

Human Evolution Out of Africa: The Role of Refugia and Climate Change

J. R. Stewart¹ and C. B. Stringer²

Although an African origin of the modern human species is generally accepted, the evolutionary processes involved in the speciation, geographical spread, and eventual extinction of archaic humans outside of Africa are much debated. An additional complexity has been the recent evidence of limited interbreeding between modern humans and the Neandertals and Denisovans. Modern human migrations and interactions began during the buildup to the Last Glacial Maximum, starting about 100,000 years ago. By examining the history of other organisms through glacial cycles, valuable models for evolutionary biogeography can be formulated. According to one such model, the adoption of a new refugium by a subgroup of a species may lead to important evolutionary changes.

Modern humans are thought to have evolved in Africa more than 200,000 years ago. By about 20,000 years ago, they had expanded to all continents except the Americas and Antarctica and had essentially replaced all archaic human species. The most familiar of these, the Neandertals, was spread across western Eurasia, but recent evidence indicates that other human forms were also present, such as the Denisovans in Siberia and *Homo floresiensis* on the Indonesian island of Flores. DNA evidence now implies that modern humans interbred with at least some of these native species. Migration and replacement occurred as climates fluctuated toward the peak of the last Ice Age. The human patterns emerging from these new data have led to debate regarding the roles of climate oscillations and the resultant refugia in the formation of these patterns.

We suggest that recent studies of changes in the biogeography of other organisms, and of their constituent populations through the Pleistocene (1–3), can provide a potential model for human evolution outside Africa. Phylogeographic (genetic biogeographical) studies of various extant organisms, paleontological studies, and ancient DNA (aDNA) techniques are beginning to reveal the important role of population contraction into refugial areas in driving the evolution of distinct lineages of species, and are leading to the implication of refugia as areas of endemism for new populations and species (2, 4–6). Additionally, aDNA analyses are showing that extinction below the species level was far more prevalent than formerly realized (7). Here, we integrate these studies with recent evidence of human migration and interactions to assess some of the factors

influencing the unique emergence of one globally distributed species of human by the end of the Late Pleistocene.

What Was the Role of Quaternary Refugia in the Evolution of Organisms in General?

The idea that species' geographical ranges changed during glacial cycles dates back as far as Darwin (8). However, it was in the 1950s that the term refugia was first used by palynologists to describe the contracted ranges of plants during the last glacial in Canada (9). Since that time it has been applied in many different environmental contexts, including tropical forests in Amazonia (10). The definition we use here is in essence that of Hewitt (4), in which a refugium is an area where a particular species survived for an entire glacial-interglacial cycle. This will generally be the smallest space occupied by the fewest numbers of individuals over time (2, 4). A species' adaptations and tolerances will influence the time and place at which the refugium occurred during a glacial cycle (6). Note, however, that a recent paper advocated that the term be dropped in favor of the alternative concept of bottlenecks (11).

In Eurasia, the concept of the refugium was originally applied to temperate-adapted taxa whose populations contracted during glacial periods. In Europe, such taxa were thought to have refugia in the southern peninsulas (Iberia, Italy, and the Balkans) as well as in the east (2, 4, 12). This conclusion was based on phylogeographical studies of animals and plants [the common meadow grasshopper (*Chorthippus parallelus*), hedgehogs (*Erinaceus* sp.), brown bear (*Ursus arctos*), and oak trees (*Quercus* sp.)], showing that genetically distinct populations of these species were distributed across Europe, but with greater continuity between populations in different southern regions and areas to the north. The inference that refugia lay to the south came from the influence of palynological studies [e.g., (13, 14)], where trees had been reconstructed as expanding out of southern

Europe as climate warmed during the Holocene. The phylogeographic patterns were in turn used to infer that populations expanded from these putative southern refugia (4). In addition to southern refugia, there seem to have been cryptic northern refugia at higher latitudes, where temperate taxa persisted through the last glacial (5, 15, 16). In contrast, the ranges of colder-adapted taxa, and especially arctic-adapted ones, decreased during interglacials such as the Holocene. For example, the ranges and abundances of species such as the collared lemming (*Dicrostonyx torquatus*) and reindeer (*Rangifer tarandus*), whose distributions are limited to the north today, and in some cases also to southern mountain ranges [such as the mountain avens (*Dryas octopetala*) in the Alps], expanded during the last glacial (6). Similarly, continental-adapted taxa [e.g., ground squirrels (*Citellus* sp.) and saiga (*Saiga tatarica*)] had expanded ranges during glacial times, whereas they are in refugia today in central Eurasia (6). Many oceanic taxa are widespread today but were in refugia during glacial times. A further scenario is that offered by the analysis of aDNA of brown bear in Europe (17), which has suggested that in some instances, species had a single larger southern refugium encompassing all the peninsular refugias, but with limited gene flow between peninsulas.

