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A genetic perspective on African prehistory

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Abstract

The various genetic systems (mitochondrial DNA, the Y chromosome and the genome-wide autosomes) indicate that Africa is the most genetically diverse continent in the world and the most likely place of origin for anatomically modern humans. However, where in Africa modern human arose and how the current genetic makeup within the continent was shaped is still open to debate. Here, we summarise the debate and focus especially on the maternally-inherited mitochondrial DNA (mtDNA) and a recently revised chronology for the African mtDNA tree. We discuss the possible origin of modern humans in southern, eastern or central Africa; the possibility of a migration from southern to eastern Africa more than 100 ka, carrying lineages within mtDNA haplogroup L0; the evidence for a climate-change-mediated population expansion in eastern Africa involving mtDNA haplogroup L3, leading to the "out-of-Africa" migration around 70–60 ka; the re-population of North Africa from the Near East around 40–30 ka suggested by mtDNA haplogroups U6 and M1; the evidence for population expansions and dispersals across the continent in the onset of the Holocene; and the impact of the Bantu dispersals in central, eastern and southern Africa within the last few millennia.

There is a consensus across the fields of genetics, archaeology and palaeoanthropology that Africa is the cradle of *Homo sapiens*. Genetically, across the genome-wide autosomal variation and the uniparental markers, the mitochondrial DNA (mtDNA) and Y-chromosome, Africa is the continent with by far the highest genetic diversity (Torroni et al. 2006; Behar et al. 2008; Li et al. 2008; Cruciani et al. 2011). However, with a few exceptions, this is where the consensus ends. A whole range of crucial questions remain highly controversial. These include: where in Africa modern humans first appeared; when each part of Africa was first colonized by modern humans; the impact of climate change on human populations; and how cultural and technological innovations helped shape the current genetic diversity in the African continent.

Genetics can contribute valuable insights into the origins and migrations of human populations. The rationale for this lies in the fact that mutations and recombination, the events promoting changes in the genome down the generations, are random phenomena that leave marker buoys scattered throughout the genome, each of which arose at a particular time and place. They can therefore serve as an inference tool to bracket the place and timing of evolutionary events.

The relatively small, maternally inherited mtDNA component (around 16,570 base pairs) has been heavily screened worldwide, initially for short segments of the fast-evolving, non-coding control-region (>150,000 samples), and more recently for the whole-mtDNA genome. By 2013, more than 15,000 whole-mtDNA genome sequences have become publicly available, including more than 2000 from African individuals. Whole-mtDNA genomes, in particular, can resolve the details of the maternal genealogy in exquisite detail. An even greater level of genealogical resolution awaits us for the male line of descent, inscribed in the non-recombining, male-specific part of the Y chromosome, or "MSY", as human genome sequencing proceeds apace. Although some analyses have suggested drastic reductions on the number of MSY lineages in the recent past due to the reproductive success of relatively few individuals, it may also be the case that the MSY often tracks important dispersals, leading to the spread of language families, that are much less evident from the mtDNA variation (Forster and Renfrew 2011). In the end, models erected using either the mtDNA or the MSY have to be tested against variation in the rest of the genome. The analysis of genome-wide autosomal markers, and increasingly complete human genomes, provides a more complete window onto the past that does not focus on one or other single line of descent.

Nevertheless, mtDNA led the way for archaeogenetics and remains an extremely valuable marker system. The mtDNA, like the MSY, is non-recombining, leading to the transmission down the generations of the genetic material in a block – essentially, a single DNA sequence. As it is passed down the generations mutations accumulate, leading to the formation of related clusters called haplogroups, each of which can trace its descent back to a single common ancestor. A haplogroup is effectively a named example of what evolutionary biologists call a clade – a group comprising an ancestor and all its descendants. Any ancestral node in the genealogical tree can, moreover, be dated using the "molecular clock" – a measure of how rapidly mutations accumulate over time – an approach that remains controversial, but which has seen considerable progress recently in all three systems, with the use of whole mtDNA genomes (Soares et al. 2009), the autosomes with the development of large-scale complete human genome sequencing (Scally and Durbin 2012) and the MSY as much larger genomic tracts of the Y chromosome start to be used (Wei et al. 2012; Francalacci et al. 2013). Thus, if a migration takes place from one region to another, new mutations unique to that region will start to accumulate there, and the age of the presence of that cluster in that region can be estimated by dating the node from which they arise. This tracking of genetic lineages (or lines of descent) in time and space by analyzing their geographic distribution and time depth is referred to as "phylogeography", and the dating of dispersals in this way in particular is called "founder analysis". The resolving power of the mtDNA genealogical tree makes mtDNA an extremely powerful tool with which to evaluate population structure and follow migrations across space and time (Torroni et al. 2006; Macaulay and Richards 2013).

Phylogeographic approaches have been criticised on a range of fronts, and have often been compared unfavourably to both more formal and supposedly robust procedures such as those based on simulation modelling or summary statistics (Nielsen and Beaumont 2009). However, hypothesis-testing procedures based on evolutionary and population-genetics theory have their own weaknesses; in particular, they suffer from the well-known gulf between the rejection of a null hypothesis and the inference of specific demographic scenarios (Bandelt et al. 2002). Although critics often dismiss phylogeographic analyses as "interpretative" and "story-telling", it is difficult to maintain a hard-and-fast distinction of this kind between the phylogeographic approach to population genetics and more formal procedures. In practice, all reconstructions based on inferences from the modern distribution of genetic variation are fraught with difficulties. Moreover, we are increasingly learning that these issues do not go away when ancient DNA comes into play – although this is not for the present an issue so far as Africa is concerned.

On the other hand, the critics sometimes fail to acknowledge both the extraordinary richness of the genetic evidence – whether it be the extraordinarily fine resolving power of mtDNA or MSY phylogenies, or the incredible autosomal profiling that is now possible – or the successes that phylogeographic reconstructions have achieved in cases where the demographic history is broadly known from other lines of evidence – such as the settlement of the Americas, the Remote Pacific, and indeed southern Africa, as we discuss below. Rather than a hard-line set of protocols in which demographic history is read from scratch from DNA sequence data using statistical tools of dubious reliability, we prefer an exploratory and interdisciplinary approach in which hypotheses are evaluated within the framework of models supplied by archaeology, palaeoanthropology, palaeoclimatology and so on.

In this chapter we focus primarily on the patterns in the mtDNA variation and review the main respects in which the phylogeographic analysis of this particular molecule can provide information about the history of the continent, in the context of some of the autosomal and MSY work. For a broader view of the mtDNA variation we can recommend the recent review by Rosa and Brehm (2011).

The maternal genealogy of Africa

The African mtDNA tree is effectively the human mtDNA tree, since the deepest two-thirds of the lineages are restricted to Africa, and the non-African lineages are only a tiny fragment of African diversity. Any phylogenetic tree comprises nodes separated by branches, in a nested array of clades and subclades – clusters of lineages that include all descendants of a given common ancestor (a subclade is simply a clade within a clade). The mtDNA tree is divided into two primary or basal clades, referred to as haplogroups L0 and L1'6, or L1'2'3'4'5'6 (Figure 1) (Torroni et al. 2006; Behar et al. 2008). For historical reasons, the deep African lineages within the mtDNA tree are all prefixed with "L" – other haplogroups around the world having already claimed most other available letters (such as A through D in Native Americans, H through K and T through W in Europeans, for example). Haplogroup labeling follows a scheme in which nested subclades within a haplogroup graced with a capital letter are then followed by a number (such as L0), and further nested subclades are given alternate letters and numbers (*e.g.* L0a, L0a1, L0a1b etc.) (Richards et al. 1998). Clades that include several

named clades can be described by concatenating the subclades, *e.g.* L0a'b. Multiply concatenated clades can be abbreviated to just the first and the last, so that L1'6 becomes just L1'6, for example.

Until the emergence of haplogroup L3, roughly between 70 and 60 ka (70,000–60,000 years ago) (Watson et al. 1997; Soares et al. 2012), the human mtDNA tree was bifurcating (separating into only two daughters) at every node, and nodes are usually separated from one another in time by many thousands of years. This pattern reflects small population sizes and a correspondingly high degree of genetic drift prior to this time. This in turn implies a high rate of extinction of lineages, and a corresponding loss of evidence as one extends inferences back into this period. Even so, some general conclusions can be drawn from the structure of the tree.

Phylogenetically, one-half of the human mtDNA tree – that is, L0 – seems to have a southern African distribution, and probably also origin (Figure 1 and 2A). L0 is divided between L0d (with a southern African distribution) and L0a'b'f'k where L0k is southern African and L0a'b'f has an eastern African distribution.

The other half of the human mtDNA tree has a much more complex genealogy and distribution, with subclades distributed throughout central, eastern and West Africa, as well as (more recently) North Africa and the rest of the world. This L1'6 clade is also much more frequent overall than L0 throughout Africa – even in most of southern Africa, where L0 is found at its highest frequencies. L1'6 then splits into L1, mainly found in central Africa (Figure 2B), and or L2'6. The latter then splits once again into L2'6 and L5. Haplogroup L5 is very rare and only found in eastern Africa. L2'6 then further divides into L2 and L3'6, with L2 most likely originating in central or West Africa (Figure 2C) and L3'6 in eastern Africa (Figure 2D for L3). Haplogroup L3 also includes two major subclades that are most likely of central or West African origin, L3b and L3d. These geographic splits in the tree represent the most ancient potential dispersals that we can detect in the mitochondrial record. L3 also includes two subclades, haplogroups M and N, which include all of the non-African (Eurasian and Australasian) diversity, excluding additional dispersals out of Africa in the last few millennia.

Modern human origins

Exactly where the so-called "anatomically modern humans" (or AMH) first appeared in Africa remains a thorny problem. Perhaps the question should not even be framed in such terms; AMH may not descend from a single group of people that lived in a specific geographic location at a particular time, but may have arisen from various groups that interacted or coalesced over time (Schlebusch et al. 2012) – a kind of "multi-regionalism in one continent".

Paleoanthropology has commonly placed modern human origins in East Africa. The Omo 1 cranium, from the Kibish River in Ethiopia and dating to ~195 ka, is the oldest known fossil to display modern human features (McDougall et al. 2005). The remains from Herto, also in Ethiopia, date to ~160 ka (Clark et al. 2003), strengthening the case for an East African origin. However, the Jebel Irhoud specimens from Morocco also date to about 160 ka (Smith et al. 2007), although with some dispute over whether or not they are anatomically fully modern (Stringer 2011), and the Skhul/Qafzeh fossils from Israel date to roughly 90–135 ka (Millard 2008). In the south of the continent, the oldest known fossil is from the Klasies River caves, with two poorly constrained pulses dating to >100 ka and 65–105 ka respectively (Deacon 1995; Millard 2008), although its status as fully modern is also contested (Rightmire et al. 2006). More archaic remains, dating between 190 and 330 ka are found at Florisbad (Millard 2008). There is also some very early evidence in southern Africa for key elements of modern human behavior, ~160 ka at Pinnacle Point (Marean et al. 2007). Clearly, the fossil record is extremely fragmentary, and any conclusions drawn from it regarding an eastern African origin for AMH are on shaky ground for the time being.

