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Mitochondrial Footprints of Human Expansions in Africa

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Summary

mtDNA studies support an African origin for modern Eurasians, but expansion events within Africa have not previously been investigated. We have therefore analyzed 407 mtDNA control-region sequences from 13 African ethnic groups. A number of sequences (13%) were highly divergent and coalesced on the "mitochondrial Eve" in Africans. The remaining sequences also ultimately coalesced on this sequence but fell into four major clusters whose starlike phylogenies testify to demographic expansions. The oldest of these African expansions dates to ~60,000–80,000 years ago. Eurasian sequences are derived from essentially one sequence within this ancient cluster, even though a diverse mitochondrial pool was present in Africa at the time.

Introduction

mtDNA has been widely used as a tool in the study of human evolution, because it is maternally inherited and nonrecombining, so that phylogenetic relationships between mitochondrial haplotypes in a sample reflect the maternal genealogical relationships between the individuals sampled. Moreover, the mutation rate of the mtDNA is high enough to provide information about the most recent phase of human evolution: the origin of anatomically modern humans during the past 150,000 years and their spread around the globe (Stoneking 1993).

Previous human mtDNA studies have demonstrated that the highest mtDNA diversity in the world is found within Africa (Cann et al. 1987; Vigilant et al. 1991; Chen et al. 1995) and thus support an "out-of-Africa" scenario for the evolution of anatomically modern humans, in agreement with more sophisticated phylogenetic analyses (Penny et al. 1995; although see Templeton 1993), as well as with most nuclear-DNA studies (Wainscoat et al. 1986; Armour et al. 1996; Tishkoff et al. 1996) and most paleoanthropological findings (Stringer and Andrews 1988; Bräuer 1989; Stringer and McKie 1996; Swisher et al. 1996). With the advent of large data sets and intraspecific phylogenetic methods, it is now becoming possible to study the geographic origins of mtDNA types in Africa, as well as the expansions within Africa that led to the settlement of Eurasia.

Although the weight of evidence now supports an African origin for anatomically modern humans, the origins of modern behavior, most clearly witnessed in the Middle-Upper Paleolithic transition ~40,000 years ago in Europe, remain controversial. In particular, it is uncertain to what extent the modern behavior of the Later Stone Age in Africa, from ~40,000 years ago, is prefigured during the preceding Middle Stone Age (Clark 1989; Deacon and Shuurman 1992; Klein 1989; Brooks et al. 1995; Yellen et al. 1995). Much also remains unclear about the origin and timing of the expansions out of Africa—for example, the significance of the presence of anatomically modern humans with a Middle Paleolithic material culture in the Middle East dated to 90–120,000 years ago, long before the Upper Paleolithic expansion into Europe (Stringer 1988; Mellars 1989; Stringer et al. 1989; Grün and Stringer 1991; Mercier et al. 1993). Furthermore, little is known about expansion events within Africa and about their relation to expansions in other parts of the world (compare Di Rienzo and Wilson 1991; Harpending et al. 1993; Sherry et al. 1994; Graven et al. 1995; Eller and Harpending 1996).

Here, we apply a novel intraspecific phylogenetic-network method (Bandelt et al. 1995), in conjunction with new outgroup information (Zischler et al. 1995) and a recent confirmation of the mitochondrial control-region mutation rate (Forster et al. 1996), to 407 published African sequences, in order to investigate these questions. We find that most African mitochondrial sequences appear to be the result of demographic expansions that started ~60,000–80,000 years ago, the earliest of which led to the colonization of Eurasia. Only a minority (13%) of sequences fall outside these expansion clusters, echoing a time, before the expansions, when the human mitochondrial gene pool was possibly more diverse (in terms of mean sequence divergence) than it is today.