Evidence shows that local extinctions can occur when a species' range is contracting (18), although it remains unknown whether this is a general phenomenon. If this does occur, then long-term refugia will generally lie where terminal populations eventually become extinct (19). The expansion and contraction of a species' range can also influence its evolution. Populations in refugia will tend to differentiate from other refugial populations through drift and natural selection in response to the specific conditions encountered; ecological variation between separate refugia could help to reinforce differences between the isolated populations (2, 4, 20). The alternative view is that differentiated populations may mix and merge again when ranges expand during more favorable conditions (21, 22).

Phylogeographic studies [e.g., (2)] have shown that when isolated populations of temperate taxa reemerged from southern refugia in Europe during interglacials, hybrid zones were formed, but a single population did not generally reform completely. The results suggest that these refugia may have been areas of endemism for temperate taxa (2, 5). An example of this process is the evolution of two hedgehog species in Europe, the western hedgehog (*Erinaceus europaeus*) and the eastern hedgehog (*Erinaceus concolor*), which appear to have expanded out of Spain and Italy and out of the Balkans, respectively (23). Evolution may also take place in cryptic refugia: For example, the polar bear (*Ursus maritimus*) is known from mitochondrial DNA (mtDNA) studies to be an arctic-adapted brown bear (24). It likely evolved when brown bears were isolated in a cryptic

¹School of Applied Sciences, Bournemouth University, Talbot Campus, Poole, Dorset BH12 5BB, UK. ²Department of Palaeontology, Natural History Museum, London SW7 5BD, UK. E-mail: jstewart@bournemouth.ac.uk (J.R.S.); c.stringer@nhm.ac.uk (C.B.S.)