Unfortunately, though, the genetic evidence does not really clarify the picture. Two genome-wide studies, one mainly based on the evidence from fast-evolving STRs (short tandem repeats) and "indels" (insertions and deletions) (Tishkoff et al. 2009), and one employing nearly 600,000 SNPs (single-nucleotide polymorphisms, or variants) (Henn et al. 2011), both pointed to a southern African origin, an early genetic legacy that left its mark particularly on the foraging and herding populations usually lumped together as "Khoisan" or "Khoe-San", belonging to the otherwise linguistically unrelated click-consonant Khoe, Tuu and Ju families (Guldemann and Stoneking 2008).

We need to digress at a moment here. The comparative method does not confirm Greenberg's linguistic thesis of a common origin for the southern African click-consonant languages, for which he took up the biological term "Khoisan", in distinction to his three more widely accepted African linguistic phyla: Afro-Asiatic, Nilo-Saharan and Niger-Kordofanian (which includes the Bantu group). Imprecision in this regard has unfortunately permeated the genetic literature on Africa, generating many inaccuracies and confusions (Mitchell 2010). Strong genetic evidence has, however, accumulated for a deep common ancestry amongst many of these groups, in distinction to both other Africans and non-Africans,

so it therefore seems reasonable to refer to them collectively as "indigenous southern Africans" or "Khoe-San", suggested as the preferred collective name of the communities themselves (Schlebusch 2010). Nevertheless, we must emphasize that this is a distinction made on the basis of inferred geographic ancestry, akin to "West Eurasian", "East Eurasian" and "Sahulian" (Saitou 1996), and not on any linguistic basis.

So, autosomal studies have been interpreted as implying a southern source for modern humans. On the other hand, studies focused on the MSY have suggested that the root of the Y-chromosome tree may lie in central/West Africa (Cruciani et al. 2011; Mendez et al. 2012). In terms of mtDNA the situation is even more opaque. As noted above, the tree splits into two primary branches or clades, L0 and L1'6; the former most likely arose in southern Africa while the latter has a more northerly origin (by "northerly" we here mean simply to the north of southern Africa). It is difficult to assess the most likely place of origin of L1'6, but the center of gravity of its frequency distribution is central Africa. The first bifurcation divides L1, with a central/West African distribution (and most probably a central African origin) and from L2'6, which includes the very rare eastern African haplogroup L5 and a West/eastern African clade (L2'3'4'6).

To try and get a further handle on this issue from the perspective of mtDNA, we can calculate diversity measures for different parts of the continent. We map the mean number of pairwise differences on the mtDNA HVS-I (hypervariable segment I of the non-coding control region) of each available population in Africa in Figure 3. These values are not likely to be highly informative, considering the time depth of the human mtDNA, and the tendency towards saturation (a leveling-off of values due to recurrent mutation) in the HVS-I beyond 50 ka or so, but nevertheless they show us which regions look especially diverse. The plotted diversity values (using the Kriging algorithm in the Surfer software) point to eastern central Africa (roughly to the west of Lake Victoria) as the most diverse region, at the intersection of the origin of the three major clades, L0, L1 and L2'6. These three major clades have ages of ~120–140 ka when dated using maximum likelihood (Yang 1997) and the molecular clock for the whole-mtDNA genome corrected for purifying selection (Soares et al. 2009) (Figure 1). This pattern might simply be generated by the meeting of very different groups of differing origins, but a central African origin might at least appear broadly compatible with the Y-chromosome conclusions, where a recently discovered deeper root in central/West Africa has been recently dated to ~340 ka (Batini et al. 2011; Batini et al. 2011; Cruciani et al. 2011; Francalacci et al. 2013).

Even so, it is difficult to assess whether or not different markers are even pointing to the same phenomena. The mtDNA and Y-chromosome analyses (although not the diversity statistics portrayed in Figure 3) are based primarily on phylogenetic reconstruction and conclusions are drawn according to phylogeographic principles. This means that although diversity measures are important in many contexts, the tree structure itself is the chief inference tool. A population might have undergone migrations, expansions and contractions that could change genetic diversity in many aspects, but the survival of an ancient branch not located elsewhere can provide an indication of ancestry in that region, even if other more recent clades prevail in the population. Such a case is observed in the Y-chromosome, where the deepest split is observed in central/West Africa although the recently detected subclade that indicates this split is very rare (Cruciani et al. 2011).

Diversity indices, however, especially measures such as linkage disequilibrium (LD) and indeed the one we employed for Figure 3, could vary for several reasons, including population substructure, bottlenecks and admixture (Pritchard and Przeworski 2001). Populations in eastern, central and West Africa probably went through major range expansions involving substantial admixture between them (as we demonstrate below), whilst Khoe-San populations appear to have been largely isolated until the Bantu expansion occurred, so patterns of LD such as those used by Henn and collaborators (Henn et al. 2011) might be misleading. A second measure supporting their conclusion of modern human origins in southern Africa was F_{st}, calculated against European populations (Henn et al. 2011). This value, which measures differentiation from Europeans and which was correlated with distance, might also have little to do with modern human origins. Eastern Africa incurred a great deal of back-to-Africa gene flow from non-African populations since the out-of-Africa exodus, both in the Pleistocene and the Holocene, especially through the Arabian Peninsula (Musilova et al. 2011; Fernandes et al. 2012). Even central and West Africa probably experienced some genetic input from non-African populations, in part due to contact with North Africa, as has also been shown for both mtDNA (Ottoni et al. 2010) and Y-chromosome variation (Cruciani et al. 2002). A more recent study focusing on southern African autosomal variation was unable to localize a geographic origin, instead pointing to a long history of "admixture and stratification" (Schlebusch et al. 2012).

A further issue is the time depth of the diversity patterns. There is little evidence for a speciation event in the emergence of *Homo sapiens,* either in the paleoanthropological record or in the genetics (Barham, Mitchell 2008). The domed cranial vault is a modern feature (Lieberman et al. 2002) that appears 150–200 ka ago, but it emerged gradually from more archaic forms in the previous few hundred thousand years. On the genetics side, despite much debate over the years, it seems that there is little evidence for a bottleneck at ~200 ka (Sjodin et al. 2012). There is no persuasive reason to consider that the mtDNA root dating at ~180 ka (Figure 1) or the Y-chromosome root, possibly now somewhat older (Cruciani et al. 2011; Mendez et al. 2012), indicate the emergence of modern humans. What makes this speculation plausible is the proximity of these ages with the emergence of modern human features in the fossil record. However, the coalescent time of the autosomes is overall much higher than in the uniparental markers (due to a higher effective population size and therefore less drift) so, when measuring autosomal diversity, we are analyzing phenomena that most likely greatly predate modern human origins.

Although it is difficult to point to a place of origin for "mitochondrial Eve", at least by ~140 ka it does seem likely from the extant distributions that there were at least two groups of modern humans living in two different parts of the continent. Given the present distribution of L0d and L0k (Barbieri et al. 2013), it seems likely that L0 (dating to ~142 ka) had a southern origin while L1'6 (~148 ka) had a more northerly origin in central or eastern Africa (Figure 4A). Furthermore, the separation between these two groups is unlikely to have happened before ~180 ka, the coalescence time of the human mtDNA tree as a whole (and age of "mitochondrial Eve") and is most likely more recent. An implication is that these two distinct groups were probably both already "anatomically modern", since there is hardly any scope for "leveling across" of anatomical features later on through admixture, given that the southern groups ancestral to modern Khoe-San populations seem to have been isolated throughout most of prehistory, at least on the maternal line of descent. The major exceptions to this isolation are two instances of gene flow, one at ~130–70 ka from southern Africa to eastern Africa, and the second only in the last two thousand years, when the Bantu expansion reached the south of the continent.

This mtDNA picture of the isolation of the two groups is also discernible in genome-wide data, for example in the neighbor-joining population tree of Tishkoff and collaborators (Tishkoff et al. 2009). Their tree separates southern African Khoe-San groups from a single group containing all of the remaining African populations with a more northerly distribution, including the tropical forest forager groups. Although one should not read too much into a population tree, one point to note is that again central Africans appear more basal in this tree than eastern Africans. Moreover, when they set the ADMIXTURE software (Alexander et al. 2009) to distinguish six populations, Henn and collaborators (Henn et al. 2011) also obtained two distinct ancestral clusters in southern hunter-gatherers and more northerly hunter-gatherers, although the separation time of these clusters is unknown. Recent more detailed analyses have confirmed this picture (Pickrell et al. 2012; Schlebusch et al. 2012; Petersen et al. 2013). Finally, using autosomal re-sequencing data, Veeramah et al. (Veeramah et al. 2012) detected an early separation between Khoe-San and other modern human populations that they dated to ~110 ka, although with large confidence intervals [52–187] ka, and other recent estimates have been similar (Schlebusch et al. 2012), although a figure of ~250-300 ka was suggested with a recent re-evaluation of the autosomal mutation rate (Scally and Durbin 2012).

Between south and east

The above-mentioned separation between southern populations and more northerly populations potentially represents the first migration registered in the human mtDNA profile, even though the direction is contentious. However, it seems likely that L0 had a southern origin. L0d is the most common clade in southern African Khoe-San populations, including both herders and hunter-gatherers, and it is also the result of the first split in L0 (Behar et al. 2008). Apart from some more recent input into eastern Africa of L0d3 sequences that we discuss below, this clade is restricted to southern African populations. This evidence for deep isolation and independent evolution across southern African indigenous populations, in genome-wide autosomes as well as the mtDNA, seems to provide some retroactive justification for the collective term "Khoe-San", despite the lack of identifiable relationships amongst the Khoe, Tuu and Ju language families, as discussed above (Guldemann and Stoneking 2008; Mitchell 2010).

After the branching out of L0d, there is a split within L0a'b'f'k, as L0k branches off. Again L0k is mostly found in southern populations. One of the subclades of L0k, L0k2, has so far been mainly in Bantu-speaking southern African populations (Rito et al. In preparation), probably the result of gene flow from the autochthonous population occupying southern

Africa into Bantu speakers as they came into contact within the last ~2 ka, since L0k has never been found in more northerly African populations.

The L0a'b'f clade has a broadly eastern African origin, but the first clade to branch off, L0f, lends additional support to an origin for L0 in the south and a migration to eastern Africa, since it has somewhat an intermediate distribution (Rito et al. in preparation). L0f has four subclades in the whole-mtDNA tree. One occurs only in southern Africa (albeit amongst Bantu speakers), but the HVS-I database allows the identification of this subclade in Zambia and Zimbabwe (*i.e.* in the northern part of southern Africa); one of the subclades is only seen in Tanzania (*i.e.* in the southern part of eastern Africa); a third only in Somalia and Tanzania; and the fourth is more widely distributed through eastern Africa, but also in central Africa. The distribution suggests that L0f probably arose somewhere between southern and eastern Africa (Rito et al. in preparation).

