

# Origins of modern human ancestry

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New finds in the palaeoanthropological and genomic records have changed our view of the origins of modern human ancestry. Here we review our current understanding of how the ancestry of modern humans around the globe can be traced into the deep past, and which ancestors it passes through during our journey back in time. We identify three key phases that are surrounded by major questions, and which will be at the frontiers of future research. The most recent phase comprises the worldwide expansion of modern humans between 40 and 60 thousand years ago (ka) and their last known contacts with archaic groups such as Neanderthals and Denisovans. The second phase is associated with a broadly construed African origin of modern human diversity between 60 and 300 ka. The oldest phase comprises the complex separation of modern human ancestors from archaic human groups from 0.3 to 1 million years ago. We argue that no specific point in time can currently be identified at which modern human ancestry was confined to a limited birthplace, and that patterns of the first appearance of anatomical or behavioural traits that are used to define *Homo sapiens* are consistent with a range of evolutionary histories.

All living humans trace their history through long lines of ancestors into the past. Some of our ancestors will have lived in groups or populations that can be identified in the fossil record, whereas very little will be known about others. Here we review the current understanding of early human population history by tracing the ancestry of present-day people into the deep past. We investigate what can be said about where human ancestors lived geographically at different points in time, and whether or not these ancestral groups are represented in the current fossil record. Within this framework, we argue that there is little empirical or conceptual reason to focus on models of a single point in time and space during which modern human ancestry originated.

## Phase 3 and the worldwide expansion outside of Africa

Present-day genetic diversity in African groups and individuals is greater than in any other part of the world<sup>1–4</sup>, a pattern that was first observed in mitochondrial DNA (mtDNA)<sup>1</sup>. Together with a turnover in fossil morphology<sup>5</sup> this was taken as strong evidence for a ‘recent African origin’, where a population carrying a subset of African diversity underwent a size bottleneck and then became the founders of worldwide expansions. This model is now strongly supported by early fossils in Africa<sup>6–8</sup>, by genomic evidence of interbreeding with archaic human groups outside of Africa<sup>9,10</sup> and by the major portion of genomic ancestry outside of Africa appearing to be nested within African ancestries, in the Holocene epoch (the past 12,000 years or so) closest to eastern African ancestry<sup>1,2,11–15</sup>. However, different scenarios have been proposed for the number and timing of into-Eurasia expansion(s).

From the fossil record it has long been clear that there were early range expansions of *H. sapiens* (the fossil lineage that includes modern humans—we make no allusions to species status by the use of these terms) from Africa into western Asia and the eastern Mediterranean.

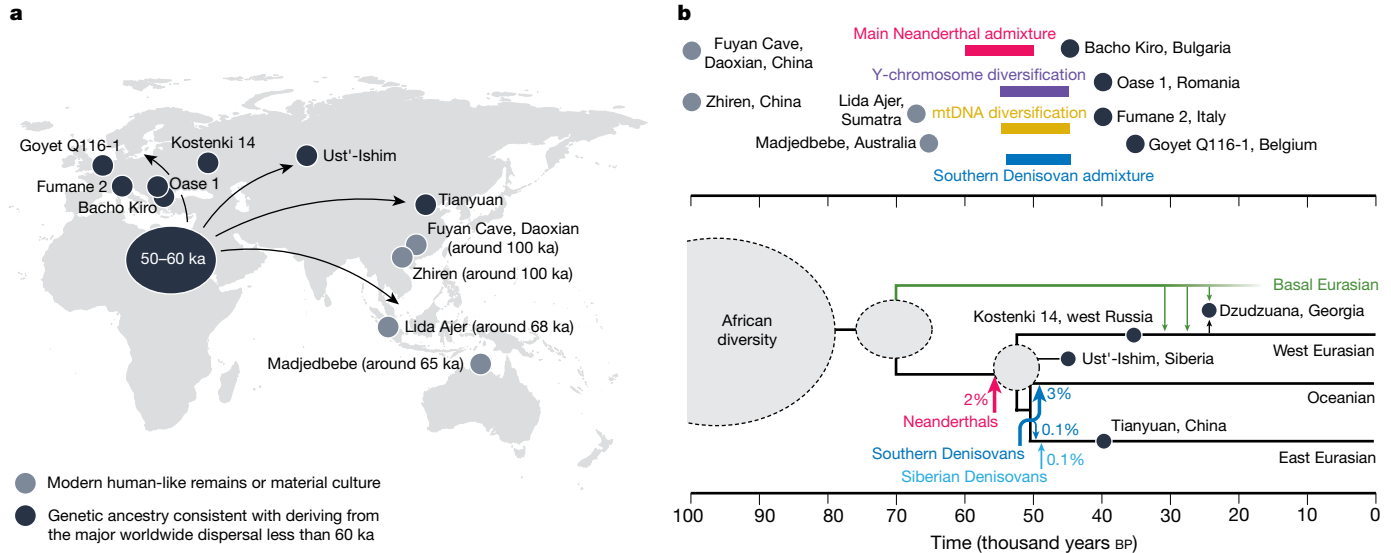
These may have occurred during favourable climate conditions in the Saharo-Arabian belt<sup>16</sup>, as recorded by fossils in the Israeli caves of Skhul and Qafzeh (dated to 90–130 ka)<sup>17,18</sup> and Al Wusta in Saudi Arabia (dated to around 90 ka)<sup>19</sup>. Even older, but more fragmentary, *H. sapiens* fossils come from Misliya Cave, Israel (dated to around 180 ka)<sup>20</sup> and Apidima Cave, Greece (dated to more than 210 ka)<sup>21</sup>. Further from the African continent, suggested earlier records include Chinese fossils estimated to date to between around 80 and 113 ka<sup>22,23</sup>, teeth from Sumatra dated to around 70 ka<sup>24</sup>, cranial and mandibular fossils at least 50 thousand years of age from Laos<sup>25</sup> and artefacts from northern Australia dated to at least 65 ka<sup>26</sup>.

