals). Though some refer to the entire last glacial stage, or marine isotope stage (MIS) 2, as the LGM (i.e., LGM sensu lato), we consider the LGM sensu stricto most pertinent to Siberian and Beringian human ecology, when Northern Hemispheric glaciers were at their greatest extent and temperatures at their minima, following Clark et al. (2009). Despite temperatures colder than today for Siberia and Beringia during the entire span of MIS 2 (Zazula et al. 2006), various paleoproxy records from these regions indicate even more extreme cold

and arid conditions during the LGM (e.g., Kuzmina and Sher 2006; Szpak et al. 2010). Here we consider the archaeological records of Siberia and Beringia in the context of the Beringian Standstill Model (BSM), a hypothesis proposed by geneticists to explain late Pleistocene dispersal of modern humans from Siberia to America. We present basic tenets and archaeological expectations of the BSM, review the region's Upper Paleolithic prehistory, and discuss how well the archaeological record meets these expectations.

A Hypothesized Beringian Standstill: The Long and Short of It

Genetic studies convincingly demonstrate that Asia gave rise to the first Beringians and Americans. Genetic data from present-day human DNA (mitochondrial, Y chromosomal, and whole genome) link all Native American ancestors to Siberia (Derenko et al. 2007; Karafet, Zegura, and Hammer 2006; Merriwether 2006; Mulligan and Kitchen 2013; Mulligan, Kitchen, and Miyamoto 2008; Perego et al. 2009; Reich et al. 2012; Schurr 2004; Schurr and Sherry 2004; Tamm et al. 2007), and new studies of ancient mtDNA and paleogenomics from early American contexts yield Asian-derived Native American relationships (Gilbert et al. 2008; Kemp et al. 2007; Raff and Bolnick 2014; Raghavan et al. 2014, 2015; Morton Rasmussen et al. 2014, 2015; Smith et al. 2005; Tackney et al. 2015). Paleogenomics indicate that first American population histories were far more complicated than we realized (Skoglund et al. 2015). Despite these advancements, we still do not know precisely when and from where these first American populations emerged or how they dispersed through Beringia and the Americas.

This northern perspective requires considering two events: (1) dispersal from Siberia to Beringia, and (2) subsequent dispersal from Beringia into the Americas. Based on estimates of lineage coalescence as well as placement and dating of the earliest archaeological sites in far northeastern Siberia and Alaska

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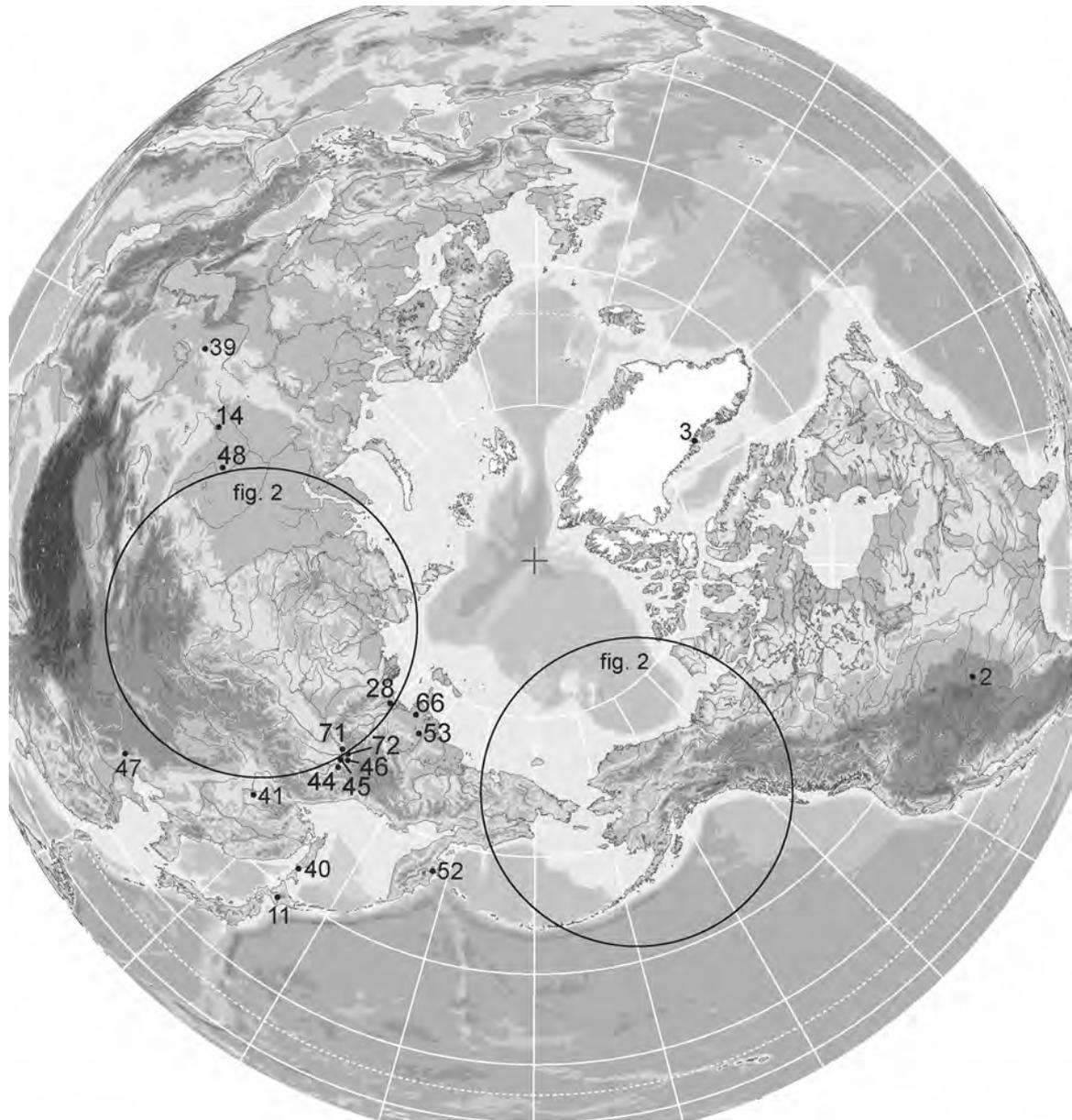
Figure 1. Map showing sites mentioned in the text. 2 (Anzick), 3 (Saqqaq), 11 (Kashiwadai), 14 (Ust' Ishim), 28 (Yana RHS), 39 (Kostenki 14), 40 (Ogon'ki 5), 41 (Ust' Ulma), 44 (Diuktai Cave), 45 (Ust'-Mil), 46 (Verkhne Troitskaia), 47 (Tianyuan Cave), 48 (Cherno'ozere), 52 (Ushki Lake), 53 (Berelekh), 66 (Lake Nikita), 71 (Ikhine), 72 (Ezhantsy). A color version of this figure is available online.

at 33 ka and 14 ka, respectively, most geneticists agree that Native Americans diverged from Asian ancestors either in northeastern Asia or on the Bering Land Bridge just before or immediately following the LGM (Bortolini et al. 2003; Goebel, Waters, and O'Rourke 2008; Hoffecker, Elias, and O'Rourke 2014; Karafet, Zegura, and Hammer 2006; O'Rourke 2009; Raff and Bolnick 2014; Raghavan et al. 2015; Schurr 2004; Schurr and Sherry 2004; Seielstad et al. 2003). Divergence was followed by a period of isolation when today's Native American genetic diversity developed. This incubation or "standstill" was origi-

nally hypothesized to have taken 15 kyr (Kitchen, Miyamoto, and Mulligan 2008; Mulligan and Kitchen 2013; Mulligan, Kitchen, and Miyamoto 2008; Tamm et al. 2007), although new studies argue it began later and lasted less than 8 kyr (Raghavan et al. 2015; table 1).

Geneticists mostly analyzing mtDNA genome data from living populations propose a long chronology where divergence between Asian ancestors and proto–Native Americans occurred about 40–30 ka as a group left Central Asia and arrived on the Bering Land Bridge by 30 ka. Divergence was immediately fol-

Table 1. Assumptions and archaeological expectations of Beringian Standstill Models (BSM)

BSM and genetic model assumptions	Archaeological expectations
Long-chronology:	
Initial divergence between a Central Asian ancestor population and proto–Native Americans >30 ka	Archaeological sites in eastern Northeast Asia dating 40–30 ka
Migration of proto–Native American population to Beringia by 30 ka	Time-transgressive distribution of sites from south to north with sites in Beringia by 30 ka
15–7.5 kyr isolation period and incubation of Native American suite of genetic variations in Beringia 30–16 ka	Archaeological sites present in Beringia 30–16 ka with new technologies and land-use strategies that differ from contemporary sites in Northeast Asia
Estimated effective population size of 8,000–10,000 individuals at 30–16 ka	Many archaeological sites dating to 30–16 ka in Beringia, reflecting proposed population
Migration of Native American founding population (~1,000 individuals) south along a Pacific coast route into the Americas	Archaeological sites along the Pacific coast dating to 16–13.5 ka
Short-chronology:	
Initial divergence between a Northeast Asian ancestor population and proto–Native Americans by about 23 ka	New archaeological technology and land-use strategy in eastern Northeast Asia by about 23 ka
Migration of proto–Native American population to Beringia immediately after the LGM (23–20 ka)	Time-transgressive distribution from south to north of sites with this new technology and land-use strategy 23–20 ka
<10 kyr isolation period and incubation of Native American suite of genetic variations in Beringia during the Late Glacial (20–14 ka)	Archaeological sites present in Beringia 20–14 ka with new technologies and land-use strategies differing from contemporary sites in Northeast Asia
Migration of Native American founding population south along perhaps both a Pacific coast and interior "ice-free corridor" route into the Americas	Archaeological sites along the Pacific coast and ice-free corridor dating to 16–13 ka

lowed by a long, 15–7.5 kyr isolation period when genetic diversification occurred through the LGM followed by dispersal of founding subclades (A2, B2, C1b, C1c, C1d, C4c, D1, D4h3, X2a) south to the Americas after 16 ka (Mulligan and Kitchen 2013). The long-chronology BSM assumes diversified subclades migrated as distinct populations south along the Pacific coastline carrying all Native American genetic diversity. Subsequent movements were hypothesized for the Holocene with migrations back to East Asia bringing C1a, a sister clade of the American C1 phylogeny, and the American A2a subclade as well as a final west–east dispersal across far-northern North America of the Siberian D2 subclade (Tamm et al. 2007). This version implies that people were in Beringia by 30 ka and that an LGM-aged Beringian biome maintained a viable human population throughout a period of global and regional climatic instability. Accordingly, we expect archaeological sites in high-latitude locations (>60°N) of Siberia from 40 to 30 ka, especially in western Beringia; the earliest archaeological sites on the Bering Land Bridge dating as early as 30 ka and through the LGM; and a Beringian archaeological record dated 30–16 ka, reflecting new tool kits and lifeways used by the new genetically varied founding population that gave rise to Native Americans. Ultimately the founding population would have left archaeological sites along the Pacific coast 16–13.5 ka.