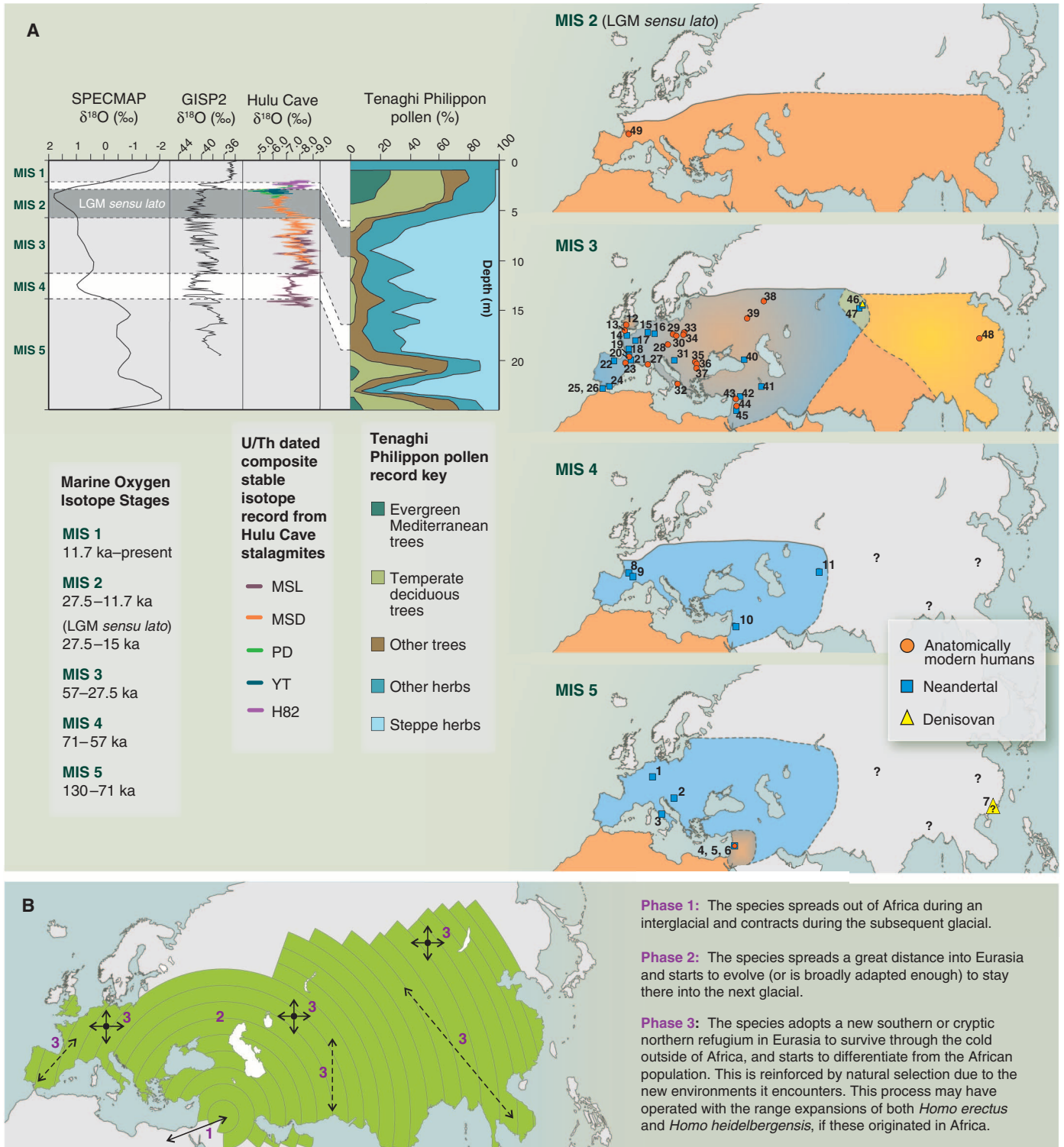


Fig. 1. Patterns and process of human distribution in Eurasia between 130,000 and 15,000 years ago in relation to climate change. **(A)** Long-term climate change curves for the Late Pleistocene, 130,000 years ago (130 ka) to the present. Included are SPECMAP chronology, GISP data, the Hulu Cave stalagmite curve, and the overview pollen record from Tenaghi Philippon (92–95). Also shown are maps of Eurasia with the distributions of selected (well-dated) sites with reliably identified human remains (Neandertals, AMH, and Denisovans) in different broad climatic episodes [marine oxygen isotope stages (MIS) 5, 4, 3, and 2, although the younger limit of MIS 2 is taken here to be the start of the first Late Glacial interstadial at ~15,000 years ago]. Table S1 is a key to the numbered

sites. The maps also include a projected maximum distribution of humans (Neandertals, AMH, and Denisovans) based on archaeology. Our confidence in the limits of these distributions varies, as indicated by the solid (more confident) and dashed (less confident) lines. **(B)** Diagram showing the three-phase process whereby human populations expanded their range out of Africa, adopted refugia in Eurasia, and eventually differentiated into distinct populations and species. These refugial areas may also have been operating during the shorter stadials. Alternatively, the human populations outside of Africa may have occupied a broad, continuous range across Eurasia during glacials, invoking a parapatric or even a sympatric evolutionary mode.

Downloaded from www.sciencemag.org on March 15, 2012

coastal northern refugium, whereupon selection favored adaptations to arctic maritime conditions (6). aDNA analyses of Quaternary fossils have supported this idea and indicated that the origin may have occurred in an area such as Ireland (25).

Ancient biomolecules have also shown that past mammals often had greater genetic variability in the Late Pleistocene than do their extant counterparts (7), suggesting that many mammals [e.g., brown bear, bison (*Bison bison*), musk ox (*Ovibos moschatus*)] underwent population bottlenecks (26–28). Such high variability is consistent with the presence of some extinct clades in the fossil record that have been interpreted morphologically as different species or subspecies, such as the cave lion (29).

Although disagreements exist about details, it is generally thought that the uniqueness of species (or populations of those species) and their specific adaptations guide the location, size, and timing of refugia for a given organism (6, 11). This perspective can be applied to different populations of the genus *Homo* through time to gain an insight into how climate change, or other natural events, affected their range and abundance. In turn, a number of predictions or hypotheses can be derived about the evolution of those human populations.

What Was the Biogeographical Pattern of Later Pleistocene Humans Outside of Africa?

Our view of the human inhabitants of Eurasia during the past 130,000 years (Fig. 1) has changed recently. There is consensus that Neandertals (*Homo neanderthalensis*) occupied the west of the continent for more than 200,000 years, although our knowledge of Neandertals in eastern Eurasia is much more limited at present. By at least 40,000 years ago they had been joined by anatomically modern humans (AMH; *Homo sapiens*) (30–32). Neandertals apparently became extinct shortly afterward (33, 34). This extinction was apparently diachronous across Europe, starting in the north and culminating in their final demise to the south (35). The last populations were evidently in southern refugia such as Iberia (36), the Balkans (37), and possibly the Levant (38). The contraction may have paused in areas such as Belgium until around 36,000 years ago (39) because southern Belgium was a cryptic northern refugium for a number of species at this time (Fig. 1) (15). The contraction of the range of Neandertals was roughly coeval with the arrival of AMH, although it is possible that the Neandertals had already disappeared from northern areas by the time AMH arrived there (30). However, many have directly linked the arrival of AMH with the disappearance of Neandertals and have cited competition between the two human species as a likely cause [e.g., (33, 40)]. Others have attributed their extinction to a combination of climatic factors and competition with AMH (41). A dominant role for climate in Neandertal extinction also has its supporters (42, 43). Earth's

climate became cooler after ~100,000 years ago, and ice sheets expanded to the Last Glacial Maximum (LGM) ~20,000 years ago. However, the overall cooling involved several abrupt episodes, and recent focus has been on the extreme cold of Heinrich event H4 (~39,000 years ago) or H5 (~48,000 years ago) as primary drivers of Neandertal extinction (30, 38, 40, 44).