Beyond Africa and western Asia, the palaeoanthropological evidence before about 65 ka thus appears increasingly in tension with genomic evidence that indicates that all present-day human populations outside of Africa derive the majority of their ancestry from a worldwide expansion after 50–60 ka (Fig. 1). A main line of evidence is the Neanderthal ancestry found in all present-day and ancient non-African modern human genomes studied to date. This ancestry is mostly consistent with originating from a single admixture episode<sup>27–32</sup>, the majority of which had ceased by 50–60 ka<sup>29,33–35</sup>. This time frame is apparent in the long Neanderthal segments that are observed in an approximately 45-thousand-year-old modern human genome from Siberia and other ancient genomes<sup>29,33</sup>, and further supported by the fact that mtDNA<sup>36,37</sup> and Y-chromosome<sup>38,39</sup> lineages outside of Africa diversified by around 45–55 ka.

## Early expansion hypotheses

Several genomic studies have suggested that ancestry from a separate, earlier worldwide expansion is present in Oceania (for example, Australia and New Guinea)<sup>40–43</sup>, in line with a ‘southern route’ hypothesis of another migration that followed the Asian coast<sup>44,45</sup>. However, such

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**Fig. 1 | Worldwide expansion and archaic admixture (phase 3).** **a**, Locations of early individuals with modern human ancestry in Eurasia, together with sites that may indicate an earlier dispersal in Asia and Sahul (the continental shelf centred on Australia). **b**, Palaeoanthropological and archaeological evidence of early modern humans far away from Africa (see older specimens in Greece and

the Levant in Fig. 2), and chronology of diversification and admixture events during the worldwide expansion that gave rise to most of the ancestry of present-day people outside of Africa. The genetic ancestry of Bacho Kiro and Fumane 2 has so far only been assessed through mtDNA. Grey circles represent uncertainty around timing or population topology. BP, before present.

analyses could be confounded by the divergent Denisovan ancestry in these populations, and other studies have found no support for this ancestry<sup>14,46–49</sup>. Thus, the fossil and archaeological records of modern humans outside both Africa and Southwest Asia that are older than around 60 ka are best reconciled with the genetic data by any earlier dispersals not contributing detectable ancestry to people living after the later, major expansion.

A recent addition to our understanding of modern humans outside of Africa is ‘basal Eurasian’ ancestry, which diverged from other non-African ancestries before these diversified, and probably lacked Neanderthal admixture<sup>50,51</sup>. It probably diverged more than 60 ka<sup>52,53</sup>, is found as early and widely as around 15 ka in Morocco<sup>54</sup> and about 26 ka in Georgia<sup>52</sup>, and expanded throughout west Eurasia and South Asia during the Holocene epoch<sup>50,51,55–58</sup>. Some ancestry in these regions thus derives from groups that diverged before the worldwide expansion of 50–60 ka. The origins of basal Eurasian ancestry most likely centred around Southwest Asia and North Africa, and are unlikely to be connected to evidence of humans further away from Africa before 60 ka.

**Episodes of gene flow from Eurasian archaic humans**

A large number of admixture events between Neanderthals and Denisovans and modern human populations have been proposed in the literature. However, we argue that currently only four of these events, one of which did not contribute to present-day ancestry, have a broad consensus and could be considered conclusively demonstrated.

**Gene flow from Neanderthals**

The first archaic admixture event resulted in approximately 2% Neanderthal ancestry in present-day populations outside of sub-Saharan Africa<sup>9,34,59</sup> and is found in all non-African modern human genomes studied to date (up to around 45 ka), including early ancient individuals in Belgium<sup>27</sup>, western Siberia<sup>29</sup> and China<sup>32,60</sup>. Neanderthal ancestry is also present in smaller amounts in East and West Africa<sup>61–63</sup>, reflecting later gene flow from Eurasia<sup>2,13,63–66</sup>. However, some African populations, such as the Central African Mbuti and the East African Dinka, lack detectable Neanderthal ancestry, as do ancient genomes of the Holocene period from Ethiopia<sup>67</sup>, South Africa<sup>13,68</sup> and Malawi<sup>13</sup>. The geographical ubiquity of Neanderthal ancestry outside of Africa

has suggested that the admixture occurred in or close to Southwest Asia<sup>9</sup>, but no explicit evidence is available so far. Despite co-occupation with modern humans for thousands of years<sup>69</sup>, late Neanderthals in Europe do not appear to have contributed ancestry to present-day populations, as these are not genetically closer to the source population than Neanderthals in the Caucasus are<sup>70</sup>.

A central feature of the geographical distribution of Neanderthal ancestry today is an approximately one fifth to one tenth lower relative proportion in western compared to eastern Eurasian populations<sup>71–73</sup>, with intermediate levels in South and Central Asia<sup>35,62</sup>. This observation has been suggested to reflect multiple admixture events<sup>74–77</sup>, but currently, the most likely explanation is a process of dilution by ‘basal Eurasian’ groups that carried little to no Neanderthal ancestry<sup>50,51</sup>.