Recently, a short-chronology BSM emerged from comparing ancient and present-day autosomal genome data, including remains from the 24 ka Mal'ta skeleton from the Baikal area (Raghavan et al. 2014), the 12.5 ka Anzick skeleton from Montana (Morton Rasmussen et al. 2014), the 9 ka Kennewick skeleton from Washington (Rasmussen et al. 2015), and the

hair from a 4 ka Saqqaq mummy from Greenland (Rasmussen et al. 2010; figs. 1, 2). Raghavan et al. (2015) found genetic ties between all modern and ancient Native American populations sampled to date and Mal'ta, indicating divergence from Asian ancestors not at 40 ka but between 23 and 20 ka, arguing incubation did not last longer than 10 kyr. This is because migration south to the Americas commenced before 13.5–13 ka, the time of Clovis, the earliest unequivocal archaeological tradition in the Americas (Haynes et al. 2007; Waters and Stafford 2007). Short-chronology BSM implies people dispersed to the Bering Land Bridge immediately following the LGM, so no archaeological sites should be expected in eastern Beringia before 20 ka. This version implies that Native American genetic variation emerged rapidly during an early late-glacial standstill.

Several geneticists agree that dispersal from Beringia to the Americas was rapid, occurred after the LGM, and potentially followed the Pacific coast with subsequent interior movements at ~16–14 ka (Fagundes, Kanitz, and Bonatto 2008; Fix 2002; O'Rourke 2009; Wang et al. 2007) and slightly later via an interior "ice-free corridor" at ~14 ka (O'Rourke 2009; Perego et al. 2009; Starikovskaya et al. 2005). A coastal route would have been viable throughout the late glacial (Mandryk et al. 2001); however, an interior route following the Yukon River basin over low divides into the Mackenzie River basin and then south to northern Alberta and Saskatchewan would have been available by about 12.6 ka (Pedersen et al. 2016, but see Munyikwa et al. 2011 and Zazula et al. 2009 for slightly earlier dates). Archaeologically, however, the oldest Pacific coastline evidence dates to the early Holocene (Dixon and Monteleone 2014), and there are no archaeological sites predating Clovis along the ice-
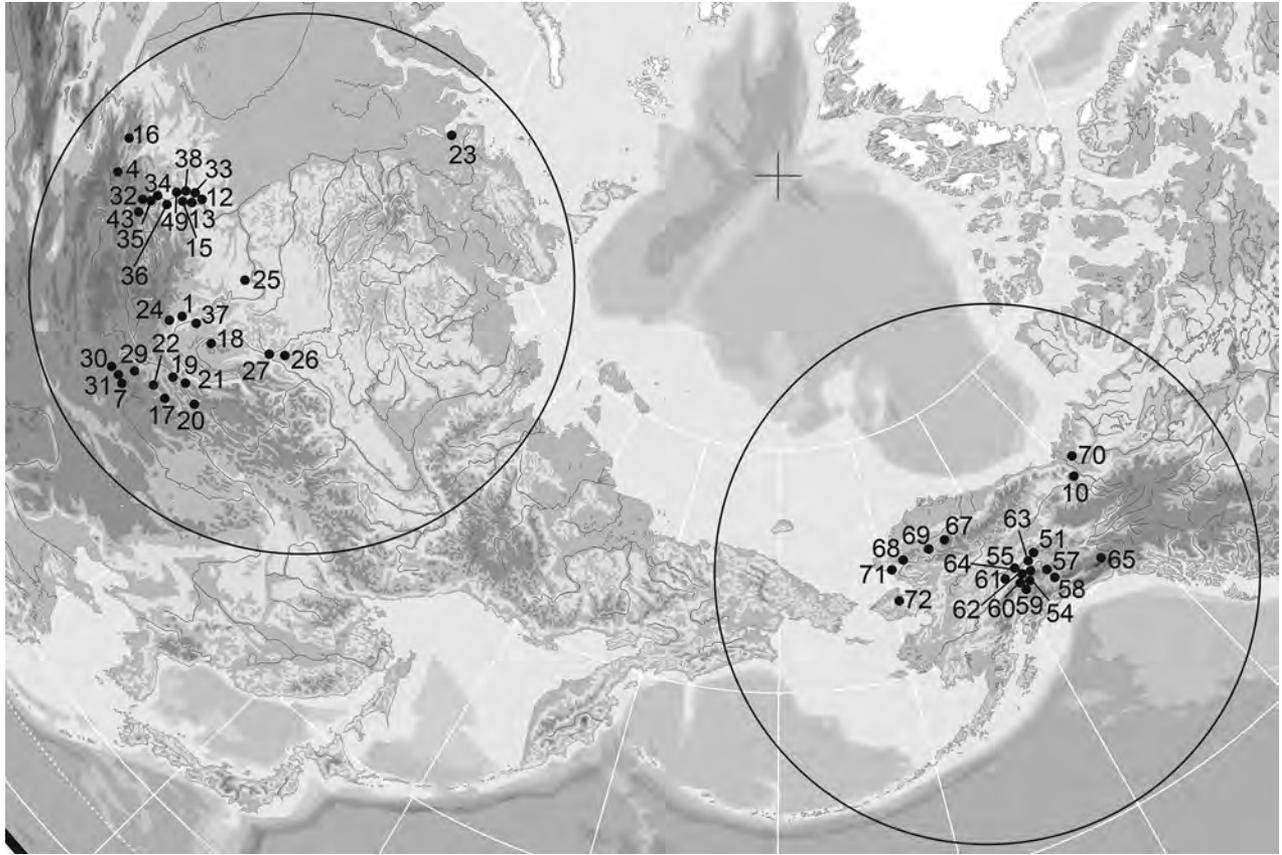
Figure 2. Map showing sites in southern Siberia and Eastern Beringia. 1 (Mal'ta), 4 (Denisova Cave), 7 (Ust'-Menza), 10 (Bluefish Cave), 12 (Afontova Gora), 13 (Listvenka), 15 (Pokrovka), 16 (Kara Bom), 17 (Tolbaga), 18 (Makarovo 4), 19 (Varvarina Gora), 20 (Khotyk), 21 (Kamenka), 22 (Masterov' Kliuch), 23 (Sopochnaya Karga), 24 (Buret), 25 (Ust'-Kova), 26 (Nepa 1), 27 (Alekseevsk), 29 (Kunalei), 30 (Chitkan), 31 (Melnichnoe, Studenoe), 32 (Ui 1), 33 (Novoselovo 13), 34 (Afanaseva Gora), 35 (Kashtanka 1), 36 (Derbina 4/5), 37 (Igeteiskii Log), 38 (Kurtak 4), 43 (Nizhnii Idzhir'), 49 (Kokorevo 1), 51 (Swan Point), 54 (Tangle Lakes), 55 (Moose Creek), 57 (Gerstle River Quarry), 58 (Upward Sun River), 59 (Carlo Creek), 60 (Dry Creek, Panguingue Creek), 61 (Owl Ridge), 62 (Walker Road), 63 (Broken Mammoth), 64 (Linda's Point), 65 (Little John), 67 (Mesa), 68 (Tuluaq Hill), 69 (Irwin Sluiceway), 70 (Engigstciak), 71 (Raven Bluff), 72 (Serpentine Hot Springs). A color version of this figure is available online.

free corridor (Ives et al. 2013), obscuring which route was used and when.

These events are based solely on genetic models. Empirical archaeological evidence is, therefore, critical for testing the long-chronology and short-chronology standstill models and determining precisely when and how humans arrived in the New World. Below we review archaeological records from southern Siberia to central Alaska in the context of both BSMs to establish which is better supported by existing evidence. Finally, in discussion, we place these records in the context of the genetic models.

The Siberian Record

The Siberian Paleolithic is primarily an archaeological record; however, some human skeletal remains have been recovered. Both archaeological and skeletal remains indicate premodern Neanderthals and Denisovans initially colonized the Altai re-

gion of southwestern Siberia more than 50 ka (Buzhilova, Derevianko, and Shunkov 2017; Derevianko 2010; Derevianko and Markin 1998; Derevianko et al. 1998, 2003; Goebel, Derevianko, and Petrin 1993; Green et al. 2010; Krause et al. 2007; Prüfer et al. 2014; Reich et al. 2010; Turner 1990), though one Denisovan specimen may be <50 ka given the difficulty in determining its exact stratigraphic correlation with remains discovered in another part of Denisova Cave (Sawyer et al. 2015; fig. 2). These premodern populations, however, may not have spread north or east of the Altai (Graf 2015, but see Lbova 2000; Tashak 2004). It was not until about 47 ka that Upper Paleolithic archaeological sites began to emerge (table 2). Regionally, they are divided into three chronological phases labeled early, middle, and late (Sapozshnikov 2004; Vasil'ev 1992) and represent dispersal of humans to the north and east, eventually making it across the Bering Land Bridge to Alaska. Only five known sites have preserved paleoanthropological remains from Upper Paleolithic contexts: Mal'ta, Afontova Gora, Listvenka, Pokrovka,

Table 2. Climatic time-stratigraphic units associated with archaeological phases, technologies, and land-use patterns of the Upper Paleolithic in Central and Eastern Siberia