Although Neandertals appear from existing data to have finally died out in southern Europe, we now know from aDNA results that their geographical range extended to Siberia at times (Fig. 1) (45, 46). It is not known whether the nearest refugium for these eastern populations was immediately south of Siberia or was farther west, although it seems unlikely that Siberia itself was a refugium, given that the Neandertals retreated south as climate cooled toward the LGM in Europe (35). Neandertal fossils in Iraq and the Levant (Fig. 1) suggest that refugia existed in such areas, in addition to western refugia such as Iberia. However, the present evidence does not clearly indicate that these populations represented different Neandertal clades, which may imply that if eastern refugia existed, they had not been operating as such for long [(45), but compare (47)].

The most unexpected result from the eastern localities was that the aDNA data—both mitochondrial and nuclear—suggested that another distinct human population, the Denisovans, lived in Siberia at the same time as Neandertals, near the time that the latter were becoming extinct. On the basis of their mtDNA, the Denisovans were originally described as different from both AMH and Neandertals (48), but they are now considered to be a sister group of Neandertals by virtue of a younger coalescence date for their nuclear DNA (49). Moreover, the three Denisovan mtDNA sequences so far obtained (from a single site) are already more diverse than all those known from the Neandertals (46). This genetic diversity in Pleistocene humans, together with the additional variation 100,000 years ago suggested by the mtDNA of the Neandertal fossil from Sladina, in Belgium (50), mirrors the genetic diversity seen in other mammals during the Pleistocene (7). Although morphological information on the Denisovans is sparse relative to the genomic data, fossils from China (e.g., Dali, Maba) and India (Narmada) might represent this Asian lineage. These have variously been regarded as related to *Homo erectus*, *Homo heidelbergensis*, Neandertals, or archaic *H. sapiens* (51).

Before the emergence of the Neandertals, Eurasia was occupied by *H. erectus*, a species that evolved perhaps 2 million years ago and is seen in Dmanisi, Republic of Georgia, by at least 1.8 million years ago (52). Several other *Homo* species followed, notably *H. heidelbergensis*, which is arguably found throughout Eurasia from about 600,000 to 400,000 years ago (51). The timing of the last *H. erectus* occurrence in continental Eurasia is uncertain, and it may well be that the species disappeared during the

Middle Pleistocene for reasons that are currently unknown. It had been thought to have survived until the Late Pleistocene at Ngandong in Java (Indonesia); however, the date of these fossils is not well established (53). The enigmatic *H. floresiensis* (54, 55), which is dated from about 95,000 to 17,000 years ago, is of uncertain affinity and is an isolated insular find. Thus, we exclude these two species from the discussion of continental refugia; unless aDNA can be retrieved from *H. erectus* and *H. floresiensis*, the precise relation between each of these species and the Neandertal, Denisovan, and AMH groups may remain uncertain. It is likely that, as with Neandertals, the extinction of other archaic humans took place in their respective refugial areas, as this is the direction toward which the last populations will have contracted in geographical range and numbers of individuals.

The earliest known AMH outside of Africa are from the Levant, dated between 90,000 and 120,000 years ago (Fig. 1A) (56). It seems likely that this was a population expansion that contracted again toward Africa or Arabia during a subsequent cold or arid event. The next expansion of AMH outside of Africa was ~60,000 years ago, when they appear to have spread into western Asia (Fig. 1A) (57). This population expansion led to their dispersal into Australasia by at least 45,000 years ago (58).

The arrival of AMH in Europe by at least 40,000 years ago (31, 32, 59) represented an expansion of their geographical range from the east, although the geographical origin of these dispersals is not precisely clear (57). After ~26,000 years ago, AMH, now the sole occupant of Europe, also retreated south and became locally extinct in northwestern Europe (Fig. 1A). This occurred as ice sheets advanced and ice-free northern environments became impoverished in terms of carrying capacity. The contraction of the AMH geographic range appears to have been a two-stage process in northwestern Europe, as there is evidence that areas such as Belgium were vacated by AMH making Aurignacian industries, only to be repopulated some time later by a population making the Gravettian stone tool industry, as interstadial conditions temporarily returned just before the LGM (60). The Gravettian industry eventually disappeared in turn, about 23,000 years ago, after which northwestern Europe lacks evidence of human occupation for about 8000 years until the area was recolonized from one or more southern and/or eastern refugia in the Late Glacial ~15,000 years ago (60). Indeed, it was as a consequence of a similar Late Glacial spread north that AMH crossed the Bering Straits and dispersed into North and South America (61).

How Did the Evolution of Archaic Out-of-Africa Humans Take Place?