Comparisons of Neanderthal DNA segments in present-day humans indicate that, while the diversity of the source population was low, more than a few individuals must have contributed<sup>49,78</sup>. Furthermore, Neanderthal ancestry today is depleted by about one third around genic regions and promoters<sup>79–81</sup>, probably due to genetic load accumulated because of low Neanderthal population sizes<sup>82,83</sup>. Little reduction in Neanderthal ancestry is observed across ancient genomes from the past 45 thousand years<sup>79</sup>, suggesting that natural selection rapidly brought an initial proportion as high as around 10% down to the present-day levels of about 2%<sup>81,83</sup>. Thus, we cannot presently rule out an ‘assimilation’ scenario in which Neanderthals were absorbed into a larger expanding modern human population.

**Gene flow from Denisovans**

The second strongly supported admixture event gave rise to up to approximately 3.5% Denisovan-related ancestry in present-day Oceanian individuals<sup>10,49,62,71</sup>. Ancestry deriving from this admixture event is present across Southeast Asia and Oceania<sup>84,85</sup>, and in very small amounts (around 0.1%) in East Asian, South Asian and Native American populations<sup>35,61,72,86,87</sup>. A major enduring question is where this admixture took place, as the Denisovan individual from Siberia is only distantly related to the source population of hypothetical ‘southern Denisovans’<sup>61,87,88</sup>. Denisovan segments in present-day Oceanian genomes are longer than Neanderthal segments, and it has therefore been estimated that this admixture occurred more recently than

Neanderthal admixture<sup>35,46</sup>, around 45–55 ka. Like Neanderthal ancestry, Denisovan ancestry today is depleted around functional regions of the genome and was therefore probably subject to a similar process of negative selection<sup>35</sup>.

The third strongly supported admixture event in the ancestry of present-day people is from a second, distinct Denisovan population into the ancestors of present-day East Asian people, found in proportions in the order of 0.1%<sup>49,87,89,90</sup>. This population appears to have been more closely related to the Denisovans from Siberia<sup>87</sup>. East Asian populations can thus trace very small amounts of ancestry to two distinct Denisovan-related groups.

### The frequency of archaic admixture outside of Africa

Another strongly supported archaic admixture event comes from analyses of an approximately 40-thousand-year-old individual from Peștera cu Oase in Romania<sup>91</sup>, who had a Neanderthal ancestor in the previous 4–6 generations<sup>92</sup>. However, this Neanderthal admixture probably did not contribute to present-day ancestry<sup>92</sup>. Together with findings of admixture between Neanderthals and Denisovans<sup>61,93</sup>, these few, but direct, observations of admixture suggest no strong biological or behavioural barriers to admixture between modern humans, Neanderthals and Denisovans.

Further archaic admixture events have been proposed, but lack consensus across the literature. These include additional pulses from Neanderthals<sup>46,71,73–77,86,94,95</sup>, Denisovans<sup>78,85,90</sup> and unknown archaic ancestries<sup>96,97</sup>. An emerging notion, fuelled by the many hypothesized events in the literature, is that archaic admixture into modern human populations occurred frequently whenever these groups came into contact. Although such admixture complexity is certainly plausible, we argue that the currently well-supported events include only those described above.

The current genomic data also do not support substantial unknown ‘ghost’ archaic ancestry in non-Africans<sup>89,98,99</sup>, for example from *Homo erectus* or other groups. More substantial amounts of such ancestry would give rise to an excess of ancestral variants in some non-African groups over others, detectable even without access to the source genome, a signal that can be confirmed for Denisovan ancestry<sup>10</sup>.

## Phase 2 and African origins

The second key phase is the diversification of present-day human ancestries. Although Africa was probably the centre of this process, neighbouring parts of Southwest Asia cannot be excluded as key areas of the history of the human population during the past few hundred thousand years<sup>100</sup>. However, an origin of present-day modern human diversity further away in Eurasia now seems to be highly unlikely. Here, we discuss what is known about modern human history in Africa between around 60 and 300 ka in a conceptual framework of models (Fig. 2a), among which only a complete replacement scenario inside Africa in the past 100 ka can currently be excluded.

### The fossil record of modern human origins in Africa

For the period from around 150 to 300 ka, African fossil crania show great morphological diversity (Fig. 2b). By contrast, Middle Stone Age technology, which emerged across Africa around 300 ka, suggests similar patterns of behaviours across diverse human populations<sup>7,101</sup>. Specimens such as Jebel Irhoud 1 and 2 (Morocco, dated to around 315 ka)<sup>7</sup> and Omo Kibish 2 (Ethiopia, dated to around 195 ka)<sup>8</sup> are often placed on the modern human lineage, but lack a globular cranial vault. In fact, despite certain dental and mandibular traits pointing to *H. sapiens* affinity<sup>7</sup>, some studies place Irhoud 1 as closer to Neanderthals than to extant *H. sapiens*<sup>102,103</sup>. On the basis of the currently available evidence, a globular cranial vault appears only by about 150–200 ka, when it is found in Omo Kibish 1 (Ethiopia, dated to around 195 ka) and Herto 1 and 3 (Ethiopia, dated to around 160 ka)<sup>8</sup>, although it might also be present in partial crania found at Apidima (Greece, dated to

more than 210 ka)<sup>21</sup> and Guomde (Kenya, dated to around 240 ka)<sup>8</sup>. The fragmentary Florisbad cranium (South Africa, dated to around 260 ka, although this date requires confirmation<sup>104</sup>) is too incomplete to determine the extent of globularity, and its relationship to modern humans is uncertain<sup>105</sup>.