Dates (ka)	MIS	Greenland ice-core climatic intervals (S. O. Rasmussen et al. 2014)	Archaeological phases	Technologies	Land-use strategies
50–34	3	Long Greenland interstadials 14–7 interrupted by short Greenland stadials 13–7	Early Upper Paleolithic	Laminar blade and flake lithic technologies; unifacial blade-tipped osseous projectile technologies	Seasonal use of sites. Too few sites to confidently interpret mobility strategies
34–24	3/2	Long Greenland stades 6–3 interrupted by short Greenland interstadials 6–3	Middle Upper Paleolithic	Blade, bladelet, flake, and bifacial lithic technologies; osseous projectile and sewing technologies; osseous mobile art	Varied site types, including special-task and base-camp sites, indicate familiarity with the landscape and a logistical-mobility strategy
26–20	2	Last glacial maximum long Greenland stades 3–2.1b interrupted by short Greenland interstadials 2.2 and 2.1			
22–12	2	Long Greenland stades 2.1b–1 interrupted by a shorter Greenland interstadial 1 (Bølling-Allerød)	Late Upper Paleolithic	Blade and flake lithic technologies; wedge-shaped microblade core technology and slotted microblade-osseous composite projectile points; osseous sewing technologies	Uniform site types (base camps), behaviors geared toward economizing lithic raw materials and maximizing tool cutting edges suggests a residential-mobility strategy

and Ust' Ishim. Of these, only the remains from Mal'ta, Afontova Gora, and Listvenka were discovered in archaeological excavations and have clear associations with Upper Paleolithic artifacts (Akimova et al. 2005; Astakhov 1999; Gerasimov 1958; Sosnovskii 1935). The other two were found in secondary fluvial settings (Akimova et al. 2010; Fu et al. 2014). All are anatomically modern *Homo sapiens* with complete autosomal genomes sequenced for Mal'ta (Raghavan et al. 2014) and Ust' Ishim (Fu et al. 2014) and some preservation of autosomal material from Afontova Gora (Raghavan et al. 2014). Below we provide a brief review of the Siberian Upper Paleolithic primarily focusing on the record east of the Altai.

Before the Last Glacial Maximum: The Early Upper Paleolithic

Anatomically modern humans appeared in Siberia about 50–45 ka in the Altai but spread into south-central and southeastern Siberia about 45–40 ka, represented by sites from the northern foothills of the Saian Mountains and Lena-Angara Plateau in the upper reaches of the Enisei, Angara, and Lena rivers. In addition to the archaeological remains, a single *Homo sapiens* femur, dating to 45 ka, was found at Ust' Ishim in Western Siberia (Fu et al. 2014).

Early Upper Paleolithic (EUP) sites are in open-air contexts along drainages, a few within alluvium, and others in colluvium or a combination of colluvial and eolian sediments. Dating these early sites has been highly problematic. First, they are situated in complicated depositional settings usually with primary contexts disturbed by LGM cryoturbation. Second, some dates were obtained on pooled bone fragments without proper pretreatment to isolate collagen and to ensure that external con-

tamination was not included. So unless these dates are statistically equivalent to other samples from the same contexts on well-prepared collagen or wood charcoal (see Douka and Higham 2017; Graf 2009), they must be viewed with skepticism. Sites with relatively diagnostic archaeological assemblages, found in understandable stratigraphic contexts with reasonably reliable chronometric dates, are few, suggesting modern humans were first in southern Siberia by about 50–45 ka at Kara Bom (Goebel, Derevianko, and Petrin 1993) and then spread east to the Makarovo 4 site immediately west of Lake Baikal perhaps as early as 45 ka (Goebel and Aksenov 1995). Dates from Varvarina Gora (45–40 ka; Bazarov et al. 1982; Kuzmin 1994), Khotyk (42 ka; Kuzmin et al. 2006), and Kamenka (40–30 ka) east of Lake Baikal suggest more substantial habitation at 45–35 ka (Lbova 2000). Other dates obtained from fauna among the cultural materials at the sites of Masterov Kliuch' (Goebel, Waters, and Mescherin 2000) and Tolbaga (Bazarov et al. 1982; Buvit et al. 2016; Goebel and Aksenov 1995; Goebel and Waters 2001; Kuzmin et al. 2011; Lbova 2005) range from about 48 to 30 ka. These Transbaikal sites are found in colluvial settings, so their long time ranges probably reflect redeposition of materials from various times. At Sopochnaya Karga weather station at 72°N latitude in the lowermost reaches of the Enisei River, a nearly complete mammoth carcass was found with several lesions that Pitulko et al. (2016) contend were made by human hunters; however, neither osseous nor lithic artifacts were found with the remains. From what we know about EUP sites, they fall within the middle part of MIS 3, a paleoclimatic warm period punctuated by several cold intervals (Bezrukova et al. 2010; Kind 1974). Radiocarbon databases, now numbering close to 1,000 dates (Buvit et al. 2016; Kuzmin et al. 2011),

signal two possible pulses of EUP occupation, one at ~50–42 ka and a subsequent one after 40 ka, both during warm intervals (GIS-12/11/10 and GIS-9/8) of the mid Upper Pleistocene. Given the limitation of radiocarbon dating near the working limit of the method as outlined by Douka and Higham (2017), we accept these age ranges with some caution.

In addition to sites discussed above, others are included in the EUP on typological and stratigraphic associations of their lithic artifact inventories (fig. 3). Together they illustrate how early modern humans made sophisticated large laminar blade-based technologies with weapons tipped by unifacial points (Derevianko and Shunkov 2005; Derevianko et al. 2005; Goebel 2002*b*; Goebel, Derevianko, and Petrin 1993; Kirillov and Derevianko 1998; Konstantinov 1994; Markin 1998; Vasil'ev and

Rybin 2009). The variety of other lithic tools, as well as osseous tools (e.g., needles, awls, retouching implements, and small antler points; Tashak 2007; Vasil'ev and Rybin 2009), indicate humans were undertaking various processing tasks and manufacturing clothing and other perishable items. Evidence from a few EUP sites confirms production of personal adornment on bone and stone (e.g., beads, bead preforms, pendants, bracelets; Derevianko and Rybin 2005; Derevianko, Shunkov, and Volkov 2008; Lbova 2010). Personal ornaments are known from EUP sites across the Old World; however, early sewing implements are known only from the northern contexts of Siberia and Eastern Europe, where they would have been germane in manufacturing warm clothing (Hoffecker 2005). During this time, people were procuring fauna as they encountered them,
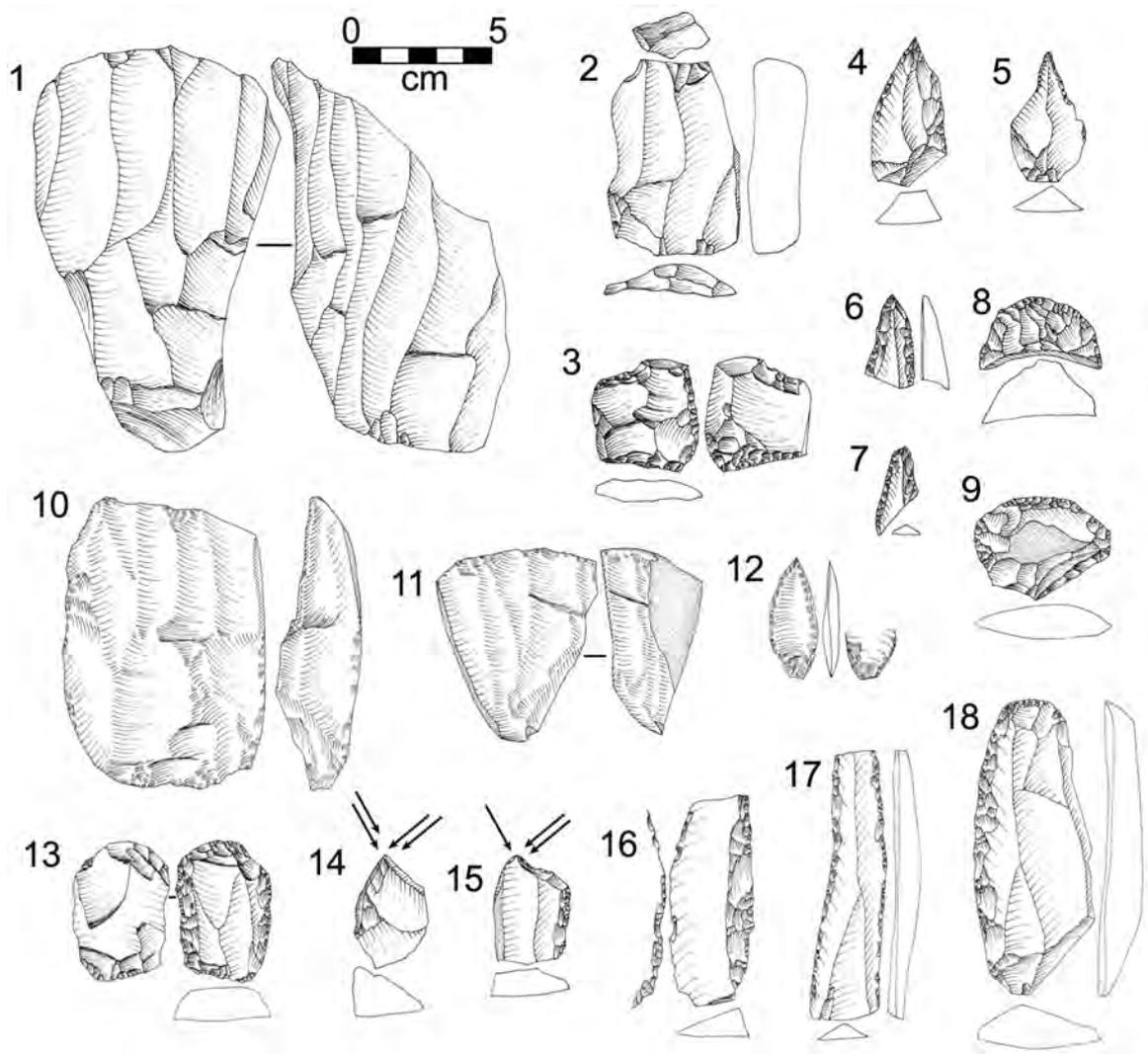
Figure 3. Representative artifacts from early Upper Paleolithic contexts (drawn by T. Goebel). Varvarina Gora: 1 (subprismatic blade core), 2 (laminar, flat-faced blade core), 3 (bipolar core), 4–5 (gravers), 6–7 (points on blades), 8–9 (end scrapers). Makarovo 4: 10 (laminar, flat-faced blade core), 11 (subprismatic blade core), 12 (point on blade). Tolbaga: 13 (bipolar core), 14–15 (burins), 16 (backed blade), 17 (retouched blade), 18 (end/side scraper on blade).

not focusing on any one taxon or type of animal (Goebel 2004*a*; Vasil'ev 2003*a*; Vasil'ev and Rybin 2009). Dense, vertically thick artifact concentrations, dwellings, and storage pits (Konstantinov 2001) indicate people were living at these sites for relatively long periods, maybe seasonally in scheduled base camps. Better seasonality data from faunal assemblages may help sort out these behaviors.