The remainder, L0a'b, has a much more northerly distribution in eastern Africa, with the rarer L0b in particular found only in Ethiopia and Kenya. Imposing a (very approximate) time depth on this reconstruction, L0 and L0a'b'f'k date to ~140 ka and 130 ka in southern Africa, and L0a'b'f dates to ~100 ka. This implies that the first steps of the south-to-east migration occurred between ~130 and 100 ka, or (less plausibly) between 100 ka and the age of L0a'b if L0f arose further south (Rito et al. in preparation) (Figure 4B). L0a'b dates to ~75 ka, suggesting that the final leg of the dispersal into eastern Africa occurred between ~100 and 75 ka (Figure 4B). Intriguingly, therefore, L0 (in the form of L0a'b or a close ancestor) may have entered eastern Africa not very long before the expansion of haplogroup L3 that would generate the out-of-Africa dispersal, ~60–70 ka (Soares et al. 2012). The timescale for the expansion from south to east also corresponds very roughly to the onset of renewed "megadrought" conditions in central Africa, beginning ~115 ka, which may, paradoxically, have facilitated the expansion of human groups by creating a more open landscape in the tropical rainforest zone (Blome et al. 2012).

Considering that the earliest evidence of symbolically-mediated behavior (engraving or ornamentation) has been claimed to be in southern Africa (*e.g.* at Pinnacle Point, dating to ~165 ka (Marean et al. 2007)) and that this symbolically-mediated behavior was part of what was once thought as the "human revolution" in the out-of-Africa populations, it is tempting to speculate that some aspects of modernity might have been carried by L0a'b'f migrants and eventually transmitted from them to eastern African populations carrying L3. This hypothesis could be invoked explain the appearance of *Nassarius* bead ornamentation in North Africa where they are found by ~85 ka (Bouzouggar et al. 2007; d'Errico et al. 2009), and of elements of symbolic behavior in the Levant, although these are present by at least 80–90 ka and possibly for longer (Millard 2008; Shea 2008). This is, of course, highly conjectural, and some dates in the north may well challenge the assumed priority of southern Africa for behavioral innovation (Barton et al. 2009).

Such a migration seems too early for the expansion of the modern Howiesons Poort industry from south to east. This industry appears to have arisen indigenously in South Africa ~65 ka from the Still Bay industry, dating to 70–74 ka, in southern Africa (Jacobs et al. 2008) and Mellars et al. have suggested that it spread into eastern Africa where similar industries are evident by ~60 ka (Mellars et al. 2013). However, given the imprecision of genetic dating (particularly at such time depth), we should not completely dismiss the possibility, particularly given the uncertainty of the place of origin of L0f. Furthermore, several alternative scenarios might provide a channel for Howiesons Poort industries to move from south to east. The earlier dispersal might have opened up a communication channel along which cultural characteristics might have been able to flow, either via contact or by sex-biased dispersal. A signal of male gene flow from south to east might be indicated by the sharing of subclades of the deep-rooting Y-chromosome A and B haplogroups between southern African Khoe-San central/eastern Africa (Semino et al. 2002; Batini et al. 2011). Alternatively, L0f might actually have arisen in southern Africa and the expansion of both it and L0a'b in eastern Africa might represent a direct, second, more recent migration from southern Africa, after ~70 ka, although the present distribution does suggest that this is rather unlikely.

It is worth noting here an apparent second, much more recent, migration involving L0 from south to east. L0d clearly has a southern African origin. L0d1'2, dating to about 70 ka, is only present in southern African, mostly Khoe-San, populations. The second subclade of L0d, L0d3, is however much less frequent and dates to only ~25 ka. Although it too is present in southern Africa, a single subclade, L0d3b, appears to be restricted to eastern Africa and is mostly seen in Tanzanian Sandawe (Gonder et al. 2007; Tishkoff et al. 2007), who speak a click-consonant language. The age of the clade is ~7.4 (SE 4.5) ka, based on HVS-I data (Rito et al. in preparation). Although the confidence intervals are very large – and with no clear linguistic evidence exists connecting southern and eastern click languages, although the possibility remains for the Sandawe (Güldemann 2008) – this genetic link to long-standing southern Khoe-San

populations might suggest an expansion of individuals speaking click-consonant languages from southern Africa into eastern Africa during the early to mid-Holocene, rather than a migration in the Pleistocene followed by contraction during the Holocene, as has been previously suggested (Tishkoff et al. 2007; Guldemann and Stoneking 2008), although the migration could have taken place any time between the age of L0d3 at ~25 ka and the age of the Sandawe clade (Figure 4D).

A mid-Holocene south-to-east dispersal has not been identified so far in other marker systems, or in the archaeological record, although it might explain the southern-African admixture detected in both East African click-consonant groups in the autosomes (Pickrell et al. 2012). However, dispersal in the reverse direction (separate from that of Bantu speakers, which we discuss below) has been proposed on the basis of MSY evidence. An east-to-south dispersal has been a long-standing hypothesis to explain the acquisition of sheep- (and subsequently cattle-) herding amongst southwest African foraging groups ~2 ka, slightly before the arrival of Bantu-speaking agriculturalists (Phillipson 2005). Henn et al. (Henn et al. 2008) identified a minor MSY haplogroup which they called E3b1f-M293, now known as E1b1b1g, which was most diverse in Tanzanian Nilotic and Afro-Asiatic-speaking groups. This suggested that it arose in East Africa, but it was also present in Khoe (or Kxoe) and Ju speakers ("!Kung"), dating (very approximately) to ~2 ka. One type was even shared between Khoe speakers and the Tanzanian Sandawe, who also speak a click-consonant language. This led them to propose a direct dispersal from Tanzania to the ancestors of Khoe-speaking herders in Angola/Namibia.

Although they argued that this dispersal was independent of the slightly later Bantu dispersals, and mediated by Nilotic speakers, an alternative for the emergence of herding in southern Africa would be exchange with the leading edge of the Bantu expansion, suggested on the basis of ceramic similarities (Phillipson 2005). Few mtDNA data are available from Khoe speakers, and they have drifted to such an extent that almost every haplogroup is represented by only a single control-region sequence (Chen et al. 2000; Güldemann and Stoneking 2008), but almost every single mtDNA sequence (in a sample of Khwe; outside the southern L0d and L0k lineages) directly matches a sequence from a Bantu speaker elsewhere in Africa. With the caveat that this is merely a preliminary look at a very limited dataset, this might support acquisition from pioneer Bantu-speaking groups, rather than a separate dispersal from East Africa.

This also illustrates, by the way, a significant point. Güldemann and Stoneking's (2008) suggestion that genetic drift confounds historical reconstruction applies much more strongly to the frequency-based approaches that they tend to stress, such as principal-components analysis, than to the genealogical approach emphasized here. The source of even a very heavily drifted lineage in the mtDNA genealogy can be readily identified phylogeographically, provided the source has been well-sampled. This latter point is important; in this case, for example, a much better characterization of the mtDNA variation of East African Nilotic (especially Southern Nilotic) speakers would be needed to clearly distinguish the alternative hypotheses. The suggestion of a predominantly southern genetic make-up with introgression from Bantu-speaking groups does, however, seem to be consistent with genome-wide autosomal data (Tishkoff et al. 2009; Pickrell et al. 2012; Schlebusch et al. 2012), albeit with possibly a smaller contribution from East African Nilotic speakers in some Khoe-speaking groups (Schlebusch et al. 2012); and an East African cluster shared with the click-consonant-speaking Sandawe is also evident in one recent data set (Petersen et al. 2013).

A possible scenario then is that the E1b1b1g MSY lineages were been assimilated into Bantu speaking groups in East Africa (where they are indeed present at lower diversity) and then dispersed southwards. Henn et al. argue that this is unlikely, since related lineages have not been found amongst central and southern African Bantu speakers; but perhaps the "pioneer phase" of the Bantu dispersal into the south may have differed in its MSY composition from groups that followed and gave rise to the majority of the Bantu-speaking populations in the south (Mitchell 2002; Phillipson 2005). If this were correct, then the dispersal may have been distinct from the main wave of Bantu expansion, but not entirely independent. Or perhaps "pastoralist" MSY lineages and "Bantu" mtDNA lineages in the Khoe speakers result from different episodes of introgression. Heterogeneity from group to group and even individual to individual is clearly very evident in the genome-wide data, emphasizing the need for larger sample sizes before drawing firm conclusions about dispersal histories. Hopefully it is clear though that whilst this issue, like many others we discuss, requires much more work, it is likely to be clarified considerably, and indeed in great detail, as more and more genetic data are brought into play.

Climate change and the out-of-Africa migration

One of the most important moments in human mtDNA evolution was the emergence of haplogroup L3. This clade gave rise to all of the ancient non-

African mtDNA lineages, which are entirely encompassed within haplogroups M and N (Macaulay et al. 2005). Given this, the age of L3 provides an upper bound for the out-of-Africa migration (Soares et al. 2012). L3 dates to between 60 and 70 ka with several methods (Soares et al. 2012) and is 61 ka in figure 1, but this estimate is based on only African lineages and seems to be an under-estimate due to the dramatic expansions of the L3e'i'x'k and L3b'd subclades. By chance, it seems that the most common African L3 subclades under-estimate the age of L3, whereas possibly the two non-African clades (M and N) might over-estimate it. The true age is likely to be ~70 ka, as estimated with ML when haplogroups M and N are included (Soares et al. 2009; Behar et al. 2012; Soares et al. 2012), better reflecting the four mutations between L3 and M (dating to ~55 ka) and the five between L3 and N (dating to ~60 ka).

Even so, the upper bound of the age of L3 virtually excludes an out-of-Africa dispersal (at least, for the maternal ancestry of non-Africans alive today) before ~74 ka, the time of the Mt. Toba volcanic super-eruption. Various archaeologists have proposed migrations out of Africa during MIS-5 (130–75 ka), either through the Levant (Baryosef 1992) or along the southern coastal route (Petraglia et al. 2007; Armitage et al. 2011), but if these putative events left any descendants living outside Africa in the present day, there is no sign of them in the maternal line of descent. Furthermore, the Y-chromosome also suggests a post-Toba out-of-Africa dispersal (Shi et al. 2010; Mellars et al. 2013).

Scally and Durbin (2012) suggest that the autosomes indicate an earlier exit, but this is based on erroneous reasoning. The date relies on a split between Yoruba (from West Africa) and non-Africans, which comes to 90–130 ka. However, West Africans diverged from eastern Africans well before the latter formed the source for the non-African gene pool, and indeed well before the emergence of L3. A simple estimate for the split time from mtDNA data would be the divergence between L3'4'6 and L2, which is indeed ~110 ka. In fact, though, these population divergence times are not appropriate for estimating the timing of the dispersal out of Africa. The mtDNA evidence shows that modern West Africans carry subclades of L3 (which arose since the dispersal out of Africa) living alongside more ancient lineages from L1 and L0. Even present-day eastern Africans would not be representative of the source of non-African mtDNAs, since L0 and L2 lineages have arrived from the south and west, since the time of the exit, presumably accompanied by autosomal lineages that would inflate any estimate of the divergence from non-Africans. The best current autosomal estimate for the timing of the dispersal from autosomal SNPs is, rather, the divergence of Europeans and Asians, at ~40–80 ka (Scally and Durbin 2012). An estimate from autosomal microsatellites is ~56 ka, with a 95% upper bound of 67.4 ka (Prugnolle et al. 2005).