With the scattered fossil evidence that is currently available, it is therefore unclear whether or not there was a specific evolutionary event between 200 and 300 ka that originated a suite of ‘modern’ traits such as the globular cranial vault, bony chin on the mandible, and a narrower and less flared pelvis. One rationale has suggested that such traits were in place before the earliest separation of present-day ancestries. However, if early separations were more gradual, as is increasingly likely and discussed further below, ‘modern’ traits could have become universal by later gene flow. The timing of modern human ancestry diversification will therefore provide only a weak constraint on the evolution of traits.

### The time depth of modern human population structure

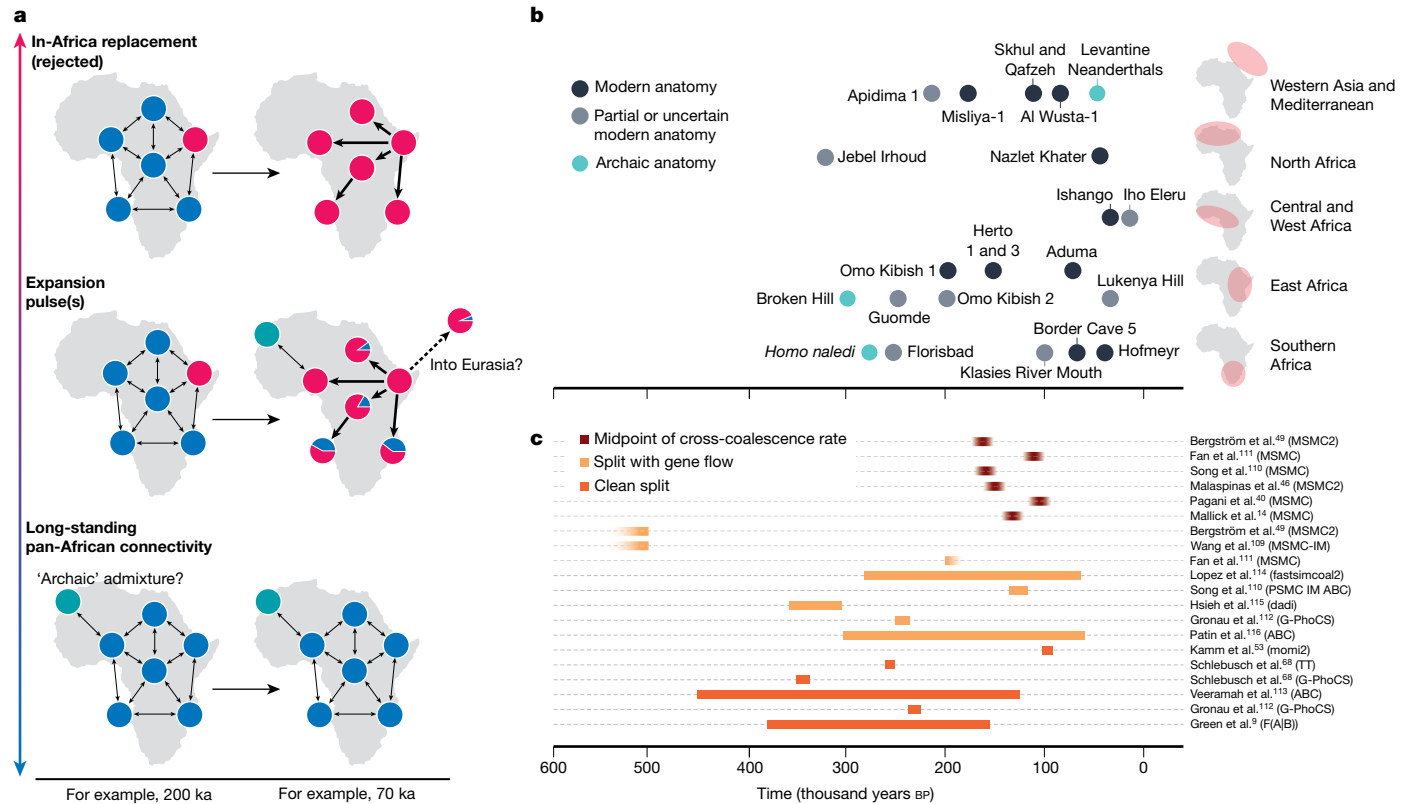
The major distinguishable strands of present-day human ancestry could be summarized as including those associated with populations in West Africa, East Africa, the Central African rainforests, southern Africa and the world outside of Africa<sup>2,11,13,15,106,107</sup>. Many African populations can then be described as having ancestry from more than one of these strands, including non-African ancestry, reflecting complex admixture processes. The diversification of these African ancestries probably postdates the divergence of Neanderthal and Denisovan ancestors, as no differences in relatedness to archaic genomes between these lineages are apparent<sup>9,13</sup>. Understanding the diversification process of early modern humans more precisely has been a major focus in the study of human origins.