Genome sequencing of the Ust' Ishim individual shows ties to a basal Eurasian population, ancestral to both Europeans and East Asians, without admixture by Denisovans, which make up none of the sequence, and little by Neanderthals, which are only 0.3%–2.3%, a similar range for present-day Europeans and East Asians. This means Neanderthal introgression in the Ust' Ishim individual's ancestral population occurred well before their dispersal to Siberia, perhaps at about 60–50 ka in Southwest or Central Asia (Fu et al. 2014).

The Onset of the Last Glacial Maximum: Middle Upper Paleolithic

The next phase of the Upper Paleolithic is broadly compared with the Gravettian of Central and Eastern Europe (Anikovich et al. 2007; Hoffecker 2002; Roebroeks et al. 2000) because of assemblages based on bladelet production (Lisitsyn 1996), a variety of utilitarian and nonutilitarian osseous technologies including art, high faunal diversity, elaborate site features, and dedicated logistical mobility with sometimes far-reaching raw material procurement (Hoffecker 2002). Russian scholars refer to the Siberian middle Upper Paleolithic (MUP) as the Mal'ta Culture (Derevianko 1998; Lisitsyn 2000; Okladnikov 1968) after the sites of Mal'ta and Buret about 160 km west of Lake Baikal.

Nearly all MUP sites have a similar west–east distribution to the EUP. In fact, MUP material overlies EUP cultural layers at several sites. One difference, however, is that MUP sites extend more than 500 km north to nearly 60°N latitude at Ust' Kova, Nepa 1, and Alekseevsk in the Enisei and Lena River valleys and as far as 71°N latitude at Yana RHS along the lowermost Yana River in northwestern Beringia, representing the oldest (~33–31 ka) MUP site occupation yet found in this far-northern context. Generally, however, Siberian MUP sites exist south of 60°N latitude and range in age from about 34 to 24 ka with at least nine belonging to the relatively warm first half of this age range (34–29 ka), when arboreal taxa are more prevalent in paleoecological records (Bezrukova et al. 2010; Derevianko et al. 2003). The majority, however, date to 29–24 ka, a period when regional conditions began to deteriorate toward the LGM (Graf 2009; Kuzmin 1995; Kuzmin et al. 2011).

MUP assemblages include both flake and blade production but show marked reliance on flake over blade production, and sites such as Mal'ta in the Angara basin; Kunalei, Chitkan, Priiskovoe, and Melnichnoe in the Transbaikal; Ui 1 in the Saian; and Novoselovo 13, Afanaseva Gora, and Kashtanka 1 in the Enisei basin show extensive use of bladelets and small flakes (fig. 4). A few assemblages (Ust' Kova and Derbina 4/5) have

bifacial projectile points (Akimova et al. 2003; Goebel 2004*b*; Medvedev 1998*b*), whereas elsewhere most projectile points were constructed of osseous materials. Processing implements include simple retouched flakes and blades and a variety of other small, functional tools (Derevianko 2005; Graf 2008, 2010; Konstantinov 1994; Terry 2010; Terry, Andrefsky, and Konstantinov 2009).

Several MUP assemblages have somewhat elaborate osseous industries compared with EUP and late Upper Paleolithic (LUP) sites. Bone, antler, or ivory implements are unslotted, are rarely decorated, come in various sizes depending on their raw material (i.e., large points made from mammoth or horse vs. smaller points made on cervid antler or bone), and are found in most MUP sites that preserve faunal remains. A few thin, >20 cm long rod-type points have been discovered at Yana RHS, Mal'ta, Buret', and Igeteiskii Log (Medvedev 1998*b*; Pitulko et al. 2013). Sites also produced osseous retouchers, awls, and needles (Abramova et al. 1991; Lisitsyn 2000; Medvedev 1998*b*; Vasil'ev 2000). MUP sites also preserve various forms of nonutilitarian osseous artifacts, mostly carved ivory pieces divided into personal adornment (undecorated and decorated beads, drop, flat-form rectangular, disk-shaped pendants made of ivory, and pendants made of fox canines and cervid incisors) and highly symbolic "mobile" art. Some stone beads and pendants are recorded from Mal'ta, Yana RHS, and Kurtak 4. Mobile art includes engraved ivory plaques or badges, enigmatic rod-shaped pieces, 3-D zoomorphic figurines including mammoths and swans or other birds, 2-D outlines of mammoths carved into ivory, and anthropomorphic forms or "Venus" ivory figurines coeval with most found in western Eurasia. However, unlike western figurines, female characteristics on Siberian examples are carved in 2-D instead of 3-D and occasionally have hooded, full-body winter clothing (Abramova 1995; Drozdov et al. 1990; Medvedev 1998*a*; Pitulko et al. 2012, 2013; Vasil'ev 2000).

Faunal lists include woolly mammoth, woolly rhinoceros, horse, steppe bison, auroch, Irish elk, argali sheep, Siberian mountain goat, saiga antelope, red deer, roe deer, reindeer, arctic fox, red fox, and hare, but unlike the EUP, not all MUP sites contain such a wide variety. Instead, some sites—for example, Ui 1 and Kashtanka 1—contain fauna specific to the geographic location and site function. At the Western Saian upland site of Ui 1, Siberian mountain goat and argali sheep (both upland biota) dominate, and at the lowland hunting camp of Kashtanka 1 in the Minusinsk Basin, reindeer and bison (both gregarious-herd taxa) were preferred (Graf 2015; Vasil'ev 2003*a*). In contrast, base-camp sites tend to have a wide variety of fauna without clear preferences (e.g., 13 taxa in relatively equal frequencies at Mal'ta and a similar pattern at Yana RHS; Medvedev 1998*b*; Pitulko et al. 2013; Vasil'ev 2003*a*). Several MUP sites preserved hearth features and associated dwellings (Konstantinov 2001; Larichev, Khol'ushkin, and Laricheva 1988; Medvedev 1998*b*; Pitulko et al. 2013; Sergin 1996; Vasil'ev 1996, 2003*b*), some more substantial than others, such as the subterranean features proposed at Mal'ta (Gerasimov 1935, but see
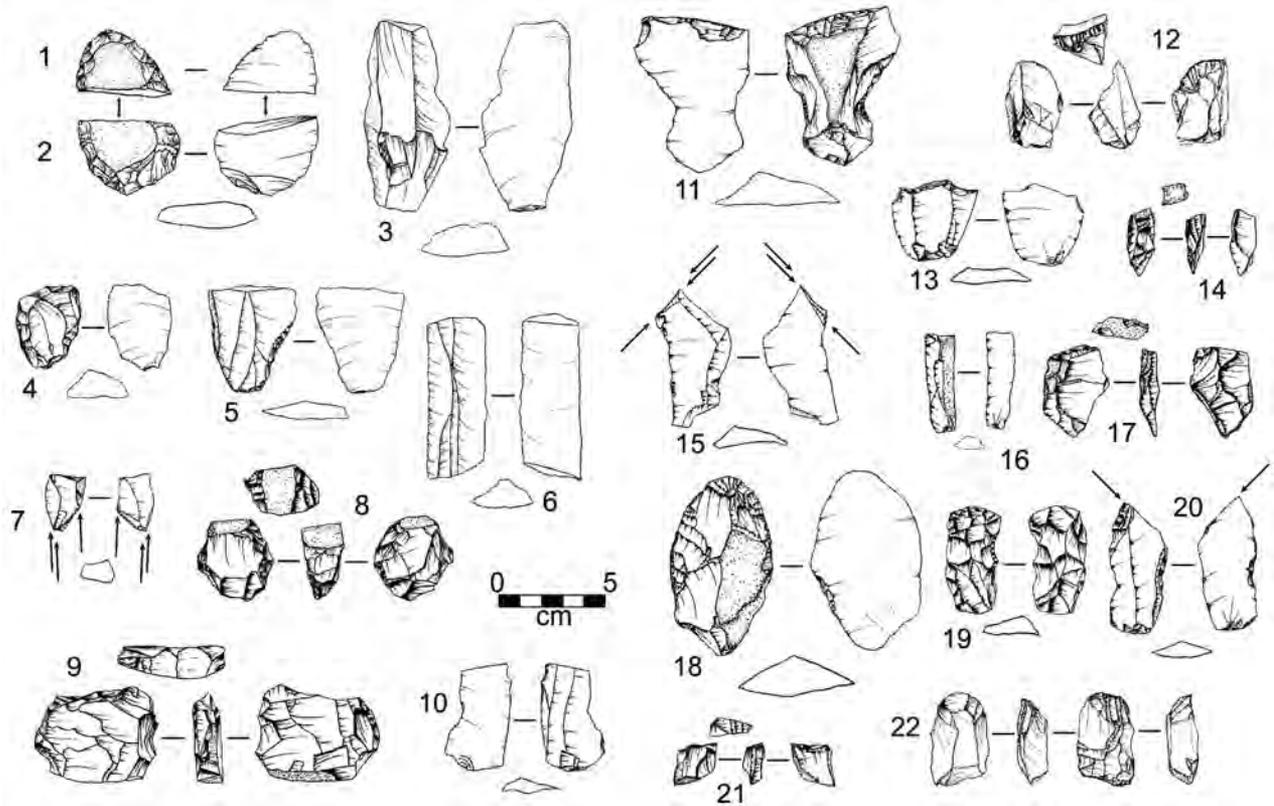
Figure 4. Representative artifacts from middle Upper Paleolithic contexts. Melnichnoe 2: 1–2 (convergent scraper fragments), 3 (blade), 4 (double convex scraper), 5 (concave single side scraper), 6 (medial blade fragment), 7 (burin), 8–9 (flake cores), 10 (proximal blade fragment). Chitkan: 11 (end scraper), 12 (subconical microcore), 13 (double notch on blade), 14 (wedge), 15 (burin), 16 (proximal blade fragment), 17 (retouched core), 18 (end scraper), 19 (irregular bifacial core), 20 (burinated double scraper), 21 (wedge), and 22 (microcore).