The fact that the age of the out-of-Africa mtDNA clades, M and N, is so close to the age of L3 (Macaulay et al. 2005; Soares et al. 2009; Soares et al. 2012) – probably within ten thousand years or so – suggests that the diversification and expansion of L3 and the out-of-Africa expansion might be all part of a continuous demographic phenomenon (Figure 4C). L3 almost certainly had an origin in eastern Africa. The large ancestral clade L2'6, dating to ~130 ka, probably originated in eastern Africa, given the extant distribution of L5, L6 and L4, although L2, dating to more than 80 ka, is very likely West African in origin. If L2'6 arose in eastern Africa, this implies a migration from eastern Africa into West Africa, crossing central Africa between ~105 ka (the age of L2'6) and ~80 ka (the age of L2), whose signal mostly disappeared in central Africa (Figure 4B). This time frame does fit the separation between Yoruba (from West Africa) and non-Africans (originating from eastern Africans) at just over 100 ka in the recent autosomal dating referred to above (Scally and Durbin 2012). Another possibility for the route into West Africa is that this hypothetical migration occurred via the Sahel belt or North Africa. North Africa has very likely been depopulated and repopulated since the time of the Aterian industry (Bouzouggar et al. 2007; Pereira et al. 2010b; Henn et al. 2012), but shows very early evidence of symbolic behavior in the archaeological record (Barton et al. 2009). More important for the issue of L3 origins, the clade L3'4'6 shows clear evidence of an eastern African origin. L4 and L6 are primarily present in eastern Africa and the Arabian Peninsula (Kivisild et al. 2004; Torroni et al. 2006; Behar et al. 2008) and L3 itself also has several basal clades in eastern Africa (L3a, L3e'l'k'x and L3h in Figure 1). Furthermore, the central African clade or clades L3b'd and the two out-of-Africa clades M and N suggest an eastern African center of gravity (Soares et al. 2012).

It has been suggested that the moister climate after ~70 ka in eastern Africa led to a dramatic increase in population size (Mellars 2006; Cohen et al. 2007; Scholz et al. 2007),. This would in turn have given rise to the oldest clear signal of population expansion seen in the human mtDNA, the radiation of L3 (Behar et al. 2008; Soares et al. 2012), that led not only to the out-of-Africa expansion but also to the probable introduction of L3b'd and possibly L3e in central Africa after 60 ka (Soares et al. 2012) (Figure 4C). The model of Scholz and colleagues (Scholz et al. 2007), rather than others suggesting an earlier

successful exit in MIS 5 (Cohen et al. 2007), therefore provides a good fit to the mtDNA chronology.

Mellars (2006) has also coupled this phase with a step-change towards behavioral modernity by analogy to the European Upper Paleolithic, implying a single process of dispersal driving change from southern Africa into Eurasia. Although increasing evidence for modernity is most visible in southern Africa during the Middle Stone Age at about 70–80 ka (Henshilwood, d'Errico, Watts 2009; Texier et al. 2010), neither an origin for L3 in the south (Compton 2011) nor an expansion of L3 into the south (Mellars 2006), providing a link between eastern and southern Africa in this time frame, are at all likely on the basis of the extant mtDNA distributions. L0 is the only haplogroup that could show a link between southern and eastern Africa in the period 130 to 70 ka, but, as we discussed earlier, whether a south-to-north dispersal ~70 ka is feasible is far from clear, at least for the mtDNA.

North Africa and the "back-to-Africa" migration

North Africa stands distinct and unique in African prehistory, as it does not carry any surviving genetic traces connecting the Middle Stone Age to the present-day populations. Moreover, its mtDNA gene pool (strongly supported by Y-chromosome and autosomal data (Henn et al. 2012)) indicates that the re-population of North Africa occurred mainly from non-African populations, representing clearly a "back-to-Africa" migration (Olivieri et al. 2006; Pereira et al. 2010b; Henn et al. 2012; Bekada et al. 2013)

There is no doubt that North Africa was populated during MIS 5 and MIS 6. Some of the oldest fossils classified (at least, by some) as anatomically modern human (the Jebel Irhoud remains, dating to ~160 ka), have been found in Morocco (Smith et al. 2007). Archaeologically, there is evidence for modern symbolically-mediated behavior by at least ~80 ka (Bouzouggar et al. 2007; d'Errico et al. 2009). At the center of the question of continuity *vs.* discontinuity in North Africa over the last 100 ka is the identification of the bearers of the Aterian industry, recently dated to between 115 and 40 ka (Barton et al. 2009).

An analysis of the mtDNA gene pool of present-day North Africans points to only two specific haplogroups with deep Pleistocene ancestry in this part of the continent, haplogroups M1 and U6 (Macaulay et al. 1999; Olivieri et al. 2006). Haplogroup M1 is a basal clade of the non-African haplogroup M, while haplogroup U6 is even more deeply embedded within the non-African haplogroup N. The second of the L3-derived non-African lineages, haplogroup N, gave rise to another large subclade that is also found worldwide, haplogroup R (Macaulay et al. 2005). Haplogroup R evolved into haplogroup U, of which one of the subclades is U6. Most probably, N originated in Arabia immediately outside Africa, soon after the exodus (Fernandes et al. 2012) and the same is likely for the R and U subclades. Although haplogroup M (aside from M1) is not found in Arabia or the Near East, and in fact Pakistan is now the most westerly place where the rest of M is found, it may also have had an origin in the vicinity of the Arabian Gulf, alongside haplogroup N, in a glacial refuge or oasis where both M and N (and then R) diversified from L3 (Richards et al. 2006; Rose 2010; Fernandes et al. 2012).

Therefore the oldest mtDNA lineages in North Africa came from outside Africa, most probably the Near East. M1 dates to ~26 ka and U6 to ~35 ka (Soares et al. 2009), and these dates provide a lower bound for their entrance in North Africa. Since they both appear to have arisen within North Africa (Pennarun et al. 2012), the age of M (55–50 ka: Soares et al. 2009) and the age of haplogroup U (~55 ka: Soares et al. 2009), the ancestors of M1 and U6 respectively, provide upper bounds for the timing of the "back-migration". North Africa was therefore probably recolonized between 55 and 35 ka, assuming that the arrival of U6 and M1 was a single process (Figure 4C) (Olivieri et al. 2006) – which seems plausible but is not entirely clear (Pennarun et al. 2012). Genome-wide data also suggest that North Africa was recolonized in the Pleistocene from a Southwest Asian source, with a similar time frame for the "indigenous" North African lineages (Henn et al. 2012).

So it is clear that the people carrying U6 and M1 lineages are not descendants of the producers of the MSA Aterian industry (Barton et al. 2009). The time of their appearance would fit with the appearance of a Eurasian-style Upper Paleolithic blade industry, the Dabban, which appears before 40 ka in Cyrenaica (Close, Wendorf 1990; Macaulay et al. 1999; Bar-Yosef 2002; Olivieri et al. 2006; Lowe et al. 2012). Since the arrival time is not closely constrained by the presence of obvious antecedent lineages in the Near East, the age of U6 and M1 probably depend primarily on genetic drift within North Africa, and do not make the posited association with the Dabban less plausible (Pennarun et al. 2012) – indeed, they seem to require it, if this is the only attested post-Aterian North African industry of this antiquity. Bayesian skyline plots (BSPs) of haplogroup U6 (Pereira et al. 2010b) and M1, which use genetic diversity to infer population-size changes (Atkinson, Gray, Drummond 2008), also suggest population growth ~20–25 ka, coinciding with the beginning of the Iberomaurusian industry in the Maghreb (Blockley et al. 2006; Bouzouggar et al. 2008). The

pattern is not identical for U6 and M1, possibly implying distinct trajectories (Pennarun et al. 2012) – although the autosomal picture from STRUCTURE-like analyses, at least at *K* = 8, implies a single autochthonous North African cluster (Henn et al. 2012). This kind of analysis partitions autosomal datasets into genetic clusters, putatively representing ancestral populations, with the clusters defined by the software but the number of clusters identified (*K*) defined by the user.

The Iberomaurusian in the Mahgreb dates to ~22 ka and overlies a non-descript MSA flake industry, from which it is separated by a sterile layer of several thousand years; and which itself overlies the Aterian (Barton et al. 2013). The pattern with U6 and perhaps also M1 implies that the modern humans who made the MSA industries were not the ancestors of those who made the Iberomaurusian, but rather that these autochthonous North African lineages spread from further east, most likely from the makers of the Dabban industry, with an ultimately Southwest Asian ancestry – at least for U6 (the source for M1 is unresolved). The fact that the Iberomaurusian is presently dated older in the Mahgreb than in Cyrenaica complicates the picture, but may either suggest further reverse dispersals, or exchange along the Mediterranean coastline. Alternatively, there may be older Iberomaurusian sites awaiting dating further east; it has been suggested that the industry may date to ~19 ka at Haua Fteah in Libya (Barker et al. 2010). Further lineages were introduced from Iberia in the early Holocene, spreading subsequently from the Mahgreb into the Sahel belt (Ottoni et al. 2010; Pereira et al. 2010a), and more recently (perhaps at least partly with the Arab conquests) also from the Near East (Henn et al. 2012).

The suggestion that M1 may have been introduced after the LGM, carried alongside Afro-Asiatic languages (Forster 2004; Forster and Romano 2007), seems less likely, since the major subclade M1a appears to have arisen within eastern Africa and dates to ~20 ka (Forster and Romano 2007; Pennarun et al. 2012). The picture overall suggests that the people carrying U6 were likely responsible for the production of the Dabban industry into North Africa and the subsequent spread west of the Iberomaurusian industry. The links back to a Near Eastern source and the Eurasian Upper Paleolithic may partly explain the suggested similarities between the robust Iberomaurusian "Mechta-Afalou" burials and European Cro-Magnon remains (Irish 2000).

The Pleistocene/Holocene transition in Africa

The late Pleistocene/early Holocene transition, ~11.5 ka, has been hypothesized from the mtDNA evidence as being a period during which major population expansions occurred across Eurasia, from Europe (Soares et al. 2010) to the Pacific (Soares et al. 2008; Soares et al. 2011). Africa is most probably not greatly different in this respect, as we have already suggested using both haplogroup L3 data (Soares et al. 2012) and U6 data from North Africa (Pereira et al. 2010b). For this chapter, we conducted two additional kinds of analysis in order to test this hypothesis further. One was a BSP analysis for the four major clades in Africa, L0 to L3, in order to observe which periods suggested population expansions associated with these haplogroups (Figure 5). We also calculated a plot representing a random sampling of the available sequences, for comparison.