When a lineage adopts a new refugial area and survives for a number of Milankovitch cycles, expanding from and contracting into that new

refugium instead of its original refugium, it is destined to evolve into a distinct population. Given enough time in isolation, it will become a new species (Fig. 1B) (4–6). Because a new refugium is unlikely to have the same flora, fauna, and ecology as the lineage's original refugium, it exerts selective pressure to adapt and diverge (2, 4, 20). The potential role of ecological adaptation could theoretically even lead to the evolution of two sympatric human species in the same refugium, particularly if heterochrony is involved (62). Therefore, when the initial expansion of archaic *Homo* out of Africa during an interglacial (52, 63) eventually suffered range contraction in the face of climatic deterioration, it was either going to go extinct locally or, because it was sufficiently broadly adapted, survive in an out-of-Africa refugium (Fig. 1B).

It may well be that a broadly adapted taxon such as *Homo* (64) was particularly well disposed to dispersals and eventual differentiation. This appears to have happened to the likely ancestors of Neandertals. *H. heidelbergensis* expanded across Eurasia around 600,000 years ago and persisted there through entire ice age cycles, where it would have become adapted to more northern environmental conditions (Fig. 1B) (65). It apparently retreated into a refugium during cold stages, given the lack of archaeological evidence from such periods in Britain (66). This would have led to a phylogenetic split from the African conspecifics, whose refugial leading edge lay in Africa, or maximally in the Levant region. The eventual result was the distinct human species known as the Neandertals (*H. neanderthalensis*). Thus, the adoption of a new refugium by an expanded part of a population is the mechanism that often leads to phylogenetic speciation within continents.

Neandertals have been described as a cold-adapted, even hyperarctic-adapted, human species (66, 67). Several of their traits, such as relatively short limbs, high body mass, and enlarged sinus cavities, have been interpreted as related to temperature regulation (68, 69). A recent alternative view is that the limb differences are more likely to be related to locomotory adaptations, whereas Neandertal mid-facial shape reflects genetic drift (43, 70). Although these alternative explanations may be valid, there are grounds to infer that Neandertals were cold-adapted to an extent, and certainly more so than were their African ancestors (71). Furthermore, they were probably better physically adapted to cold conditions than the succeeding AMH populations, who instead possessed additional behavioral adaptations that allowed them to cope well with the Late Pleistocene Eurasian environment (71). An interesting contrast here is the evolution of the polar bear (*Ursus maritimus*) when compared with the closely related brown bear (*U. arctos*). Polar bears were and are in refugia during interglacials and were probably more widely distributed during glacial stages—the opposite situation to the Neandertals and many other species.

The age of the most recent common ancestor of Neandertals and AMH could restrict the possible explanations for how and when the various evolutionary events took place. Genetic and craniometric findings suggest that this divergence occurred ~350,000 years ago, but with assumption-based uncertainties such as calibration and generation time (72, 73). The uncertainty is too great to determine whether the divergence took place during a glacial or an interglacial, although the biogeography of other organisms suggests that it was initiated during an interglacial and consolidated during a subsequent cold stage. *H. heidelbergensis*, the presumed ancestor of both *H. sapiens* and *H. neanderthalensis*, is most likely to have spread from Africa or western Asia during an interglacial, when its population was expanding. This expansion ultimately led to the hypothesized divergence between the population of *H. heidelbergensis* that remained in Africa and evolved into *H. sapiens* and the population that spread in Eurasia to eventually evolve into Neandertals (58).

Implications of Pleistocene Interbreeding Between Eurasian Humans

Paleogenomic data imply that there was some interbreeding between Neandertals and AMH, as well as between Denisovans and AMH, during the Late Pleistocene in Eurasia (49, 74). The present-day traces of archaic human introgression are, however, not localized to the same regions as the aDNA sources. Although such interbreeding may undermine the biological species concept as applied to fossil human groups, recent research has shown that hybridization is not uncommon in the wild today between closely related species (75), and it has been recorded in an increasing number of higher vertebrates (76) and primates (77, 78).

Two biogeographic scenarios may lead to interbreeding between populations of organisms in general. In one scenario (4, 79), two populations may meet during their expansive population phases and form hybrid zones. The results of this process show up in Europe as a genetic pattern where longitudinal areas occur from north to south, apparently caused by the spread of the distinct populations from different southern refugia. In the other scenario, species hybridize during periods of environmental disturbance (76) or if the species are rare, such as has been documented for Darwin's finches (80). So two distinct climatic and biogeographic phases (glacial refugial and interglacial expansive) could have led to the hybridization. It may be that Neandertals and AMH interbred when AMH were expanding out of Africa, causing range overlap with Neandertals. This is likely to have been an interstadial expansion that brought AMH out of Africa and into the Levant (44), where interbreeding with the contracted-range Neandertals, albeit during an interstadial, may have occurred. Given that a modern European genome has no higher levels of introgression than a Chinese or a Melanesian

one, the inferred introgression of Neandertal DNA may have happened before those populations diversified but after the notional separation from sub-Saharan Africans, suggesting a likely time of ~60,000 years ago. Alternatively, the consistently small amount of Neandertal introgression may instead be a measure of the ineffectiveness of hybridization in separate interbreeding events, reflecting intrinsic limits on the process caused by biological, social, or demographic factors (81).