Vasil'ev 2000) where there was a child burial and there were storage pits (Gerasimov 1935; Medvedev 1998b).

High MUP intersite artifact, faunal, and feature variability indicates a wide variety of site functions with less diverse, smaller artifact assemblages at short-term, logistical camps and with more diverse, more concentrated lithic artifact assemblages and hordes of interesting decorative and artistic pieces at long-term, residential base camps. Faunal assemblage compositions and the types of domestic features also support this interpretation. A variety of sites with different functions indicate a logistically organized land-use strategy with residential bases and associated special-task locations (see Kelly 1983).

Results of genome sequencing of the Mal'ta child signal that people of the Siberian MUP descended from a central Eurasian rather than East Asian population and, therefore, they had already begun to diverge from initial Siberian founding populations (Ust' Ishim) by ~24 ka (Raghavan et al. 2014). In addition, the Mal'ta skeleton shares many derived alleles with the sequenced, 36 ka (early MUP) Kostenki-14 skeleton from the Central Russian Plain (Seguin-Orlando et al. 2014). As expected given its location, the Kostenki skeleton was found to be closely related to present-day Europeans, sharing more de-

rived alleles with Mal'ta than either shared with Ust' Ishim. These results indicate Siberian MUP populations were genetically isolated from East Asians but not each other at some point, and they shared immediate common ancestry with at least some Eastern European MUP populations. Another interesting result from the Mal'ta analyses is its relatively substantial 38%–14% contribution to the Native American genome, with the remainder derived from ancient East Asians, signaling a relatively recent and considerable introgression from MUP Siberia into populations migrating to the Western Hemisphere.

During the LGM: The Times They Were A-Changin'

In the 1970s geologist Tseitlin (1979) proposed Siberian LGM depopulation, specifically between about 23 and 21 ka. Since then, much debate has emerged around this hypothesis with Goebel (1999, 2002a, 2004b) advancing it based on detailed reviews of Russian excavation reports as well as his own fieldwork at sites chronologically around the LGM (Goebel, Waters, and Mescherin 2000; Goebel et al. 2000). After compiling nearly complete lists of radiocarbon dates from Siberian Upper Paleolithic sites in English, Kuzmin (2008) and colleagues

(Fiedel, Kuzmin, and Keates 2007; Kuzmin and Keates 2005) found no evidence for depopulation. Then, after revisiting original Russian reports on dates in these comprehensive lists, Graf (2005) discovered several inconsistencies in their reporting as well as uncritical acceptance of clearly aberrant ages. When obviously problematic measurements were removed, several >1 kyr gaps emerged that were associated with climatically cold periods including the LGM.

This has led us to conclude that while limited occupation occurred during parts of the global LGM, both the Enisei (Graf 2009, 2015) and Transbaikal (Buvit et al. 2015, 2016) regions were abandoned or reduced to archaeological invisibility for at least 2–3 kyr between about 24.8 ka and 22.7 ka. Calibrated radiocarbon dates from the Altai, Saian, and Angara (Kuzmin et al. 2011) indicate population decline during the LGM, but their gaps and occupations are temporally offset from each other and from gaps and occupations reported in the Enisei and Transbaikal. If this pattern bears out, then it may demonstrate a generally continuous LGM occupation of Siberia but one in which population sizes were low and people moved between these areas, perhaps between uplands and valleys. The question of complete abandonment at some point remains open, but given the archaeological record, LGM environmental factors, sampling, standard-error ranges, and important considerations about site formation, it does seem likely. Where southern Siberians exactly went remains unclear, but with humanity's overall resilience and propensity to migrate instead of perish, likely destinations would have been south and east to more moderate environments. Currently there is no evidence humans avoided inhospitable LGM conditions of southern Siberia by moving north to Yakutia and Beringia.

Recolonization Immediately following the Last Glacial Maximum: Late Upper Paleolithic

Across Siberia are dozens of LUP sites distributed much more broadly than before from Western Siberia to the Russian Far East, Kamchatka, and western Beringia (Abramova 1975; Abramova et al. 1991; Derevianko 1998; Goebel 2002a; Kuzmin 2000; Kuzmin and Orlova 1998; Kuzmin et al. 2011). Chronologically, we see a general time-transgressive pattern from south to north, arguably reflecting humans returning from LGM refugia, especially for the eastern half of Asiatic Russia where the LUP may ultimately derive from sites found farther east in pristine depositional contexts and dating to ~27–25 ka in Hokkaido, Japan (Izuho 2013).

Siberian sites with the clearest, earliest, and most trusted evidence of LGM-dated LUP occupations are Studenoe 2 and Ust'-Menza 2 in the Transbaikal. There, hearths from chronologically overlapping, briefly occupied dwelling features were found in vertically accreted alluvium conducive to preservation (Goebel et al. 2000; Konstantinov 1994, 2001; Kuzmin, Jull, and Razgildeeva 2004) and date to 22.7–20.9 ka (Buvit et al. 2016). The next youngest LUP site is Nizhnii Idzhir' from the upper reaches of the Enisei. Lithic artifacts found surrounding

a hearth feature in a paleosol formed on eolian deposits date to ~21–20 ka (Asktakhov 2008). Given that the earliest appearance of the LUP has been found at the Kashiwadai site on the southern tip of a peninsula formed by Sakhalin, Hokkaido, and some of the southern Kuril Islands (Paleo-Sakhalin-Hokkaido-Kuril [PSHK]), we expect sites dating to the LGM to be found between Hokkaido and Transbaikal. At Ogon'ki 5, located on Sakhalin Island, five radiocarbon dates on wood charcoal from features in the same cultural layer date to 35–20 ka (Vasilevskii 2005, 2008). These dates span the LGM, but cultural materials and dating samples were found in colluvial deposits and are probably not in a primary context. The Ust' Ulma site, located to the west in the Selemdzha River valley, has LUP artifacts and two radiocarbon dates on wood charcoal from a single hearth feature dated to 23.6–23 ka (Derevianko and Zenin 1995), but similar to Ogon'ki, these materials were found in a colluvial depositional setting. More work is needed in the Russian Far East to bridge the gap between PSHK and Siberia.

The Siberian LUP continues through the end of the Pleistocene, evidenced by scores of sites found in good contexts (Abramova 1986; Abramova et al. 1991; Buvit and Terry 2011; Buvit et al. 2015; Graf 2009; Ineshin and Teten'kin 2011; Konstantinov 1994; Mochanov and Fedoseeva 1996, Slobodin 2011, Vetrov et al. 2007). Conservatively, we can say by about 17–15.5 ka, the LUP spread as far as the middle Aldan River in southwestern Beringia represented at the Diuktai Cave, Ust' Mil', and Verkhne Troitskaia sites (Mochanov 1977; see discussion of dating problems with these sites in Yi and Clark 1985). Unfortunately, there are no well-dated LUP sites found east of the Aldan River in far northeastern Siberia/western Beringia (Slobodin 2011). Investigations of ^{14}C-dated Siberian LUP occupation frequencies through the late glacial illustrate a gradual increase in human populations through time with small spikes during warm intervals (i.e., Bølling, Allerød) and nadirs during intervening cold events (e.g., Oldest Dryas, Older Dryas; Buvit and Terry 2011; Goebel 1999; Graf 2005, 2009; Kuzmin and Keates 2005; Vasil'ev 2011).