One way to conceptualize the time depth of current human population structure is to focus on the earliest point in time at which groups existed that contributed more genetic ancestry to some present-day individuals than to others. There would also have been structure before this point, but any earlier groups would be symmetrically related to everyone alive today. The current absence of ancient DNA from Africa from before 15 ka means that most insights into this question have come from estimates of divergence timing between present-day African groups, reliant on various modelling assumptions and therefore associated with considerable uncertainties. It is becoming clear that early divergences within Africa were not sudden splits, but were instead much more gradual, with long-standing gene flow over tens or even hundreds of thousands of years<sup>49,108,109</sup>. Estimates that can be interpreted as a midpoint of the separation process result in relatively recent dates of 104 to 162 ka<sup>14,40,46,49,110,111</sup>, whereas models assuming instantaneous separation without gene flow yield dates of 230–340 ka<sup>9,68,112,113</sup>, and models that include gene flow yield dates of 125–340 ka<sup>110–112,114–116</sup> (Fig. 2c). Different approaches may therefore partly capture different aspects of the gradual separation processes. We argue that it is not conceptually meaningful to describe the time depth of the population structure of early modern humans with point estimates, and that future studies should aim to be more explicit about what aspect of the separation process their estimates reflect.

The question then becomes how we should describe the timing of the emergence of present-day human population structure. Looking backwards, the majority of the genetic ancestry of modern humans might converge between around 100 and 250 ka, with a minority fraction of ancestries deriving from populations that had diverged earlier than that, possibly before 500 ka<sup>49</sup> or even one million years ago (Ma)<sup>109</sup>. Many different scenarios could underlie this observed timescale of shared ancestry and, other than rejecting models of recent African-wide replacement, current data do not clearly distinguish between them<sup>117,118</sup> (Fig. 2a).

### Possible ‘archaic’ admixture in Africa

Questions about the time depth of the structure among present-day populations are inextricably linked to claims of admixture with more divergent human groups within Africa. Some of the few later fossils



**Fig. 2 | Modern human origins and diversification in Africa in the past 300 thousand years (phase 2).** **a**, African ancestry origins can be conceptualized as a range of models, most of which cannot be rejected using the current data. Models along this spectrum (indicated by the colour gradient of the arrow) include, among others, a recent complete replacement from a single region (top), a recent expansion overlaid on older structure (middle), and long-term continuity and connectivity across all of Africa (bottom). Here East Africa is a hypothetical origin of expansions (indicated by the red dot in the top and middle rows), but other regions could represent hypothetical origins too.

in western and Central Africa (Iho Eleru, Nigeria, dated to around 13 ka<sup>119,120</sup>, and Ishango, Democratic Republic of the Congo, dated to about 20–25 ka<sup>121</sup>) show apparent archaic features, which may indicate either very late survival of early *H. sapiens* morphologies, or gene flow from archaic (with morphology outside the range observed today) human lineages.

Several studies have suggested the presence of very deep population structure in Africa based on present-day genetic variation<sup>122–124</sup>, including suggestions of admixture from genetically unsampled ‘archaic’ human groups that are not closely related to Neanderthals or Denisovans<sup>115,125–128</sup>. In these genomic studies, the term ‘archaic’ is used not with reference to morphology as in the original meaning of the term, but rather to imply an early genetic divergence. The term ‘archaic’ is potentially problematic as it risks being misinterpreted as ‘less evolved’<sup>117</sup>. Given its long-standing usage, we argue that in a genomics context the term should only be applied to groups that are explicitly hypothesized to have separated chronologically from the majority of modern human ancestry at least as early as Neanderthals did.

Most studies that aimed to identify highly divergent ancestry in Africa have looked for segments of the genome that are both unusually long and deeply divergent from other segments<sup>122–124</sup>. Although these observations have been shown to match models of archaic admixture best in simulations<sup>115,125–128</sup>, it is challenging to rule out that such segments could represent the upper tails of the divergence distributions of high-diversity African populations. The concepts of ‘long-standing structure’ and ‘archaic admixture’ might thus be viewed

as a continuum of models (Fig. 2a). However, support for deep admixture also comes from derived alleles shared with Neanderthals at the rare and high-frequency ends of the spectrum in modern human populations<sup>129</sup>. Some models of African population history have also included gene flow from lineages that diverged as early as, or before Neanderthals<sup>106</sup>, but simpler models have not been excluded. In our view, it is premature to refer to these various findings as archaic admixture, and they do not come with the same level of confidence as Neanderthal and Denisovan admixture, for which direct genomes from the source populations are available. Nonetheless, admixture from highly divergent groups inside Africa could help to explain the observed complex timing of early modern human separations.

**The search for a modern human birthplace**

We argue that, with current evidence, it is not possible to pinpoint more precisely where in Africa the common ancestors of present-day people lived. In the absence of a full time series that demonstrates how ancestry was distributed in the past, a strong line of evidence for an origin in a given geographical region could be if the majority of human ancestry was ‘nested’ inside the greater diversity of that region, accounting for admixture. However, although such a criterion currently identifies Africa as the birthplace of modern humans, it does not pinpoint a specific region inside Africa.

Another rationale suggests that the highest levels of genetic diversity are found at the origin of expansions<sup>3,130,131</sup>, and this ‘serial founder’ model has been used to suggest a southern African origin of modern

humans<sup>2,12</sup>. However, present-day diversity levels reflect not only loss of diversity due to population bottlenecks, but also increased diversity due to admixture<sup>132–134</sup>, as exemplified by how a pattern of greater diversity in Europe compared to East Asia today was not present in ancient populations<sup>58</sup>. Furthermore, diversity levels of major sub-Saharan populations are all within around 10% of each other, without strong geographical trends<sup>11,14,107,111</sup>. In a recent whole-genome panel<sup>14</sup>, the population with the highest diversity was the Central African Biaka, who have a history of recent admixture<sup>2,135</sup>.