Our knowledge of the Denisovans is too limited to say much about the location and timing of the hypothesized introgression with AMH, but given the geographically limited impact—in Australasians and neighboring populations only (49, 82, 83)—it most likely occurred as modern humans spread eastward, after 60,000 years ago but before the arrival of AMH in Australasia (~50,000 years ago). It possibly took place during the refugial contraction phase of the Denisovans during a colder stadial, as AMH were spreading toward Australasia. Also, because there is evidence that grasslands spread south within southeast Asia into the subtropical region during cold conditions (84), the Denisovan range may have moved south at that time (Fig. 1A).

Given the limits of aDNA preservation, these southerly locations unfortunately may never provide genetic evidence of hybridization events from their fossil record (85). Recent evidence of introgression also appears in modern African populations, such as the San and Biaka pygmies, who may also harbor archaic human DNA acquired as recently as 35,000 years ago (86). Physical evidence of such introgression may come from Later Stone Age fossils showing archaic features, such as at Ishango, Congo (87), and Iwo Eleru, Nigeria (88).

Outlook

A number of questions concerning the evolution of humans outside of Africa remain unanswered. Many of the unknowns involve the pattern of genotypes among archaic humans and ancient and living AMH. Until recently this information was completely unavailable, but as the field of paleogenomics develops, it would be valuable to know how the different archaic fossils relate to each other genetically as well as morphologically. It is intriguing that the Denisovans were evidently more genetically variable than the Neandertals (46), and thus there was apparently more human genetic variation overall in the east of Eurasia during the Pleistocene than in the west. Further findings in this area may reopen the question of where the Neandertals evolved—was it in southern Europe or in Asia? Whatever the case, it may be that the ancestors of Neandertals and Denisovans (presumably *H. heidelbergensis*) went eastward before radiating, resulting eventually in the two Late Pleistocene archaic populations. The distribution of the Neandertals during the cold of MIS 4 and AMH during the LGM *sensu lato* (27,500 to 15,000 years ago) could

suggest that both human species had cryptic northern refugia to the east of Europe, unless they were more continuously distributed (Fig. 1).

To date, only about 20 Neandertals and far fewer fossil AMH have yielded aDNA (89), and the Denisovans are barely represented in the fossil record. It is possible that the Denisovans lived farther west, at least at times, and have not yet been recognized. Additional, complete, Denisovan fossils would help to establish their morphological differences with respect to Neandertals and may clarify how Neandertals and Denisovans relate to *H. heidelbergensis*, *H. antecessor*, and Asian *H. erectus*. However, the distinct but overlapping geographic ranges of these various individualistic human populations imply that they possessed different adaptations.

The phenotypic effect of the introgression of archaic humans with AMH is one current research direction. A recent study found that living *H. sapiens* in Europe and Asia may have acquired a part of their immune system from archaic humans (90). This hypothesis needs confirmation, but it does prompt questions as to the effects of this interbreeding.

Many researchers have used archaeological industries as proxies for Neandertals and AMH [e.g., see (35)]. Now that we have evidence of another distinct population in the Late Pleistocene as well as hybridization between past populations, we need to consider how this affects interpretations of the archaeological industries. The cultural evidence from Denisova needs further clarification, as the layers containing the fossils also contain elements of both Middle and Upper Paleolithic technologies (46). Furthermore, as AMH and Neandertals both made “Middle Paleolithic” and “Upper Paleolithic” stone tool industries at different times and places, the reality may have been even more complex. Contact between populations may well have extended beyond exchanges of genetic material to the transfer of behavior and technology, so even greater caution may be necessary when using behavioral markers as proxies for human species or populations.

Note added in proof: Cryptic northern refugia (15) at higher latitudes have now been confirmed for boreal species (91).