LUP artifact assemblages are internally consistent with lithic industries based on flake, blade, and wedge-shaped microblade core production with many assemblages containing more flakes than blades (see fig. 5). Microblade-osseous composite projectile technology was nearly ubiquitous throughout the LUP, evidenced by microblade cores, microblades, and slotted points, some with microblades still in place (e.g., at Cherno'ozere in Western Siberia [Petrin 1986] and Listvenka [Akimova et al. 2005] and Kokorevo 1 [Abramova and Grechkina 1985] in the Enisei River valley). This technological strategy, which incorporated microblades detached from diagnostic wedge-shaped cores, resulted in highly standardized products. Moreover, processing tools found in these LUP assemblages (e.g., scrapers, burins) were typically formal with long use-life histories (Graf 2010, 2011; Kuzmin, Keates, and Shen 2007; Terry, Buvit, and Konstantinov 2016). Though production of osseous materials centered mainly on utilitarian implements, items of personal adornment exist, but other art forms do not (although see
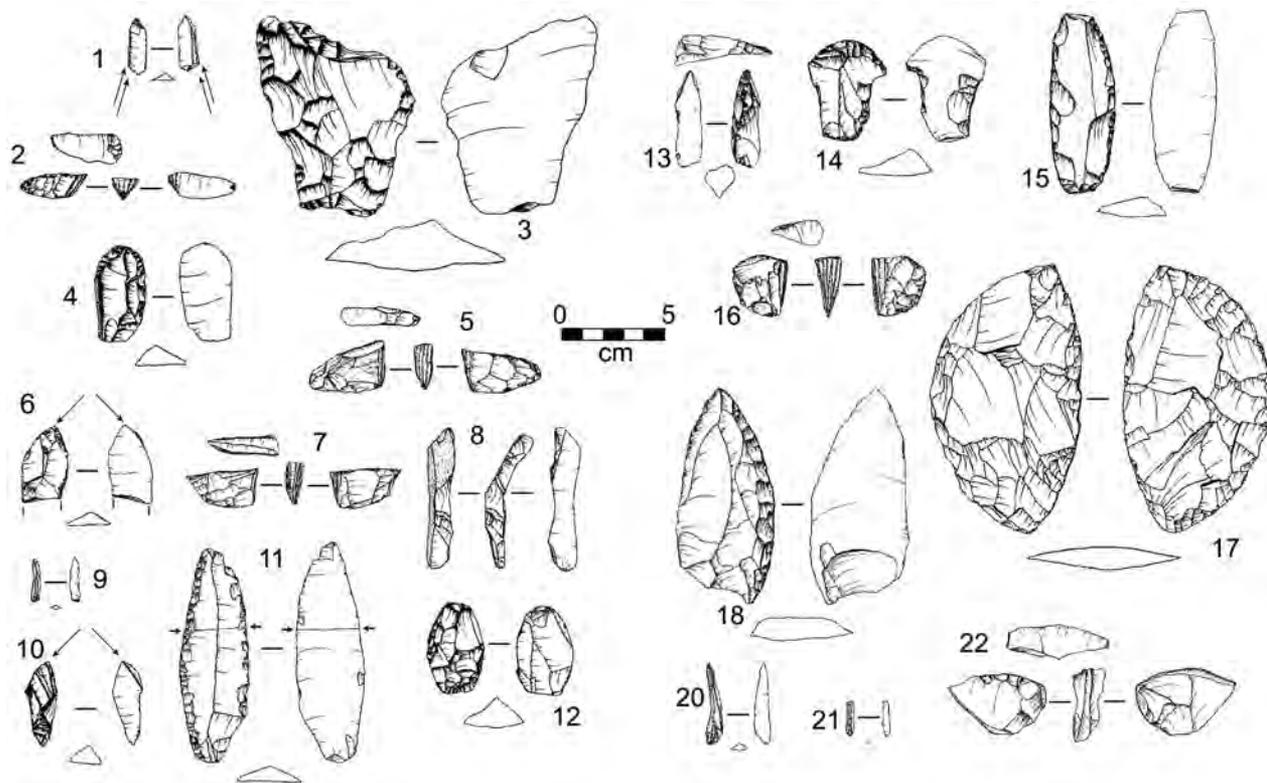
Figure 5. Representative artifacts from later Upper Paleolithic contexts. Studenoe 2: 1 (burin), 2 (subwedge-shaped microblade core), 3 (wedge), 4 (end scraper), 5, 7 (wedge-shaped microblade core), 6 (burin), 8 (ski spall), 9 (microblade), 10 (burin), 11 (convergent scraper), 12 (biface). Ust' Menza 1: 13 (ski spall), 14 (hafted end scraper), 15 (convergent scraper), 16, 22 (wedge-shaped microblade cores), 17 (bifacial foliate), 18 (convergent scraper), 20–21 (microblades).

Vasil'ev 1983 for an example of a small anthropomorphic human statue from the Maina site in the Saian that may date between 16 and 13 ka). The faunal record indicates a focus on specific, primarily large-game, gregarious-herd taxa. This pattern, coupled with a highly standardized and formal lithic technology and the near lack of any long-term dwellings, suggests people of the LUP were on the move, perhaps frequently traveling between sites. Provisioning and tool richness in the Enisei and Transbaikal demonstrate individuals were being outfitted to emphasize group mobility, and most LUP sites reflect short-term residential bases (Graf 2010; Konstantinov 2001; Terry 2010). LUP hunter-gatherers were arguably what Kelly (1983) would characterize as highly mobile, frequently moving residences across the landscape.

Summary of the Siberian Record

All archaeological and aDNA data from the EUP indicate modern humans arrived in southwestern Siberia by about 50–45 ka, spreading from the Altai to the Transbaikal by ~40 ka. Certainly modern humans were present as far north and east as Beijing, China, by this time at Tianyuan Cave (Fu et al. 2013; Shang and Trinkaus 2010). Interestingly, aDNA indicates initial Sibe-

rian populations may have been genetically close to the Tianyuan Cave inhabitants; however, they were not directly ancestral to them because Ust' Ishim is equally related to the MUP Mal'ta child who does not share derived alleles with Tianyuan Cave or present-day East Asians. Therefore, ancestors of the initial Siberian population split from early East Asians before arrival in Siberia (Fu et al. 2014; Raghavan et al. 2014). Archaeological materials found above the arctic circle at Yana RHS may represent the endpoint of an EUP dispersal to Beringia (Pitulko et al. 2013); however, elsewhere in Siberia there is at least a 2 kyr gap (and given depositional and pretreatment problems of radiocarbon dates, this may be more like 5–7 kyr) between latest EUP and earliest MUP sites, artifacts from Yana are distinctively MUP, and Siberian paleoecologists have determined the intervening years (40–35 ka) between the EUP and Yana RHS were cold (Bezrukova et al. 2010; Kind 1974). Yana may represent the first far-northern incursion of people using MUP technology at 33 ka during the warm GI-5 (or Lipovo-Novoselovo interstade, 35–30 ka; Bezrukova et al. 2010).

Despite decades of work by Russian archaeologists, the geographical distance between Yana RHS and other MUP sites to the south is probably in part the result of sampling bias because

much research to date has been undertaken around current population bases in southern Siberian cities. The taiga of central Siberia, especially in active permafrost conditions of the far north (Pitulko 2008), is logistically difficult for fieldwork, and very few roads into these areas mean far less archaeological survey has been done than southern regions. But the pattern of more and younger MUP sites in southern Siberia is also not surprising given that after 33 ka the Northern Hemisphere was beginning to cool with glaciers expanding from 33 to 26 ka (Clark et al. 2009). Colder, dryer conditions probably kept populations to the south during the onset of the LGM. The MUP record indicates hunter-gatherers were living in base camps and procuring resources relatively nearby. DNA from the Mal'ta child, one member of this MUP population, implies close genetic ties between Siberian and Eastern European MUP populations (Seguin-Orlando et al. 2014), either maintained from a recent common ancestor (45–36 ka) or possibly after occasional aggregation and mate exchange (see Binford 2001; Fix 1999). Given recognized similarities in lithic technologies and symbolic art forms between the Siberian MUP and the Eastern European Gravettian, the latter hypothesis may have more explanatory power, but we must keep in mind that to date we only have one Siberian MUP genome that probably does not represent all genetic variability of the Siberian MUP population.

The lack of archaeological sites dating to 24–21 ka across much of southern Siberia indicates MUP populations living in this region before the LGM were not maintained or that they were quite small and archaeologically unrecognizable. With such little aDNA preservation, we are still uncertain about exactly how the Afontova Gora individual was related to the Mal'ta child or other Upper Paleolithic skeletons. If southern Siberian populations were stressed enough to become archaeologically imperceptible during the LGM and human migrations to escape the inhospitable conditions were localized or had trajectories to the south and east, we find it highly unlikely that humans persisted in the far north.

Toward the end of the LGM, humans using an LUP adaptive strategy based on standardized formal lithic technology, specialized hunting, and high residential mobility arrived in Siberia from the east, where microblades emerged first during the LGM in Hokkaido (Izuho 2013) but perhaps were conceptually conceived from MUP small blade and flake technologies that were present in Siberia, northern China, and Korea just before the LGM (Derevianko et al. 2003; Lee 2015; Lisitsyn 2000; Seong 2011; Terry, Buvit, and Konstantinov 2016; Yi et al. 2016). Although so-called microlithic technology has been found in these places at the onset of the LGM, conceptual techniques and cognitive, technological steps used to make these small blades and flakes are different from techniques and steps to produce Yubetsu and other wedge-shaped microblade core types found in LGM and late-glacial contexts associated with the LUP (Gómez Coutouly 2012; Graf 2008, 2010; Kobayashi 1970; Nakazawa et al. 2005; Takakura 2012; Terry, Buvit, and Konstantinov 2016; Yoshizaki 1961). Despite imperfect resolution of the exact timing and location of its origin, we argue

formal, developed microblade technology emerged outside southern Siberia and spread north and west with dispersing human groups at the end of the LGM, continuing the journey into higher latitudes of eastern Siberia as climates ameliorated during the late glacial.

The Beringian Record

To better understand the spread of humans from Northeast Asia to the New World, we now review Beringian archaeology starting with coverage of the two earliest sites, Yana RHS and Swan Point, followed by the late-glacial record (table 3).

The Earliest Beringian Sites: 33 ka and 14 ka

Yana RHS, discovered on the lower Yana River in northwestern Beringia, preserves an MUP component dating to 33–31 ka. Its stone artifacts are characteristically MUP, with flake-core reduction and an elaborate osseous technology of both utilitarian and nonutilitarian symbolic pieces, in some cases incredibly similar to southern Siberian MUP sites (Pitulko et al. 2013). Uncharacteristic of southern Siberian MUP sites, where resource extraction was primarily local, at Yana anthraxolite and amber were procured ≥600 km away. Subsistence pursuits were directed at large (e.g., mammoth, horse, bison) as well as smaller (reindeer and hare) game (Pitulko et al. 2004, 2013). As mentioned above, similarly aged sites exist elsewhere in northern Eurasia (Abramova et al. 1991; Graf 2009; Hoffecker 2002; Kuzmin et al. 2011; Lisitsyn 1996, 2000) but not in eastern Beringia, although questions remain regarding the correlation of humans with modified faunal remains at the Bluefish Caves sites in Yukon, Canada (see Bourgeon, Burke, and Higham 2017; Morlan 2003).

In our opinion there are currently no convincing archaeological sites dating to the LGM in Beringia (but see Pitulko, Pavlova, and Nikolskiy 2017). Instead, the next-oldest, unequivocal Beringian site is Swan Point in the Tanana Valley, central Alaska, dating to 14.1 ka (Holmes 2001, 2011), with a lithic assemblage most similar to the Siberian LUP found in the Aldan sites in southern Yakutia and countless others to the south, especially in southern Siberia (Abramova et al. 1991; Goebel 1999; Graf 2010; Mochanov 1977; Terry 2010) and Hokkaido (Izuho 2013). The 17 kyr hiatus between Yana and Swan Point begs the question, do the two sites represent both ends of early Beringian populations predicted by the long-chronology BSM (Mulligan and Kitchen 2013), or do they represent two separate dispersal events—an early one irrelevant to the peopling of the Americas (which did not reach Alaska) and a later one during the late glacial, possibly supporting a short-chronology BSM (Raghavan et al. 2015)?