The tendency of populations from southern Africa to display the deepest divergence times, and to occupy the earliest branching positions in tree-like models of history<sup>2,11,15,113</sup>, has also been interpreted as evidence for a southern African birthplace. However, trees are poor representations of genetic history, and branching events always have two symmetrical descendant branches, neither of which is more ancestral than the other. More recent studies that allow for gene flow have suggested that strands of ancestry that are at least as divergent as southern African ancestry are present in western<sup>13</sup> as well as Central and eastern Africa<sup>106</sup>. More importantly, as people are likely to have moved from where their ancestors lived more than 200 ka, there is no strong expectation that the geographical location of the people carrying the most divergent ancestry today would correspond to a point of origin. Similarly, although a mitochondrial ‘Eve’, a hypothetical female ancestor of everyone alive today, will have existed and probably lived about 200 ka<sup>1,136</sup>, the location where she, or her Y-chromosomal ‘Adam’ counterpart<sup>137</sup>, lived is not necessarily expected to be the birthplace of all human ancestry. Furthermore, the small mitochondrial history traces just one out of a multitude of paths through the greater human genealogy. In many other parts of the genome, the most divergent branch will be found elsewhere in Africa, or sometimes outside of Africa.

For these reasons, current genomes simply do not contain enough information on where our early ancestors lived geographically. Recently, increasing attention has been given to the hypothesis that the ancestors of modern humans lived in distinct but interconnected populations across large parts of the African continent<sup>101,117</sup>, but such ‘pan-African’ origin hypotheses (Fig. 2a) are similarly difficult to test against genomic evidence. A richer and geographically more representative fossil record, and ancient DNA or proteins from earlier time periods, might be more informative about past distributions of humans within Africa.

### A possible Late Pleistocene expansion across Africa

In population history models that include deeply diverging ancestries in West<sup>13,106</sup> and Central<sup>106</sup> Africa, the second major ancestry in these regions tends to be related to East African populations. A speculative suggestion that could explain this is an expansion across Africa of an ancestry similar to that which expanded into Eurasia after around 60 ka<sup>13,106</sup>. This could also explain the spread of the Y-chromosomal CT lineage, for which African and non-African lineages had a common ancestor around 65–80 ka<sup>38,138</sup>. An analysis of divergence times between segments of present-day genomes similarly suggested substantial admixture from a source related to the ancestors of non-Africans, but lacking Neanderthal admixture, into all African populations studied<sup>139</sup>. This ancestry might never have left the African continent, but could represent an across-Africa expansion concurrent with the into-Eurasia expansion (Fig. 2a), and its spread could potentially be a major contributor to the complex genetic relationships observed among present-day African populations.

### Phase 1 and the divergence from archaic groups

The most characteristic Neanderthal fossils are known from Europe from about 40 to 250 ka<sup>140</sup>, with currently more limited time spans known across Asia, as far as southern Siberia<sup>61,141</sup>. Although the identity of Denisovans in the fossil record is currently poorly known, sediment

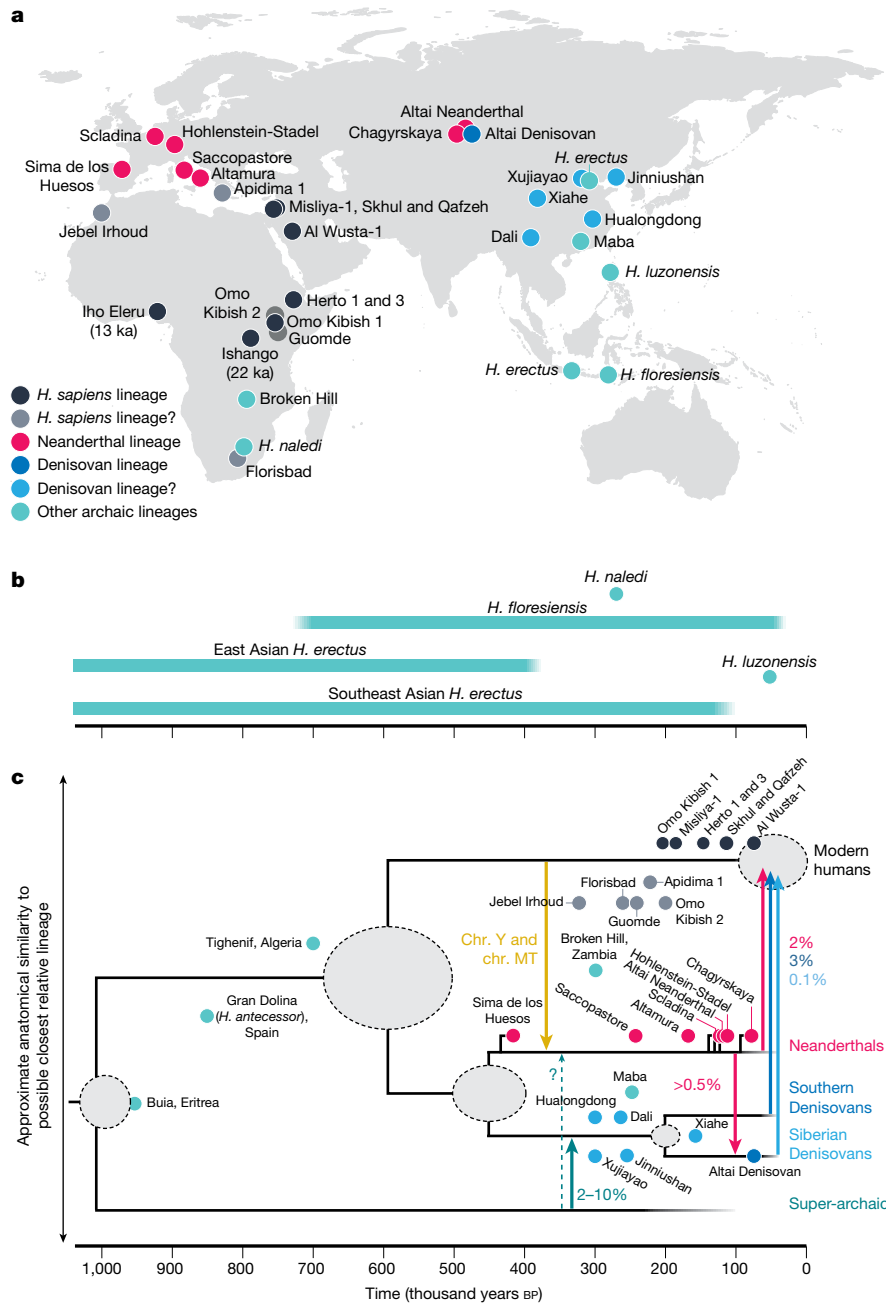
mtDNA confirms their presence on the Tibetan plateau between at least around 60 and 100 ka<sup>142</sup>, and the growing fossil record from China for the period from 200 to 600 ka contains specimens that show differentiation from earlier Asian *H. erectus*<sup>143</sup>. The Dali skull has sometimes been grouped with *Homo heidelbergensis*, but shows a combination of a massive supraorbital torus, an archaic-shaped cranial vault and a rather modern-looking, but very wide face<sup>144</sup>. This is a distinctive morph, which is perhaps mirrored in other Chinese fossil crania such as those from Jinniushan<sup>145</sup> and Hualongdong<sup>146</sup> that also lack characteristic features of *H. erectus*, *H. heidelbergensis* and Neanderthals. These could thus represent candidates for early Denisovans, along with the mandibles from Xiahe and Penghu<sup>147</sup>. Neanderthals and Denisovans share some ancestry after the separation from modern humans, but they probably diverged from each other before 400 ka<sup>61,148</sup>.