References and Notes

1. J. A. Avise, *Phylogeography: The History and Formation of Species* (Harvard Univ. Press, Cambridge, MA, 2000).
2. G. Hewitt, *Nature* **405**, 907 (2000).
3. J. Provan, K. D. Bennett, *Trends Ecol. Evol.* **23**, 564 (2008).
4. G. Hewitt, *Biol. J. Linn. Soc.* **58**, 247 (1996).
5. D. T. Bilton *et al.*, *Proc. R. Soc. B* **265**, 1219 (1998).
6. J. R. Stewart, A. M. Lister, I. Barnes, L. Dalén, *Proc. R. Soc. B* **277**, 661 (2010).
7. M. Hofreiter, I. Barnes, *BMC Biol.* **8**, 46 (2010).
8. C. Darwin, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (John Murray, London, 1856).
9. C. J. Heusser, *Can. J. Bot.* **33**, 429 (1955).
10. J. Haffer, *Science* **165**, 131 (1969).
11. K. D. Bennett, J. Provan, *Quat. Sci. Rev.* **27**, 2449 (2008).
12. P. Taberlet, L. Fumagalli, A. G. Wust-Saucy, J. F. Cosson, *Mol. Ecol.* **7**, 453 (1998).
13. B. Huntley, H. J. B. Birks, *An Atlas of Past and Present Pollen Maps of Europe, 0–13,000 Years Ago* (Cambridge Univ. Press, Cambridge, 1983).
14. K. D. Bennett, P. C. Tzedakis, K. J. Willis, *J. Biogeogr.* **18**, 103 (1991).
15. J. R. Stewart, A. M. Lister, *Trends Ecol. Evol.* **16**, 608 (2001).
16. S. A. Bhagwat, K. J. Willis, *J. Biogeogr.* **35**, 464 (2008).
17. C. E. Valdiosera *et al.*, *Mol. Ecol.* **16**, 5140 (2007).
18. L. Dalén *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 6726 (2007).
19. A. M. Lister, A. J. Stuart, *C. R. Geosci.* **340**, 615 (2008).
20. J. R. Stewart, *J. Evol. Biol.* **22**, 2363 (2009).
21. G. R. Coope, in *Diversity of Insect Faunas*, L. A. Mound, N. Waloff, Eds. (Blackwell Science, London, 1978), pp. 176–187.
22. K. D. Bennett, *Evolution and Ecology: The Pace of Life* (Cambridge Univ. Press, Cambridge, 1997).
23. F. Santucci, B. C. Emerson, G. M. Hewitt, *Mol. Ecol.* **7**, 1163 (1998).
24. S. L. Talbot, G. F. Shields, *Mol. Phylogenet. Evol.* **5**, 477 (1996).
25. C. J. Edwards *et al.*, *Curr. Biol.* **21**, 1251 (2011).
26. I. Barnes, P. Matheus, B. Shapiro, D. Jensen, A. Cooper, *Science* **295**, 2267 (2002).
27. B. Shapiro *et al.*, *Science* **306**, 1561 (2004).
28. R. D. E. MacPhee, A. N. Tikhonov, D. Mol, A. D. Greenwood, *BMC Evol. Biol.* **5**, 49 (2005).
29. J. Burger *et al.*, *Mol. Phylogenet. Evol.* **30**, 841 (2004).
30. U. C. Müller *et al.*, *Quat. Sci. Rev.* **30**, 273 (2011).
31. T. Higham *et al.*, *Nature* **479**, 521 (2011).
32. S. Benazzi *et al.*, *Nature* **479**, 525 (2011).
33. P. Mellars, *Nature* **439**, 931 (2006).
34. R. Pinhasi, T. F. Higham, L. V. Golovanova, V. B. Doronichev, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 8611 (2011).
35. T. H. Van Andel, W. Davies, Eds., *Neanderthals and Modern Humans in the European Landscape During the Last Glaciation, 60,000 to 20,000 Years Ago: Archaeological Results of the Stage Three Project* (McDonald Institute for Archaeological Research, Cambridge, 2003).
36. C. Finlayson *et al.*, *Nature* **443**, 850 (2006).
37. T. Higham, C. B. Ramsey, I. Karavanić, F. H. Smith, E. Trinkaus, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 553 (2006).
38. M. Belmaker, E. Hovers, *Quat. Sci. Rev.* **30**, 3196 (2011).
39. P. Semal *et al.*, *Am. J. Phys. Anthropol.* **138**, 421 (2009).
40. W. E. Banks *et al.*, *PLoS ONE* **3**, e3972 (2008).
41. C. Stringer, in *Neanderthals Revisited: New Approaches and Perspectives*, K. Harvati, T. Harrison, Eds. (Springer, New York, 2006), pp. 315–323.
42. C. Finlayson, *Trends Ecol. Evol.* **20**, 457 (2005).
43. J. R. Stewart, *Quat. Int.* **137**, 35 (2005).
44. M. Bradtmöller, A. Pastoors, B. Weninger, G.-C. Weniger, *Quat. Int.* **247**, 38 (2012).
45. J. Krause *et al.*, *Nature* **449**, 902 (2007).
46. A. Gibbons, *Science* **333**, 1084 (2011).
47. V. Fabre, S. Condemi, A. Degioanni, *PLoS ONE* **4**, e5151 (2009).
48. J. Krause *et al.*, *Nature* **464**, 894 (2010).
49. D. Reich *et al.*, *Nature* **468**, 1053 (2010).
50. L. Orlando *et al.*, *Curr. Biol.* **16**, R400 (2006).