The second was a founder analysis, aiming to detect periods of migration between two regions (Richards et al. 2000). One difficulty with founder analysis is defining source and sink regions, and this is particularly acute for Africa where there has been substantial gene flow across the continent throughout prehistory. For the last 20 ka or so, however, some broad haplogroup distributions within Africa can be established: L1, L2, L3b'd and L3e are found in central/West Africa; L4, L5, L6, L0a'b'f and L3 (except L3b'd and L3e) are found in eastern Africa, and L0d and L0k are restricted to southern Africa. North Africa meanwhile harbors the "back-to-Africa" U6 and M1 lineages, with some lineages from south of the Sahara; the majority are more recent migrants from Europe and the Near East. We therefore used the founder analysis and an HVS-I dataset of nearly ten thousand African individuals to check if migrations occurred between the different regions.

We performed the following founder analyses: (a) from eastern Africa to central Africa for the eastern African haplogroups; (b) from central/West Africa into eastern Africa for L1, L2, L3b'd and L3e; (c) from central, West and eastern Africa to North Africa for all the Sub-Saharan lineages and (d) from central to West Africa for L1, L2, L3b'd and L3e. The latter is much less well-defined than the others, since the L1 and L2 tree suggests that it is difficult to identify with any confidence the source or sink for many links, but even so the founder analysis can point to common clades that expanded more extensively in the region. We then performed a final founder analysis (e) which considered all haplogroups moving into southern Africa.

The results are displayed in figure 6. We discuss them in what follows; the more general reader may skip to the summary at the end of this section. Since, apart from the southern African founder analysis, the results correspond to only a fraction of the population profile (excluding the autochthonous haplogroups of each region over the last 20 ka) we

will not refer to frequencies of the founder in the analysis, but simply indicate the major founders contributing to each migration.

The Late Glacial period in tropical Africa is now thought to have gone through a mega-drought between 16 and 17 ka comparable to that observed before 70 ka (Stager et al. 2011). From ~11.5 ka and for a few thousand years thereafter, the climate was warm and humid, except for the northern and southern extremes of the continent (Kuper, Kropelin 2006; Weldeab et al. 2007). The Holocene climatic optimum would likely have allowed populations to expand, and movements of people probably took place at this time. We detected the strongest population expansions in the time window of 15 to 8 ka in the random dataset and in the L3 data. The L2 data also indicated a population expansion from ~12 ka until recent times, but (probably due to poor phylogenetic resolution) it was not separated clearly from the more recent increase observable in all the data (probably due to the Bantu expansion, as discussed in the next section). Haplogroups L0 and L1 did not show any signal of expansion until the last few millennia before the present, again with the Bantu expansions. However, some subclades of these haplogroups were indeed likely to have been involved in postglacial expansions, as we discuss below.

The migration scan from eastern Africa to central Africa (Figure 6A) reveals a clear single peak at ~11 ka, closely matching the onset of more humid conditions in tropical Africa. Lineages from two major clades, L3f and L0a, dominate the results for this peak (Figure 4D). The distribution of L3f3 has previously been highlighted as possibly representing a pastoralist migration (Cerny et al. 2009), but the age estimates here suggest that its expansion might have been earlier. We have already pointed to L3f as a signal of postglacial expansions from eastern Africa to central Africa (Soares et al. 2012), but the results here show that lineages from the L0a clade are equally represented in these migrations.

The analysis of the whole-mtDNA tree supports this result: the L0a1a clade, dating to about 16.5 ka, shows a mainly central African distribution, although with some possibly basal clades in eastern Africa. Its derived subclade, L0a1a2, lives in central Africa and dates to 13.4 [8.4;18.5] ka, similar to the time obtained in the founder analysis. The L0a1b'c'd clade has two subclades that are found in eastern Africa (L0a1c and L0a1d,) but the third (L0a1b) is central African and dates to 14.8 [7.6;22.3] ka. In L0a2, several other lineages might also have moved in this period. L0a2b, dating to only 5.5 [1.3;9.7] ka, is present in central African forest forager groups, but shares a link with eastern Africa dating to ~18 ka. L0a2a1 (dating to 14.2 [7.6; 21.0] ka) is mostly central African. An important issue to note here is that, apart from L2 lineages in central Africa, L0a lineages will be the most important mtDNA components on the migration south during the Bantu expansion.

The migration scan from central Africa to eastern Africa (Figure 6B) again indicates a major peak at ~10 ka, and a second one close to the present. A minor peak seems to be located between the two, at ~2.2 ka, visible as a small hump. We previously detected a peak containing L3b and L3d, probably related to gene flow from Bantu speakers from central/West Africa into the east (Soares et al. 2012). These lineages still show the same signal, but the signal of haplogroup L2 is much stronger in the present dataset, and a postglacial signal at ~10 ka is much more striking in the new analysis (Figure 4D). L2a1 is the lineage that provides most of the signal: more specifically, the lineage or lineages carrying the variant (relative to the Cambridge Reference Sequence) at position 16189, and those carrying both the 16189 and 16192 variants.

It is difficult to check with confidence the whole-mtDNA genome tree on this issue, for two reasons. One is the fact that the sampling in the tree is biased (since samples are rarely selected at random for whole-mtDNA sequencing), and there are not many L2 sequences available at present from eastern Africa. The second is the fact that these HVS-I sequences match two independent subclades within haplogroup L2a1, L2a1+143+16189(+16192) and L2a1+16189(+16192). However, the former (L2a1+143+16189, dating to 15.3 [9.9;20.8] ka) and its derived subclade with the 16192 variant (dating to 12.5 [8.3;16.8] ka) show basal eastern African (or Arabian) lineages or subclades that roughly support the founder analysis results with HVS-I data. The third most frequent founder is another subclade of L2, L2a1d, which appears to belong to eastern Africa in the whole-mtDNA genome tree and dates to 11.5 [4.7;18.6] ka.

A migration scan from tropical Africa to North Africa (Figure 6C) indicates a smaller recent peak, possibly related to the recent slave trade across the Sahara (Harich et al. 2010), and a major one dating to ~6.5 ka (Figure 4D). Several lineages display founder age estimates that suggest an arrival during the mid-Holocene. However, in the two founder analyses described above, only a few lineages were responsible for most of the signal. Here in addition to two or three frequent lineages there is also an array of lineages with intermediate frequencies which probably also entered North Africa in the Holocene, suggesting that the Sahel belt was probably home to extensive gene flow at this time (Cerny et al. 2007).

We focus on the three major founders. The most frequent is the HVS-I root type of L1b. It is difficult to

know here if we are looking at several dispersing lineages or just a single major one (given the weak phylogenetic resolution of HVS-I), so the dating is uncertain. Even so, if the founder age (~9 ka) were indeed an average of several lineages, it would still be hard to reconcile with a mixture of lineages some of which arrived in the Pleistocene (which would be very unlikely due to the strength of the Sahara barrier) and some in much more recent times; so the early Holocene is still the most probable time for the arrival of L1b. L1b1a is by far the most frequent of the L1b subclades, and since it does not display any defining HVS-I motif, it matches the HVS-I founder type. L1b1a dates to 11.8 [8.5;15.1] ka in the whole-mtDNA tree, and it displays several nested starlike subclades that might suggest expansion (although not detected in the BSP analysis of L1). But very few North African sequences are yet available in the L1b whole-mtDNA tree, even though L1b can reach frequencies up to 5-10% in some North African populations.

The second most common HVS-I lineage showing an arrival in North Africa in the early Holocene is L3e5 (Soares et al. 2012, Podgorna et al. in press). This lineage is mainly restricted to Northwest Africa, but is also found in central Africa, where it probably arose (Podgorna et al. in press), and it dates to ~12 [8.8-15.2] ka. The third most frequent founder is L0a1, due to its high frequency in Egypt and the vicinity. It is possible that L0a1 dispersed directly from eastern Africa into Northeast Africa, but the whole-mtDNA tree suggests that the L0a1 subclade in North Africa matches the one found in central Africa that we mentioned above, L0a1b (in the founder analysis from eastern to central Africa). A movement from North Africa to central Africa is also possible. It is worth mentioning that the next two most frequent Holocene founders in North Africa also match founders detected as participating in postglacial migrations above, the L3f and the L2a1 founders that were detected in central and eastern Africa respectively. This implies that we are most probably detecting a single major process of expansion that spread in several directions at the same time.

A scan between central and West Africa (Figure 6D) indicates two peaks, one at about ~2.5 ka and the second, more major, one at ~9.5 ka. It is difficult to judge whether or not the directionality of the migration we have imposed (central to West Africa) is correct for many of the lineages (in particular, within L2, which seems to be of overall West African origin). But it does indicate that postglacial range expansions were probably also occurring between central and West Africa. The major contributor to this signal is the L2 HVS-I root type, which should mostly include members of L2c (again, it does not contain any defining HVS-I motif). This clade dates to 18.4 [14.4;22.6] ka and the star-like pattern, which is also observed in its major subclades, suggests an early expansion. Another major founder is the root type of L3b1, which is central African in origin. A third is L3e4, also of central African origin, but very poorly represented in the whole-mtDNA trees.

The final scan (Figure 6E) corresponds to a full population founder analysis for southern African populations. The small hump at ~50 ka corresponds mainly to L0d. L0d is much older than this, but it is difficult to date HVS-I sequences much beyond ~40–60 ka due to saturation, where back-and-forth recurrent mutation begins to swamp the signal. In any case, the important point is that between this ancient peak and the much stronger second peak at ~2 ka there is no signal of any genetic input into southern Africa from more northerly populations whatsoever. (Minor early Holocene expansions seem to have occurred in the opposite direction, from south to east, perhaps taking click-consonant languages into eastern Africa earlier in the Holocene, as discussed above.)

In summary, the BSPs and the founder analyses suggest that the late Pleistocene and early Holocene were periods of major gene flow between populations in West, central, eastern and North Africa, accompanied by population growth. Southern Africa is exceptional, suggesting by contrast a history of continuous isolation and lack of any demographic growth signal throughout this period, despite archeological evidence for an increase in the number of sites and areas occupied in the early Holocene. A similar pattern is evident in a much larger recently published sample from across southern Africa. Minor recent growth signals in some L0d and L0k lineages may be the result of their incorporation into Bantu communities; indeed some of the rarer L0k subclades have been more commonly found in Bantu speakers today, but must have been assimilated from indigenous southern Africans within the last 2 ka or so (Barbieri et al. 2013).

Late Holocene dispersals

The most recent major demographic phenomenon to reshape the genetic landscape of sub-Saharan Africa is thought to have been the so-called “Bantu expansion”, which was attested both linguistically and archaeologically before it was investigated genetically (Heine and Nurse 2000; Pereira et al. 2001; Salas et al. 2002; Phillipson 2005). There has been a great deal of controversy about the origins and spread of the Bantu languages, which are dispersed over a huge swathe of sub-Saharan Africa from roughly Cameroon in the west to Kenya in the east and down to South Africa (Phillipson 2002;

Eggert 2005; Phillipson 2005; Holden and Gray 2006; Marten 2006). Bantu languages have been assigned a source in the Cross-Benue region of northwest-central Africa purely on the basis of lexical comparisons, initially by Greenberg (Greenberg 1963), and the comparative method (which is standard in, for example, Indo-European and Austronesian studies) has never been applied. Although the Cameroon origin is widely accepted, it is not reflected in the internal diversity within the Bantu subgroup, and the substructure – which has huge implications for the proposed pattern of dispersal of the speakers – has been difficult to pin down, likely due to rapid radiation in the Western Bantu languages (thought to be due to coastal and riverine dispersals) and extensive borrowing, likely to some extent within the context of dialect chains, in the East and eastern-central languages, followed by rapid starburst radiation once again in the south (Holden and Gray 2006).