Analyses of genomes have identified, in addition to Neanderthal, Denisovan and modern human ancestry, a fourth, highly distinct ancestry that would have existed during the time period before 300 ka (Fig. 3), but which currently cannot be linked to any populations apparent in the fossil record: the ‘super-archaic’ ancestry proposed to be present in Denisovan genomes<sup>71</sup>. The primary evidence is that all modern humans, including African populations with little or no Neanderthal admixture, share more genetic variants with Neanderthals than with Denisovans<sup>71</sup>, and particularly so for variants that became fixed in early modern humans—with super-archaic ancestry diluting the frequency of these variants in Denisovans. This super-archaic group would have diverged from the common ancestor of modern humans, Neanderthals and Denisovans between 0.9 and 1.4 Ma<sup>61,149</sup>, or earlier<sup>61,150</sup>. Denisovans also carried a highly distinct mitochondrial lineage that diverged from others around 0.7–1.4 Ma<sup>151,152</sup> and that was probably obtained from this population. Although it is tempting to speculate that this super-archaic population could correspond to *H. erectus* or some related group, its genetic divergence seems too recent to align with the first appearance of fossil *H. erectus* at least around 1.8 Ma<sup>153</sup>. Populations related to *Homo antecessor*<sup>154</sup> might be an alternative.

The ancestors of Neanderthals and Denisovans are estimated to have diverged from the ancestors of modern humans between 500 and 700 ka<sup>9,49,53,61,62,68,155</sup>. Although it has been suggested that this was a sudden rather than a gradual separation process<sup>49</sup>, evidence against complete genetic separation since more than 500 ka comes from the mtDNA of modern humans and Neanderthals diverging only around 350–450 ka<sup>151,152,156,157</sup>, and a similar time frame for Y chromosomes<sup>158</sup>. This apparent discrepancy could be explained if the uniparental chromosomes moved between the ancestors of Neanderthals and modern humans by gene flow, in either direction, at some point after about 450 ka.

An important data point in resolving this history is DNA from the more than 400-thousand-year-old<sup>159</sup> site of Sima de los Huesos in Spain, where skeletons with Neanderthal-like physical traits also have an affinity to Neanderthal rather than Denisovan genomes<sup>148</sup>. However, individuals from Sima de los Huesos carry a version of the highly diverged mtDNA lineage that is found in Denisovans<sup>156</sup>, suggesting that it once could have been carried by all early Neanderthals, but was replaced by gene flow from the ancestors of modern humans<sup>148,152,158</sup>. Later Neanderthal mtDNA lineages diversified around 270 ka, suggesting that the gene flow into Neanderthals occurred before this date<sup>152</sup>, although it is possible that part of this diversity was present earlier.

Gene flow from the modern human lineage into Siberian, but not European, Neanderthals has been suggested<sup>160</sup>, but higher-quality genomes have not corroborated this<sup>62</sup>. Instead, later studies have statistically inferred modern human gene flow on the order of a few per cent into the ancestors of all Neanderthals studied to date<sup>63,160,161</sup>. Such inferences are subject to many of the same modelling challenges as analyses of archaic admixture in Africa. Regardless, any such gene flow would need to have come from a population that diverged mostly before the diversification of present-day modern human ancestries,



**Fig. 3 | Separation of modern human and archaic ancestries in the past one million years (phase 1).** **a**, Locations of key *H. sapiens*, Neanderthal, Denisovan and other archaic human fossils from the past 500 thousand years. Pale colours indicate uncertain but possible lineage assignments. **b**, Chronology of archaic human populations that are unlikely to have contributed to modern human ancestry. These include *Homo naledi*, *Homo floresiensis* and *Homo luzonensis*<sup>143</sup>. The timeline is the same as in **c**. **c**, Chronology and probable ancestry history of

the separation between modern human and archaic human ancestries. Selected fossils older than 80 thousand years and their possible lineage attributions (as in **a**) are indicated. The placement of the fossils along the vertical axis reflects our assessment of how closely related they might be to the genetic ancestries. Chr. MT, mitochondrial chromosome; chr. Y, Y chromosome. Grey circles represent uncertainty around timing or population topology.

more than 200 ka, but could correspond to the same event that led to the transfer of the uniparental chromosomes.