51. C. Stringer, *Philos. Trans. R. Soc. London Ser. B* **357**, 563 (2002).
52. J. S. Carrión, J. Rose, C. Stringer, *Quat. Sci. Rev.* **30**, 1281 (2011).
53. E. Indriati *et al.*, *PLoS ONE* **6**, e21562 (2011).
54. P. Brown *et al.*, *Nature* **431**, 1055 (2004).
55. M. J. Morwood, W. L. Jungers, *J. Hum. Evol.* **57**, 640 (2009).
56. R. Grün *et al.*, *J. Hum. Evol.* **49**, 316 (2005).
57. C. Stringer, *The Origin of Our Species* (Allen Lane, London, 2011).
58. P. Endicott, S. Y. Ho, C. Stringer, *J. Hum. Evol.* **59**, 87 (2010).
59. E. Trinkaus *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 11231 (2003).
60. C. Gamble, W. Davies, P. Pettitt, M. Richards, *Philos. Trans. R. Soc. London Ser. B* **359**, 243 (2004).
61. T. Goebel, M. R. Waters, D. H. O'Rourke, *Science* **319**, 1497 (2008).
62. C. P. E. Zollikofer, M. S. Ponce de León, *Semin. Cell Dev. Biol.* **21**, 441 (2010).
63. R. Dennell, *Episodes* **31**, 207 (2008).
64. R. Potts, *Evol. Anthropol.* **7**, 81 (1998).
65. M. J. Walker, J. Ortega, K. Parmová, M. V. López, E. Trinkaus, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 10087 (2011).
66. C. Stringer, *Homo britannicus: The Story of Life in Britain* (Allen Lane, London, 2006).
67. T. W. Holliday, *Am. J. Phys. Anthropol.* **104**, 245 (1997).
68. C. S. Coon, *The Origin of the Races* (Knopf, New York, 1962).
69. E. Trinkaus, in *Aspects of Human Evolution*, C. B. Stringer, Ed. (Taylor & Francis, London, 1981), pp. 187–224.
70. T. C. Rae, T. Koppe, C. B. Stringer, *J. Hum. Evol.* **60**, 234 (2011).
71. T. W. Holliday, *J. Hum. Evol.* **32**, 423 (1997).
72. T. D. Weaver, C. C. Roseman, C. B. Stringer, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 4645 (2008).
73. P. Endicott, S. Y. Ho, M. Metspalu, C. Stringer, *Trends Ecol. Evol.* **24**, 515 (2009).
74. R. E. Green *et al.*, *Science* **328**, 710 (2010).
75. J. Mallet, *Trends Ecol. Evol.* **20**, 229 (2005).
76. M. L. Arnold, *Natural Hybridization and Evolution* (Oxford Univ. Press, Oxford, 1997).
77. C. J. Jolly, *Am. J. Phys. Anthropol.* **116** (suppl. 33), 177 (2001).
78. D. Zinner, M. L. Arnold, C. Roos, *Evol. Anthropol.* **20**, 96 (2011).
79. G. M. Hewitt, *Mol. Ecol.* **10**, 537 (2001).
80. P. R. Grant, B. R. Grant, *Am. Nat.* **149**, 1 (1997).
81. M. Currat, L. Excoffier, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 15129 (2011).
82. D. Reich *et al.*, *Am. J. Hum. Genet.* **89**, 516 (2011).
83. M. Rasmussen *et al.*, *Science* **334**, 94 (2011).
84. M. I. Bird, A. Taylor, C. Hunt, *Quat. Sci. Rev.* **24**, 2228 (2005).
85. C. I. Smith, A. T. Chamberlain, M. S. Rile, C. Stringer, M. J. Collins, *J. Hum. Evol.* **45**, 203 (2003).
86. M. F. Hammer, A. E. Woerner, F. L. Mendez, J. C. Watkins, J. D. Wall, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 15123 (2011).
87. I. Crevecoeur *et al.*, *Am. J. Phys. Anthropol.* **550**, 87 (2010).
88. K. Harvati *et al.*, *PLoS ONE* **6**, e24024 (2011).
89. S. Ghirotto, F. Tassi, A. Benazzo, G. Barbujani, *Am. J. Phys. Anthropol.* **146**, 242 (2011).
90. L. Abi-Rached *et al.*, *Science* **334**, 89 (2011).
91. L. Parducci *et al.*, *Science* **335**, 1083 (2012).
92. J. Imbrie *et al.*, in *Milankovitch and Climate*, A. L. Berger *et al.*, Eds. (Reidel, Dordrecht, Netherlands, 1984), pp. 269–305.
93. D. A. Meese *et al.*, *J. Geophys. Res.* **102**, 26411 (1997).
94. J. Pross *et al.*, *Sci. Drill.* **5**, 30 (2007).
95. Y. J. Wang *et al.*, *Science* **294**, 2345 (2001).

Acknowledgments: We thank J. Cole, M. Dover, S. Bello, R. Housley, A. Shaw, B. Scott, and W. Davies for help with Fig. 1. J.R.S. is an associate and C.B.S. is a member of the Ancient Human Occupation of Britain project, funded by the Leverhulme Trust. C.B.S.'s human origins research is supported by the Human Origins Research Fund and the Calvea Foundation.

Supporting Online Material

www.sciencemag.org/cgi/content/full/335/6074/1317/DC1
Table S1
References (96–128)

10.1126/science.1215627