At least to some degree we should also consider the hiatus between Yana and Swan Point to be an artifact of sampling—difficulties accessing today's far Northeast Asian, Alaskan, and submerged Bering Land Bridge landscapes (Hoffecker, Elias, and O'Rourke 2014)—or it could mean sustained human set-

Table 3. Climatic time-stratigraphic units associated with archaeological phases, technologies, and land-use patterns of Beringia

Dates (ka)	MIS	Greenland ice-core climatic intervals (S. O. Rasmussen et al. 2014)	Archaeological phases	Technologies	Land-use strategies
33–31	3	Greenland interstadial 5.2	Middle Upper Paleolithic (Yana RHS)	Mostly flake lithic technology; osseous projectile and sewing technologies; osseous mobile art	Large base camp with many tasks represented
31–14.5	3/2	Long Greenland stadials 5–2 interrupted by short Greenland interstadials 5–2			
14.5–14	2	Greenland interstadial 1	Late Upper Paleolithic (Swan Point)	Wedge-shaped microblade technology similar to the Siberian late Upper Paleolithic. No slotted points from the site reported	Camp with hunting-related tasks represented
13.9–12.8	2	Allerød Greenland interstadial 1 interrupted by two to three 200–100 yr cooler events	Nenana Complex	Flake, blade, and bifacial lithic technologies; triangular and teardrop-shaped lithic projectile points	Varied site types, indicating a possible logistical-mobility strategy. More sites needed
12.8–11.7	2	Younger Dryas Greenland stadial 1	Denali Complex	Wedge-shaped microblade core and flake and bifacial lithic technologies; microblade-osseous composite and lanceolate bifacial projectile points	Sites evidence mostly hunting-related activities. Too few sites to confidently identify land-use strategy
12.8–11.7	2	Younger Dryas Greenland stadial 1	North Paleo-Indian	Bifacial and flake lithic technologies; unfluted and fluted lanceolate bifacial projectile points	Sites evidence mostly hunting-related activities. Too few sites to confidently identify land-use strategy

tlement of Beringia only occurred after the LUP adaptive strategy emerged in southeastern Siberia/East Asia during the LGM and spread to northwestern North America afterward (Abramova et al. 1991; Buvit et al. 2015, 2016; Goebel 1999; Goebel and Slobodin 1999; Graf 2013, 2015; Vasil'ev 1992). Indeed, Swan Point contains distinctive Yubetsu microblade and burin technologies similar to Upper Paleolithic sites in eastern Siberia, Japan, and Korea (Andrefsky 1987; Gómez Coutouly 2011, 2012; Hirasawa and Holmes 2017; Holmes 2001, 2011; Mochanov 1977; Morlan 1978; Nakazawa et al. 2005; Yoshizaki 1961). Apart from Swan Point is a series of other late-glacial Beringian sites without microblade and burin technologies— the so-called early Ushki culture in Kamchatka, Berelekh, in northeastern Yakutia, and the Nenana complex in central Alaska, all dating to 14–13 ka (Dikov 1968; Goebel 2004b; Mochanov 1977; Pitulko 2011; Pitulko and Pavlova 2010; Powers and Hoffecker 1989). Could these actually represent an autochthonous Beringian population, pre-LGM holdovers predicted to have first inhabited Alaska?

Beringia from 14 to 12 ka

Much lithic variability exists in Beringia after 14 ka, with some late-glacial sites producing microblade technologies but not others (Goebel and Buvit 2011a; fig. 6). Although some archaeologists assemble Beringia's varied industries into a single group (i.e., Beringian tradition; Dumond 1977, 1980, 2001;

Holmes 2001; Potter, Holmes, and Yesner 2013; West 1996), such lumping masks meaningful behavioral variability (Goebel and Buvit 2011a, 2011b; Hoffecker and Elias 2007). Others have recognized at least three technological complexes in early Beringia: (1) Denali, with a developed microblade component (Ackerman 2001, 2011; Ackerman, Hamilton, and Stuckenrath 1979; Anderson 1970, 1988; Goebel and Bigelow 1996; Potter et al. 2011; West 1967); (2) Nenana, with a flake and blade technological strategy distinctly without microblade technology (Goebel, Powers, and Bigelow 1991; Goebel et al. 1996; Gore and Graf 2018; Graf et al. 2015; Hamilton and Goebel 1999; Hoffecker, Powers, and Goebel 1993; Pearson 1999; Powers and Hoffecker 1989; Powers, Guthrie, and Hoffecker 2017; Yesner 1996, 2001; Yesner, Crossen, and Easton 2011); and (3) Northern Paleo-Indian, with a variety of bifacial stemmed and lanceolate points (Alexander 1987; Bever 2008; Cinq-Mars et al. 1991; Clark 1981; Rasic 2011; Smith, Rasic, and Goebel 2013).

Originally defined in central Alaska (West 1967) but now known to occur across large parts of Beringia from Kamchatka to southeast Alaska (Ackerman 2001, 2011; Ackerman et al. 1979; Dikov 1968; Dumond 1980; Powers and Hoffecker 1989; West 1996), Denali sites (e.g., Dry Creek component 2, Moose Creek component 2, Tangle Lakes sites, Gerstle River Quarry), typically dating from 12.5 to 10 ka, are generally characterized by wedge-shaped microblade cores, microblades, transverse burins, lanceolate bifacial points, and knives (Hoffecker, Powers,
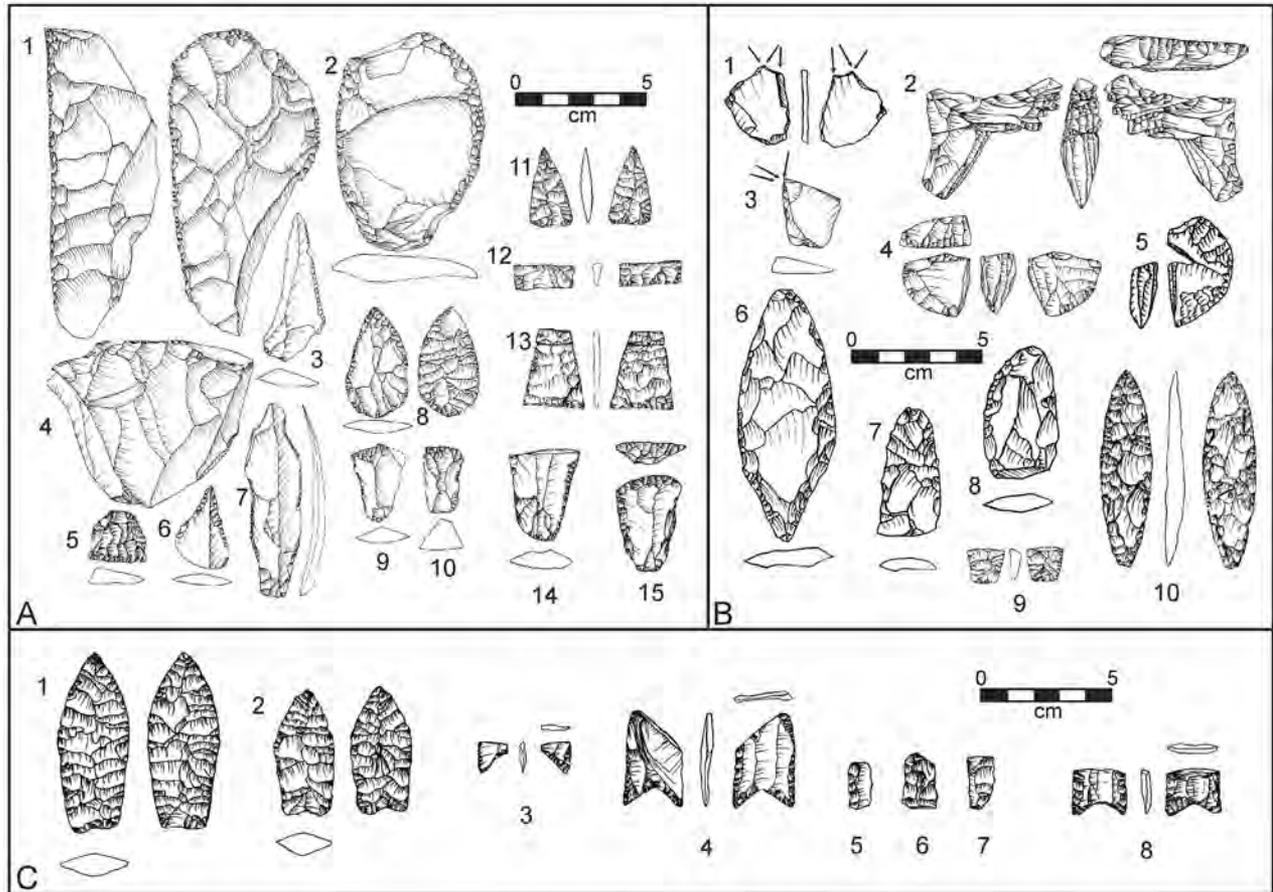
Figure 6. Representative artifacts from eastern Beringia. *A*, Nenana Complex artifacts from Walker Road: 1 (planoconvex cobble tool), 2 (unifacial side scraper), 3, 7 (utilized bladelike flakes), 4 (subprismatic blade core), 5 (bipolar flake core), 6 (bifacial drill), 8 (teardrop-shaped bifacial point), 9–10 (unifacial end scrapers; modified from Goebel and Buvit 2011); Dry Creek: 11–12 (triangular-shaped bifacial points), 14 (retouched blade), 15 (end scraper on blade; redrawn from Hoffecker, Powers, and Bigelow 1996); Owl Ridge: 13 (triangular-shaped bifacial point). *B*, Denali Complex artifacts from Donnelly Ridge: 1 (burin), 5 (wedge-shaped microblade core), 6–8 (bifaces; modified from Goebel and Buvit 2011); Dry Creek: 2 (wedge-shaped microblade core refit with a ski spall and core tablets), 3 (burin), 4 (wedge-shaped microblade core), 9 (bifacial lanceolate point base; redrawn from Hoffecker, Powers, and Bigelow 1996); Owl Ridge: 10 (bifacial lanceolate point). *C*, Northern Paleo-Indian projectile points from Mesa: 1–2 (lanceolate bifacial points; modified from Goebel and Buvit 2011); Serpentine Hot Springs: 3–4 (fluted bifacial point base), 5–7 (flute (channel) flakes); Raven Bluff: 8 (fluted bifacial point base).

and Goebel 1993; Potter 2007; Powers and Hoffecker 1989; West 1967). Occasionally, Denali occupations lack microblades (e.g., Carlo Creek component 1, Panguingue Creek component 1, Upward Sun River; Bowers 1980; Goebel and Bigelow 1996; Graf and Bigelow 2011; Potter et al. 2011).