Three possible ancestry strands that contributed to Neanderthals and Denisovans have therefore been hypothesized, with the strands having different degrees of divergence from present-day humans: (1) ‘super-archaic’ ancestry that diverged around 1 Ma; (2) the originally hypothesized ‘middle’ archaic ancestry, which diverged from the ancestors of modern humans between around 500–700 ka to give rise to both Denisovan and Neanderthal ancestry; and (3) ‘recent gene flow from modern human ancestors’ around 200–400 ka. Super-archaic

ancestry has been inferred for Denisovans<sup>61</sup>, and recent gene flow for Neanderthals<sup>148</sup>, but it is also possible that both archaic populations carried both of these strands of ancestry in different proportions<sup>88</sup>. Although it is commonly believed that both Denisovans and Neanderthals derived the majority of their ancestry from the ‘middle’ archaic population, it may be possible that the inferred archaic–modern human divergence of 500–700 ka<sup>49,53,61,62,68</sup> is due to statistical averaging of the ‘super-archaic’ and ‘recent gene flow’ ancestries. No ‘middle’ population and expansion of Neanderthal ancestors between 500 and 700 ka would be necessary in that alternative scenario<sup>88</sup>.

## The last common ancestor of modern and archaic humans

Once the majority of the ancestry of modern humans, Neanderthals and Denisovans has converged before 500 ka, genomes provide little or no information about who those common ancestors were. Fossils from around 300–700 ka have revealed many anatomically distinct groups of humans, and the period has been called the ‘muddle in the middle’<sup>162</sup> of human evolution. It is impossible to identify any early Middle Pleistocene fossils as definitively representing the common ancestral population for *H. sapiens*, Neanderthals and Denisovans, but it is possible to identify groups that probably are not, namely Asian *H. erectus*, facially derived *H. heidelbergensis* across Africa and West Eurasia, and the Neanderthal-like Sima de los Huesos hominins. Possible alternative candidates for our early ancestors might include *H. antecessor* from Europe, the Tighenif fossils from Northwest Africa<sup>163</sup> and the Buia material from Northeast Africa<sup>164</sup>.

Although it is commonly assumed that our ancestors would have lived in Africa before 500 ka, it is still too soon to exclude that they could have lived in Eurasia. A Eurasian origin during this period would also require fewer migrations between Africa and Eurasia to explain currently understood relationships between modern human, Neanderthal, Denisovan and the super-archaic ancestries<sup>88</sup>. Proteomic data from European *H. antecessor*<sup>165</sup>, which shows the potential of ancient protein preservation in the deep past, suggests that it might have been closely related to the common ancestor, but the ancestry information provided by dental enamel proteins is still of low resolution. In any case, with the earliest generally accepted evidence of hominins outside of Africa at around 2 Ma<sup>166</sup>, the fossil record strongly suggests that all human ancestors before this point, until the common ancestor with chimpanzees, lived in Africa.

## Outlook

Although a common understanding views modern humans as having an African origin in the last few hundred thousand years ago (for example, ‘200 ka’), what such an ‘origin’ entails is often not well defined. It is increasingly important to differentiate the evolution of traits—that is, when our ancestors became sufficiently similar to present-day humans in terms of anatomy<sup>6–8,167</sup>, behaviour, physiology or cognition—from genetic ancestry. Definitions from a genetic perspective may instead focus on a period in time in which most of the genetic ancestry of present-day people was found in a specific geographical area, with or without a particular set of traits. Asking when and where modern human ancestry originated is a different question from asking when and where modern humans, as defined through our traits, originated, and the answers to the first question that we have reviewed here may only weakly inform on the latter. Any strict definition of origin thus risks oversimplifying the continuous and complex, and in many aspects unknown, nature of the deep human past. For example, current evidence identifies Africa and Southwest Asia as the region of origin of humans during the period of 100–300 ka, but does not yet provide further geographical precision, and before 300 ka there is even greater uncertainty about where our ancestors lived.

Over the next decade, these insights will probably also shift the geographical focus of palaeoanthropological fieldwork to regions that previously have been considered peripheral to perceived centres of human evolution, such as Central and West Africa, the Indian subcontinent and Southeast Asia. As more spatially and temporally representative palaeoanthropological and genetic data from across Africa and the rest of the world become available, it will be possible to refine our understanding of ancestry through the human past as described here. The success of direct genetic analysis so far highlights the importance of a wider ancient genetic record. This will require continued technological improvements in ancient DNA retrieval from skeletal material<sup>60,71,168</sup>, biomolecular screening of fragmentary assemblages for human material<sup>93,169</sup>, analysis of sedimentary DNA<sup>142,170</sup> and improvements in the evolutionary information provided by ancient

proteins<sup>147,165</sup>. Interdisciplinary analysis of this combined record will undoubtedly reveal new surprises about the roots of modern human ancestry.

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