Nevertheless, even using lexical data, and in particular by using network rather than tree models to reconstruct relationships (Holden and Gray 2006), some broad outlines are widely agreed (Nurse 1997), although circular reasoning between archaeologists and historical linguists (and now also geneticists) remains an issue in this field, in the same way as has been the case with studies of Austronesian languages (Oppenheimer and Richards 2001; Eggert 2005). The agriculturalist expansion may have started perhaps ~5–4 ka from the region of the Cameroon/Nigeria border (Barker 2006), but the early stages are attested primarily on the basis of the languages, as the forest zone has so far yielded rather little in the way of archaeological evidence. There was an initial (but archaeologically invisible) dispersal from west to east, either north or south of the rainforest, reaching the Great Lakes region of Uganda by ~3 ka. In Kenya and northern Tanzania – although there is no archaeological evidence for this in Uganda – the local communities were already herding cattle. The early settlers may have been already beginning to cultivate cereals which could supplement the tuber crops (and perhaps also some cereals such as millet) presumed to have been brought from Cameroon, as well as becoming familiar in the following centuries with iron-working (Vogel 1997b; Holden 2002; Phillipson 2005; Holden, Gray 2006). With this combination of new and existing elements of a farming economy, controversy has centered primarily on the extent to which the process was fuelled by large-scale migrations or by smaller-scale processes involving contact and assimilation (Vansina 1995; Eggert 2005).

Populations expanding into the south have been most evident on the eastern side of the continent (Pereira et al. 2001; Phillipson 2005), within the last 2.5 ka. The signature of this in the archaeological record is widely agreed to be Phillipson's Early Iron Age "Chifumbaze complex", which arose to the west of Lake Victoria ~500–200 BC (Phillipson 2005). This expanded rapidly into central and southern Africa over a period of a few centuries, ~2 ka, reaching Mozambique by ~1.8 ka and South Africa, where the limits of the summer rainfall belt were reached, by ~1.5 ka (Vogel 1997a; Phillipson 2005). The Eastern Bantu languages are thought to have been distributed by this "eastern stream" of dispersal. An earlier dispersal south via the river system into the rain-forest, from the Cameroon region by ~3.5 ka, the "western stream", may have been responsible for the spread of the Western Bantu languages as far south as Angola (Vansina 1995; Vogel 1997b; Phillipson 2005), with the two streams intermingling across central Africa.

The Bantu expansion is clearly attested in the mtDNA record (Bandelt et al. 2001; Pereira et al. 2001; Salas et al. 2002; Plaza et al. 2004; Beleza et al. 2005), as we can see in the skyline plots discussed in the last section. There is a sharp increase in all of the major tropical African clades in the period between 1–4 ka (Figures 4A, 4B, 4C, 4D). Haplogroup L2 (Figure 5C) shows a continuum from a population expansion that began ~12 ka, but even so a population-size increment is observable in the late Holocene. Not surprisingly a random sampling of African samples shows this same steep increment (Figure 5E).

Our analyses suggest that southern Africa was mostly isolated for around the last 150 ka, since gene flow in this period probably occurred only from south to north, with the possible exception of the pastoralist dispersal from East Africa discussed above. Here, however, the effect of the Bantu expansion was massive. Bantu speakers in Mozambique carry almost entirely lineages from the north, although there is a much higher level of assimilation of L0d and L0k lineages in South Africa. L0d is common in many more southern Bantu groups and, as mentioned above, some southern lineages such as L0k2 are seen mainly in Bantu speakers, even though we can plausibly assume that they descend from much earlier southern African settlers. Khoe-San populations display the most distinctive mtDNA profiles in southern Africa, with haplogroup L0d dominating, but even in these groups some minor genetic input from Bantu-speaking populations can be seen (Salas et al. 2002; Tishkoff et al. 2009).

In the founder analysis, we obtained a well-defined peak at ~2.4 ka, which, given the clear archaeological picture, provides some level of corroboration for both the method and the molecular clock we have employed, albeit slightly preceding the archaeologically dated arrival in the far south. The

most common founder cluster detected was L2a1b1 (8.2%). This clade is, unfortunately, under-represented in the whole-mtDNA tree, but it does include two samples from Mozambique and one from Kenya, and dates to ~2.6 ka overall, supporting the founder analysis. A second founder cluster from L2 that also shows a significant frequency is L2a1a2 (5.1%). This clade dates to 8.6 [5.6;11.6] ka, and it also includes southern African samples, although insufficient at present to test the time of the expansion into the south using whole-mtDNA genomes. The clade has mostly West African representatives but central and eastern lineages are much less well-characterized at the whole-mtDNA level.

The second and fourth most common founders in the dataset are within the L0a haplogroup. One (at 4.0%) is L0a1 in the HVS-I, but most probably corresponds to L0a1b in the whole-mtDNA tree, where there is a fair number of southern African representatives. The other one, which is the more common (7.7%), is the HVS-I root of L0a. Inspection of the whole-mtDNA tree suggests that it most probably corresponds to L0a2a. These two founders were major components of a postglacial dispersal from eastern to central Africa, so disentangling where they were picked up by Bantu speakers is a challenge that will require further data and analysis. It remains possible that they may be the result – at least in part – of the original Bantu arrivals in the inter-lacustrine region of eastern Africa coalescing with the indigenous Great Lakes herding populations (Salas et al. 2002), but despite their ultimate eastern African ancestry, their distribution suggests that many of the lineages might have been assimilated within central Africa during the Bantu spread southwards (Figure 4E).

Broadly, the results for the expansion into the far south match the combined evidence of archaeology and linguistics quite closely. As already mentioned, this concordance (which rarely arises, except in other particularly straightforward dispersal scenarios, such as the settlement of virgin territory in the Remote Pacific, or an expansion facilitated by the use of iron-working, as here) is extremely valuable for validating the genetic methodologies. This in turn comes into its own when other lines of evidence are less forthcoming. It should be noted though that this example can be compared to the spread of Austronesian languages in another way. The final stages of the expansion, involving profound founder effects into effectively empty space are rather clear; this is not to dismiss the role of the indigenous population but, as we have said, the evidence suggests that southern Bantu-speaking groups largely carry genetic lineages from outside the region. However, the earlier stages of the putative linguistic dispersal (in central Africa, as in island Southeast Asia) are far more difficult to disentangle. Some geneticists doubt whether there was ever an "Austronesian expansion" in the sense proposed by historical linguists – that is, all the way from Taiwan to Oceania (Soares et al. 2011) – and it is not yet entirely clear whether the situation with Bantu speakers – outside southern Africa, at least – might be analogous in this regard too.

The advantage of the genetic analyses in this context is that, again as in Southeast Asia, they can also begin to illuminate the complexities of the Bantu expansion so far undisclosed by archaeology, providing a line of evidence independent of the linguistics. The founder analysis from central/West Africa to the east establishes several possible founder lineages for Bantu speakers (the most frequent being L3e3 and L2a2), but at low levels in the sampled populations. This is not surprising, since the impact of Bantu speakers on eastern Africa, where herding populations were already taking hold, was much less profound than in the south. In West Africa, during the same period, some minor founders from central Africa can be detected in clades L3e2, L2a, L3d and L2c, but with no suggestion of a large-scale migration, considering the small size of the peak at this time.

We can now reassess the demographic impact of the Bantu expansions, and in particular the extent of assimilation of indigenous populations in eastern and central Africa (Newman 1995). Both earlier mtDNA analyses and genome-wide autosomal analyses have suggested a substantial eastern African input into southern African Bantu-speaking populations, implying heavy levels of assimilation of local populations after Bantu-speaking groups arrived from further west (Salas et al. 2002; Tishkoff et al. 2009), but our present analysis points to a primary source in central Africa (although the precise location remains uncertain) and questions the scale of eastern African assimilation.

It is also very difficult to make a clear distinction between western and eastern streams, although there seems to be a more diverse array of central African mtDNA lineages in the southwest (including a much higher level of central African L1c lineages) and fewer instances of strong founder effect than those from the southeast (Plaza et al. 2004; Richards et al. 2004; Beleza et al. 2005). There is no trace to be seen of Khoe-San (L0d/k) introgression in this region (Plaza et al. 2004). Our analyses here emphasize the role of central Africa, since it seems that many eastern lineages, especially within L0a, had expanded into central Africa, as far as Cameroon, by the early Holocene.

Some Y-chromosome analyses have also suggested a more profound signal of expansion from central/West

Africa, unlike the mtDNA largely erasing the signal of earlier populations in central Africa (Berniell-Lee et al. 2009). A correlation has been suggested between parts of the MSY tree and the linguistic tree for not only Bantu languages, but Niger-Kordofanian more generally (de Filippo et al. 2011), but recent analyses here too have also complicated the picture by demonstrating unexpectedly high levels of diversity in the western forest zone (Montano et al. 2011) and links between central African forest foraging populations and southern African Bantu speakers, as with the mtDNA (Batini et al. 2011). Without secure genetic dating for the MSY, it is difficult to test whether or not links between distinct foraging groups in central and southern Africa, for example, are evidence for ancient common ancestry or due to assimilation and dispersal by Bantu speakers, although progress is being made (Batini et al. 2011). The autosomal data are also throwing up intriguing complexities (Sikora et al. 2011). It appears, then, that even this very recent, and in many ways quite clearly attested, expansion presents a highly complex genetic picture that will require far more work to elucidate it clearly.

Final remarks

As a last comment, pulling back and looking at African mitochondrial phylogeography more generally, it is worth drawing attention to the peculiarity of the history of haplogroup L0. L0 had an origin in southern Africa ~140 ka ago, migrated into eastern Africa in the form of L0a'b'f between 130 and 75 ka, and evolved into L0a in eastern Africa ~45 ka, not long after the out-of-Africa dispersal occurred. In the early Holocene, several L0a clades migrated into central Africa when the climate improved, and they later became an important component of the Bantu-speaking agriculturalist populations that would migrate south within the last two millennia – bringing L0 back to the south in a quite different form (L0a) to the ones that evolved *in situ* (L0d and L0k).

L0 therefore bears witness to some of the most significant events in the demographic history of sub-Saharan Africa, and is unique in this respect (Rito et al. in preparation). This illustrates the challenge in reconstructing prehistoric movements in Africa from mtDNA variation, but also the extent to which, even in the face of such palimpsest-like patterns, the challenge is beginning to be met. Geneticists will never have all of the answers, and in the past have not even always managed to address the right questions. Even so, we are convinced that, with much more extensive and careful sampling, along with closer inter-disciplinary collaboration with archaeologists, climatologists, anthropologists and linguists, the potential for studies of genetic variation to help resolve many of the issues we have discussed here should not be under-estimated.