Several sites stretching from western to eastern Beringia share a common technological complex reflecting an adaptive strategy different from the Siberian LUP. Based on stratigraphic correlation and a suite of radiocarbon ages from the lowest components of the Dry Creek, Owl Ridge, Moose Creek, and Walker Road sites in the Nenana River valley (Goebel, Powers, and Bigelow 1991; Graf and Bigelow 2011; Graf et al. 2015; Pearson 1999; Powers and Hoffecker 1989), Nenana complex sites date to 13.5–13 ka. These lithic industries lack microblade and burin technologies but include blade and flake

cores, small teardrop-shaped and triangular Chindadn points on flake blanks, and unifacial tools such as end scrapers, side scrapers, and gravers on flakes and blades (Goebel, Powers, and Bigelow 1991; Gore and Graf 2018; Graf et al. 2015; Hoffecker, Powers, and Goebel 1993; Powers, Guthrie, and Hoffecker, 2017). The lowest cultural components at the Broken Mammoth and Linda's Point sites in the middle Tanana River valley (Alaska) and Little John site in the upper Tanana River valley (Yukon) date about 13.5–13 ka and may be attributable to Nenana (Yesner 1996, 2001; Yesner, Crossen, and Easton 2011; Younie 2015; Younie and Gillespie 2016). Three sites in western Beringia—Lake Nikita and Berelekh (14–13.5 ka) on the lowermost Indigirka River, and cultural layer 7 at the Ushki Lake sites (13 ka) in central Kamchatka (Dikov 1968; Goebel, Waters, and Dikova 2003; Goebel, Slobodin, and Waters 2010; Kuzmin and

Tankersley 1996; Pitulko 2011; Pitulko and Pavlova 2010)—are contemporaneous and share similar lithic industries with Nenana. These assemblages seemingly form a cohesive Beringian-wide complex dating to a relatively short, 1 kyr interval with very similar technological strategies.

The Northern Paleo-Indian tradition includes sites found across the northern reaches of eastern Beringia from the Seward Peninsula to the Yukon. These sites contain finely flaked, lanceolate bifacial points that are sometimes end thinned or even fluted. Alaskan fluted points similar to Paleo-Indian varieties in temperate North America at 12.5 to 11.5 ka clearly postdate Clovis and have been found in datable contexts at sites such as Serpentine Hot Springs on the Seward Peninsula and Raven Bluff in the western Brooks Range of northern Alaska (Ian Buvit, William Hedman, Steven Kuen, and Jeff Rasic, "Formation, age, and depositional environments of the Raven Bluff fluted point site, northwest Alaska," unpublished manuscript; Goebel et al. 2013). Unfluted lanceolate bifacial points have been found at the sites of Tuluaq Hill, Irwin Sluiceway, and Mesa in the Brooks Range and Engigstciak in far northwestern Yukon. These all date to ~12.5–11 ka, with the exception of the Tuluaq Hill with dates of ~13–12.8 ka (Kunz, Bever, and Adkins 2003; Rasic 2011; Smith, Rasic, and Goebel 2013).

Beringian archaeologists recognize much variability among late-glacial sites even within the three complexes considered here. In central Alaska, for example, some early Denali sites lack microblades but still have signature lanceolate bifacial points and transverse burins. In northern Alaska, Mesa (Bever 2008) and Raven Bluff (Ian Buvit, William Hedman, Steven Kuen, and Jeff Rasic, "Formation, age, and depositional environments of the Raven Bluff fluted point site, northwest Alaska," unpublished manuscript) have microblades stratigraphically associated with otherwise Paleo-Indian-looking assemblages. Explanations of the patterns of variability generally fall into three working hypotheses: (1) different populations or cultural groups, (2) different technological activities or seasonal use of sites within a single adaptive strategy, or (3) diachronic changes in adaptive strategies as early Beringians responded to climate change (Goebel and Buvit 2011a, 2011b; Graf and Bigelow 2011; Potter, Holmes, and Yesner 2013).

Discussion: An Archaeological Test of the Beringian Standstill Models

Does archaeological evidence support a long-chronology BSM? The Siberian Upper Paleolithic archaeological record indicates that the peopling process of this vast region was episodic and punctuated by inclement climatic events such as the LGM (Graf 2008, 2009, 2010; Hamilton and Buchanan 2010). As mentioned above, paleoecological proxy records from Siberia and Beringia indicate both regions similarly experienced very extreme cold and arid conditions during the LGM. This means that despite humans pushing as far as the Yana RHS site in western Beringia during the warm GI-5 event, populations across the north decreased during the LGM to archaeologically

imperceptible levels (Buvit et al. 2015; Graf 2009, 2015; see also Mussi 2015 for evidence for LGM abandonment of Europe). Therefore, the current Siberian and Beringian archaeological records do not support expectations of the long-chronology BSM: no archaeological sites date to the LGM, demonstrating maintained human populations in far-northern Siberia and Beringia from 30 to 16 ka.

Does archaeological evidence support a short-chronology BSM? Considering Siberian and Beringian depopulation during the LGM as we do, the initial dates in the Transbaikal of the sudden presence of formal microblade technology as part of an LUP adaptive strategy and a subsequent time-transgressive spread of this technology and way of life north and west through eastern Siberia, we maintain that a population of people dispersed north from East Asia on the heels of the LGM as climate began to ameliorate. The aDNA of Mal'ta and its relationship to Native Americans suggests at least one introgression event into some East Asian populations after 24 ka coincidental with reintroduction of microblades and dispersal of this technology north to Beringia (Graf 2013; Raghavan et al. 2014, 2015). We hypothesize introgression may have occurred somewhere between the PSHK and Lake Baikal. During the LGM, the MUP population dwindled in southern Siberia, but remnants may have persisted farther east, possibly toward the coast of the Sea of Japan or on PSHK, where conditions were much more conducive to human habitation than they were farther inland (Igarashi 2016; Momohara et al. 2016). During the late stages of the LGM, an East Asian population with some western admixture utilizing an LUP lifeway, technologically focused on microblades, pushed west into the Transbaikal region by 22.7 ka and eventually north to Yakutia by about 17–15.5 ka when LUP sites appear in the Aldan River valley. Subsequent dispersal east could have placed humans, with a highly mobile LUP-based land-use strategy, in Alaska 2 kyr later, by ~14 ka, when the Swan Point site was inhabited. Exact locations of events remain unknown, but filling the geochronological and technological gaps and making a direct connection between Diuktai and Swan Point seem more tenable than filling gaps and directly linking Yana with Swan Point. Further, the marked archaeological variability that emerged in Beringia following initial occupation at Swan Point is temporally patterned. We contend it resulted from human response to late-glacial climatic and environmental changes. After initially arriving in Beringia as a genetically diverse population equipped with "institutional knowledge" of Siberian flake, blade, and microblade forms, these first Americans switched between technological and food-procuring strategies in response to environmental and associated resource distribution changes.

Currently, archaeological records best fit the short-chronology BSM for timing, but we predict the incubation event did not take place in Beringia but in the Russian Far East or on PSHK during the LGM before dispersal back into Siberia. The sudden emergence and rapid spread of the LUP lifeway as well as the proposed genetic makeup of Asian ancestors of first Americans may support this hypothesis with inland migration to Beringia

and the Americas; however, more skeletons are needed to test a Northeast Asian standstill.

Conclusions and Future Directions

The peopling of Siberia and Beringia was episodic, taking tens of thousands of years and with more than one dispersal attempt evidenced. We know from emerging LGM records that humans did not continuously occupy the far north above 60°N latitude until after 15 ka. No LGM-aged archaeological sites have yet been found on the Bering Land Bridge, but after initial arrival of humans after the LGM, the Beringian archaeological record becomes highly diverse through the late glacial as the immediate ancestors of the first Americans adapted to fluctuations in resource availability. Siberian and Beringian archaeological records thus support Raghavan et al.'s (2015) short-chronology BSM.

Future research to confirm or refute the BSMs requires a continued search for archaeological sites providing not only artifacts, features, and ecofacts but also human remains in the hard-to-reach regions between Lake Baikal and Alaska/Yukon where it is predicted by the models that either LGM or post-LGM sites exist. Similarly, when possible, excavations need to be carried out with the goal of answering questions about formation processes, prehistoric lifeways, and site function. Every effort should be made to revisit key sites (esp. Aldan sites in Yakutia and Bluefish Caves in Yukon) to resolve questions about chronology, prehistoric landscapes, and stratigraphic associations. These sites and others may provide important links between southern Siberia and North America and empirical evidence for the location of the standstill or homeland of the genome of first Americans.

We also need to better characterize the relationship between Beringian and LUP lithic assemblages of southern Siberia, the Far East, PSHK, and Paleo-Honshu with more sophisticated analytical techniques that allow for comparable results, such as recent morphometric analyses to explain cultural transmissions of artifact forms (Davis et al. 2015; Smith, Smallwood, and DeWitt 2014). These, in addition to detailed, systematic investigations of lithic raw material sourcing and technological provisioning and organization studies (Coffman and Rasic 2015; Gore and Graf 2018; Graf 2010; Kuzmin et al. 2008; Nakazawa and Yamada 2015; Reuther et al. 2011; Terry, Andrefsky, and Konstantinov 2009) will help link together the strategies employed from southern Siberia to eastern Beringia.

Acknowledgments

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