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Figure legends

Figure 1. Schematic tree of the African mtDNA diversity. Age estimates were calculated using maximum likelihood in PAML (Yang 1997) and the molecular clock corrected for purifying selection described by Soares et al. (Soares et al. 2009).

Figure 2. Frequency distribution of haplogroups L0 (A), L1 (B), L2 (C) and L3 (D) plotted using the Kriging algorithm in Surfer software.

Figure 3. Mean pairwise differences of the HVS-I of mtDNA across Africa. Data was plotted using the Kriging algorithm in Surfer.

Figure 4. Outline sketch of the major human dispersals within Africa suggested by mtDNA phylogeography. Arrows indicate directionality only and are not intended to represent migratory routes. Point estimates for the ages of each clade are based on the tree in Figure 1. Age estimates of haplogroup U, U6 and M1 are from Soares et al. (2009), calculated using the same methodology. Estimated dispersal times displayed within the arrows were obtained using HVS-I data and a founder analysis approach (Richards et al. 2000). Selected time intervals were chosen solely in order to provide a clear representation. The periods are: 200 to 120 ka (A), 120 to 70 ka (B), 70 to 30 ka (C), 30 to 5 ka (D) and 5 ka to present (E).

Figure 5. Bayesian Skyline Plots of haplogroups L0 (A), L1 (B), L2 (C), L3 (D) and random sample (E).

Figure 6. Founder analysis migration scans for migrations from eastern Africa to central Africa (A), from central/West Africa into eastern Africa (B), from central, West and eastern Africa to North Africa (C), from central Africa to West Africa (D) and from central/eastern Africa into southern Africa (E).

Figure 1.

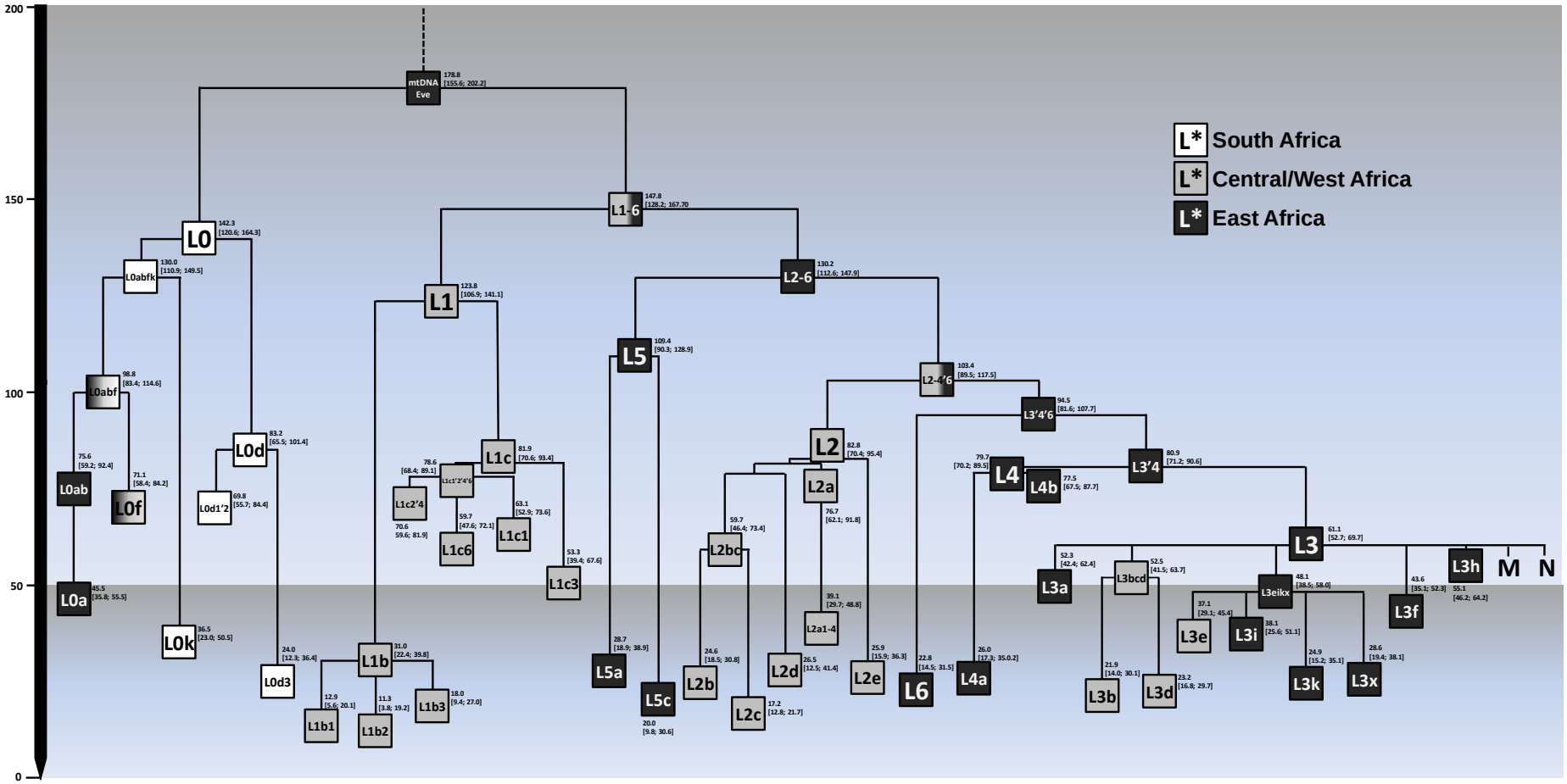

200
150
100
50
0
mtDNA Eve
178.8 [155.6; 202.2]
L0
142.3 [120.6; 164.3]
L0abfk
130.0 [110.9; 149.5]
L0abf
98.8 [83.4; 114.6]
L0ab
75.6 [59.2; 92.4]
L0f
71.1 [58.4; 84.2]
L0a
45.5 [35.8; 55.5]
L0k
36.5 [23.0; 50.5]
L0d
83.2 [65.5; 101.4]
L0d1'2
69.8 [55.7; 84.4]
L0d3
24.0 [12.3; 36.4]
L1-6
147.8 [128.2; 167.70
L1
123.8 [106.9; 141.1]
L1b
31.0 [22.4; 39.8]
L1b1
12.9 [5.6; 20.1]
L1b2
11.3 [3.8; 19.2]
L1b3
18.0 [9.4; 27.0]
L1c
81.9 [70.6; 93.4]
L1c1'2'4'6
78.6 [68.4; 89.1]
L1c2'4
70.6 59.6; 81.9
L1c6
59.7 [47.6; 72.1]
L1c1
63.1 [52.9; 73.6]
L1c3
53.3 [39.4; 67.6]
L2-6
130.2 [112.6; 147.9]
L5
109.4 [90.3; 128.9]
L5a
28.7 [18.9; 38.9]
L5c
20.0 [9.8; 30.6]
L2-4'6
103.4 [89.5; 117.5]
L2
82.8 [70.4; 95.4]
L2a
76.7 [62.1; 91.8]
L2a1-4
39.1 [29.7; 48.8]
L2bc
59.7 [46.4; 73.4]
L2b
24.6 [18.5; 30.8]
L2c
17.2 [12.8; 21.7]
L2d
26.5 [12.5; 41.4]
L2e
25.9 [15.9; 36.3]
L3'4'6
94.5 [81.6; 107.7]
L4
79.7 [70.2; 89.5]
L4b
77.5 [67.5; 87.7]
L6
22.8 [14.5; 31.5]
L4a
26.0 [17.3; 35.0.2]
L3'4
80.9 [71.2; 90.6]
L3
61.1 [52.7; 69.7]
L3a
52.3 [42.4; 62.4]
L3bcd
52.5 [41.5; 63.7]
L3b
21.9 [14.0; 30.1]
L3d
23.2 [16.8; 29.7]
L3eikx
48.1 [38.5; 58.0]
L3e
37.1 [29.1; 45.4]
L3i
38.1 [25.6; 51.1]
L3k
24.9 [15.2; 35.1]
L3x
28.6 [19.4; 38.1]
L3f
43.6 [35.1; 52.3]
L3h
55.1 [46.2; 64.2]
M
N
L* South Africa
L* Central/West Africa
L* East Africa

Figure 2.

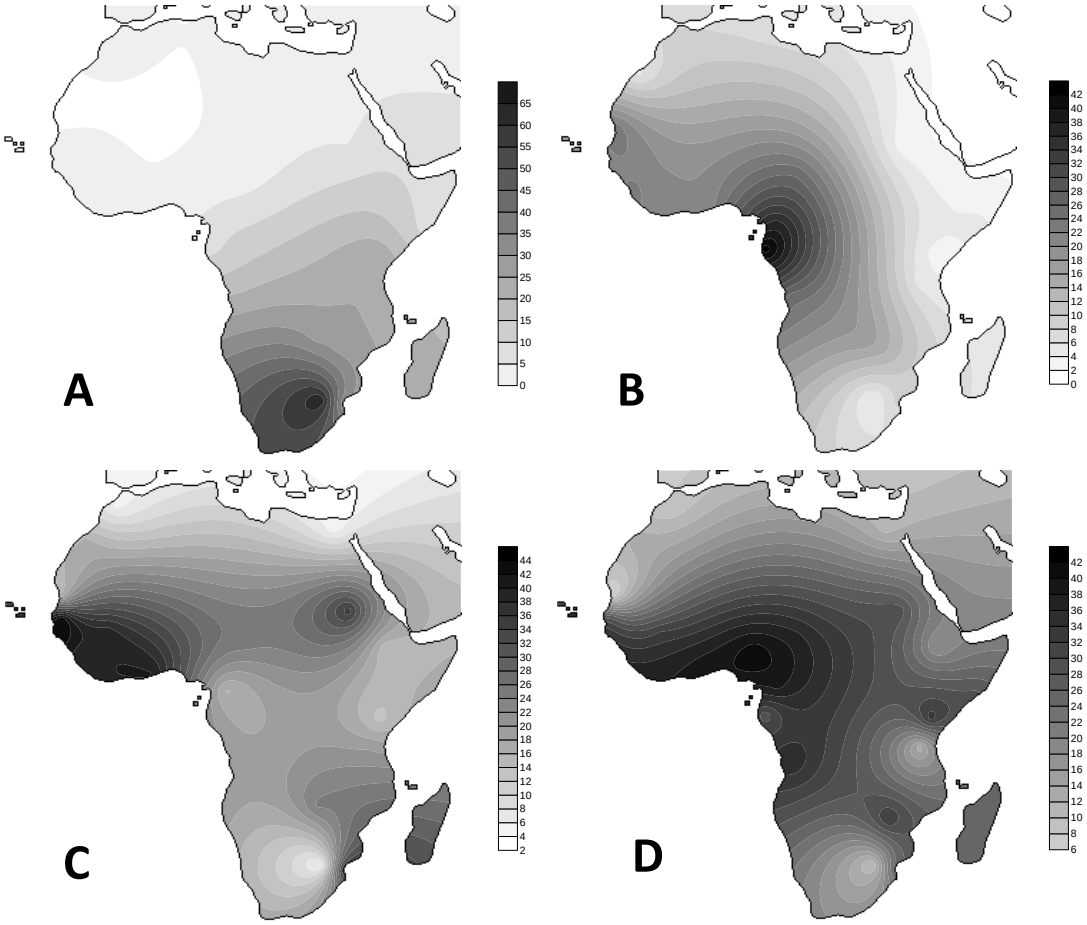


Figure 3.

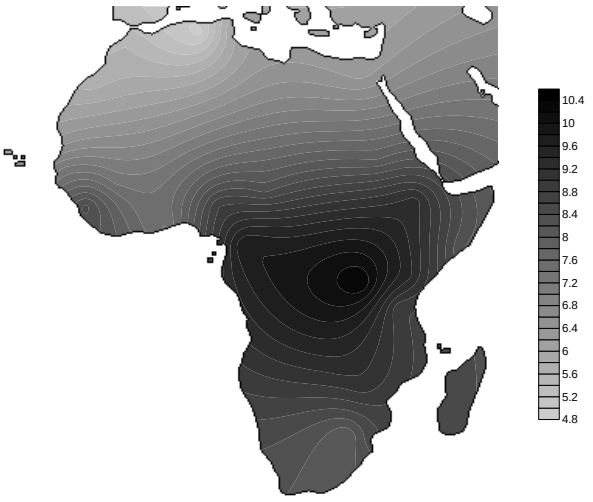


Figure 4.

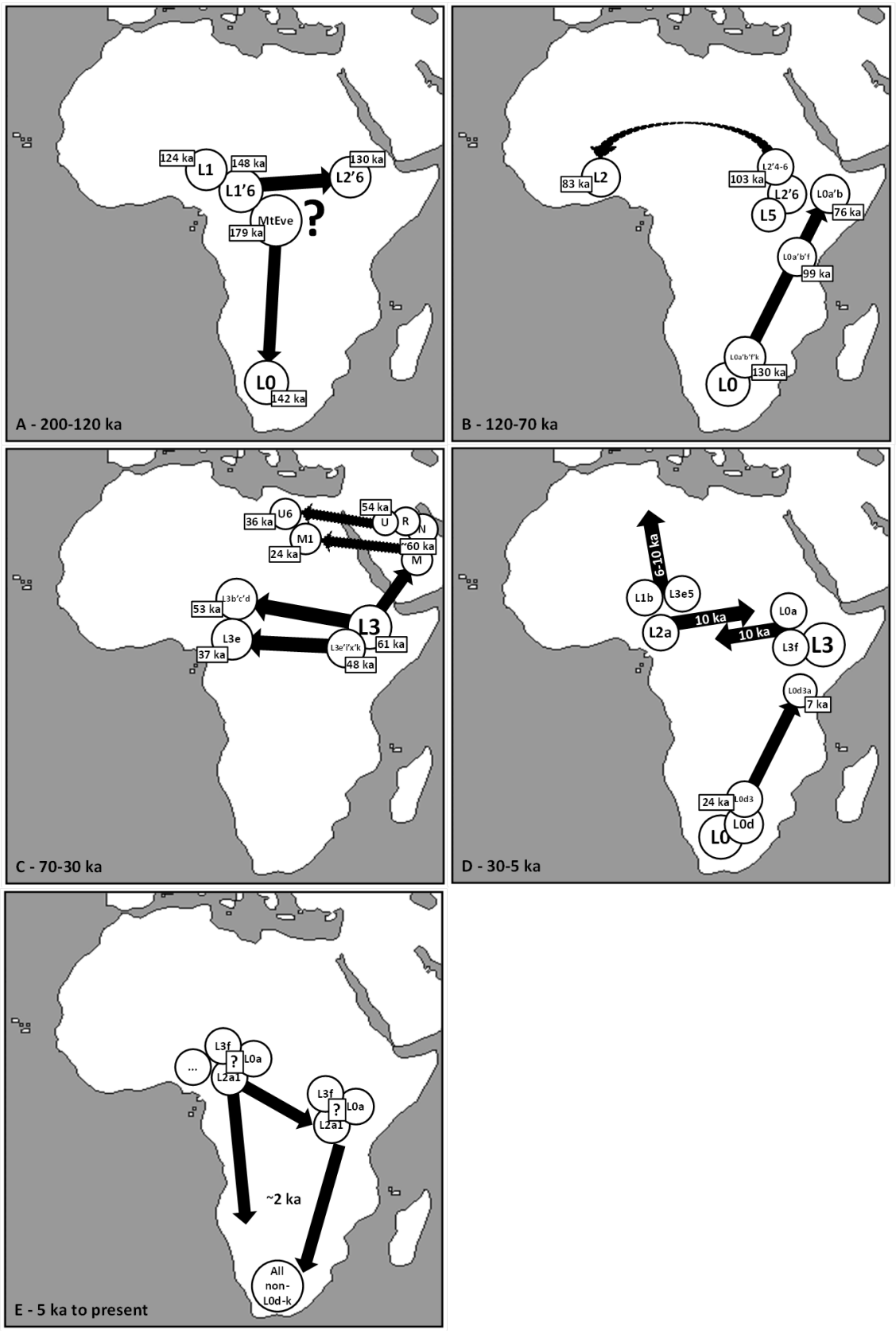

124 ka
L1
148 ka
L1'6
130 ka
L2'6
MtEve
?
179 ka
L0
142 ka
A - 200-120 ka
83 ka
L2
103 ka
L2'4-6
L2'6
L5
L0a'b
76 ka
L0a'b'f
99 ka
L0a'b'f'k
130 ka
L0
B - 120-70 ka
54 ka
U6
36 ka
U
R
N
M1
~60 ka
24 ka
M
L3b'c'd
53 ka
L3
L3e
37 ka
L3e'i'x'k
61 ka
48 ka
C - 70-30 ka
6-10 ka
L1b
L3e5
L2a
10 ka
10 ka
L0a
L3f
L3
L0d3a
7 ka
24 ka
L0d3
L0d
L0
D - 30-5 ka
L3f
...
?
L0a
L2a1
L3f
?
L0a
L2a1
~2 ka
All non-L0d-k
E - 5 ka to present

Figure 5.

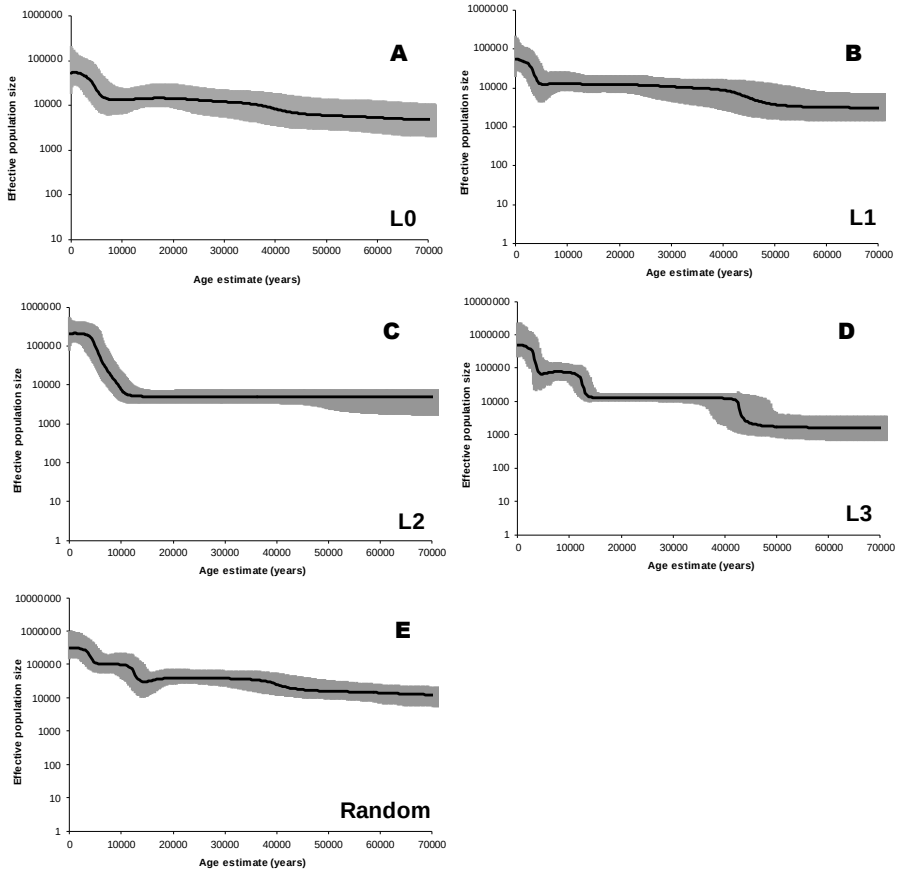
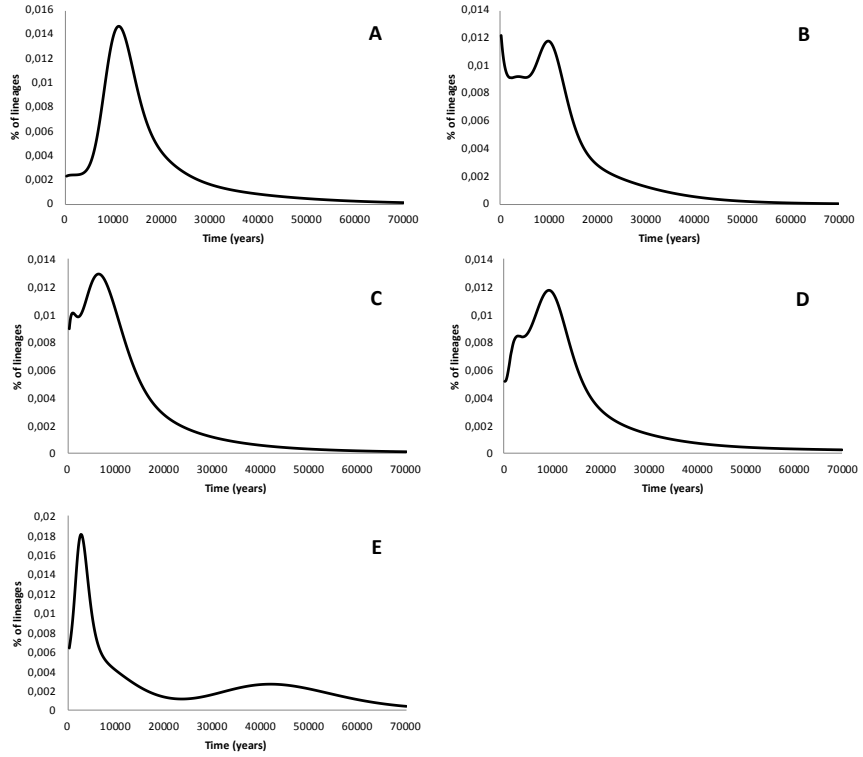


Figure 6.



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