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Table 1

Sampled Populations

Population	Code	Reference(s)	Sample Size(s)	Language Phylum[a]
!Kung	SK	Vigilant (1990)	19	Khoisan
Mbuti	CM	Vigilant (1990)	13	Nilo-Saharan
Biaka	CB	Vigilant (1990)	17	Niger-Kordofanian
Mandenka	WM	Graven et al. (1995)	110	Niger-Kordofanian
Songhai	WS	Watson et al. (1996)	10	Nilo-Saharan
Tuareg	WT	Watson et al. (1996)	23	Afro-Asiatic
Yoruba	WY	Vigilant (1990), Watson et al. (1996)	21, 12	Niger-Kordofanian
Hausa	WH	Watson et al. (1996)	20	Afro-Asiatic
Fulbe	WF	Watson et al. (1996)	60	Niger-Kordofanian
Kanuri	WK	Watson et al. (1996)	14	Nilo-Saharan
Turkana	ET	Watson et al. (1996)	37	Nilo-Saharan
Kikuyu	EK	Watson et al. (1996)	24	Niger-Kordofanian
Somali	ES	Watson et al. (1996)	27	Afro-Asiatic

[a] According to Greenberg (1963).

Subjects and Methods

Mitochondrial control-region DNA–sequence data from 236 individuals from nine African populations studied by Watson et al. (1996) were combined with data from 171 published sequences from four additional African populations (Vigilant 1990; Graven et al. 1995), to obtain a data set representative of the major linguistic and geographic subdivisions in sub-Saharan Africa (table 1). The sequences (see Appendix) have been deposited in the GenBank database, under accession numbers U93919–U94161. Five sequences (68, 445, 454, 464, and 472) from the study by Watson et al. (1996) were omitted from the present analysis, because of possible documentation errors. Two additional sequences submitted to GenBank represent single samples from other African populations and were therefore also disregarded in the present paper. RFLP status at two positions—the *Hpa*I site at np 3592 and the *Ava*II site at np 16390, known to be informative in Africans (Scozzari et al. 1988; Chen et al. 1995; Graven et al. 1995)—was tested either for all individuals (*Hpa*I) or for approximately half the individuals (*Ava*II) studied by Watson et al. (1996) and incorporated into the network analysis. Phylogenetic analysis was performed by use of the median algorithm of Bandelt et al. (1995). Reduced median networks display the principal character relationships present in the data and resolve likely parallel events while retaining character conflicts in the form of reticulations when ambiguity remains. Sites were unweighted in the analysis, since, despite some rate heterogeneity in the first segment, a rigorous weighting scheme is unavailable at present and ad-hoc weighting (based, e.g., on Wakeley 1993) has little effect on the outcome in this instance. Clusters were labeled according to the scheme of Chen et al. (1995). Geographic distribution of clusters was investigated in the spirit of the phylogeographic approach of Avise et al. (1987) and Templeton et al. (1995, and references therein). The statistic ρ was calculated as the mean divergence from an inferred root haplotype and was converted to a coalescence time, with one transition in the region np 16090–16365 corresponding to 20,180 years, by use of the numbering system of the Cambridge reference sequence (CRS) (Anderson et al. 1981), with transversions, insertions, and deletions being disregarded, as described elsewhere (Forster et al. 1996). Standard (sampling) errors (SEs) for ρ were calculated. It should be noted that this method does not account for either uncertainty in the calibration of the mutation rate or errors in the phylogeny estimation, although we believe both to be small (Forster et al. 1996). In addition, ancient, severe demographic bottlenecks can result in a biased sampling of the original haplotype diversity, increasing the variance of the age estimate. This error is also likely to be small, given the geographic and phylogenetic evidence that we present for expansion of the African clusters.

Results

Phylogenetic Dissection of African Sequences

To identify human expansions, we first defined a simple criterion to detect sequences that may reflect recent expansion events. Any major demographic-expansion event would be expected to be accompanied by a concomitant geographic expansion. We therefore identified all sequences that were shared between at least two populations, subjected these matches to a network analysis (fig. 1) to distinguish derived from ancestral character states, and then identified in the remaining data set those sequences sharing the sequence motifs of these matches. The criterion proved to be surprisingly effective: 87%

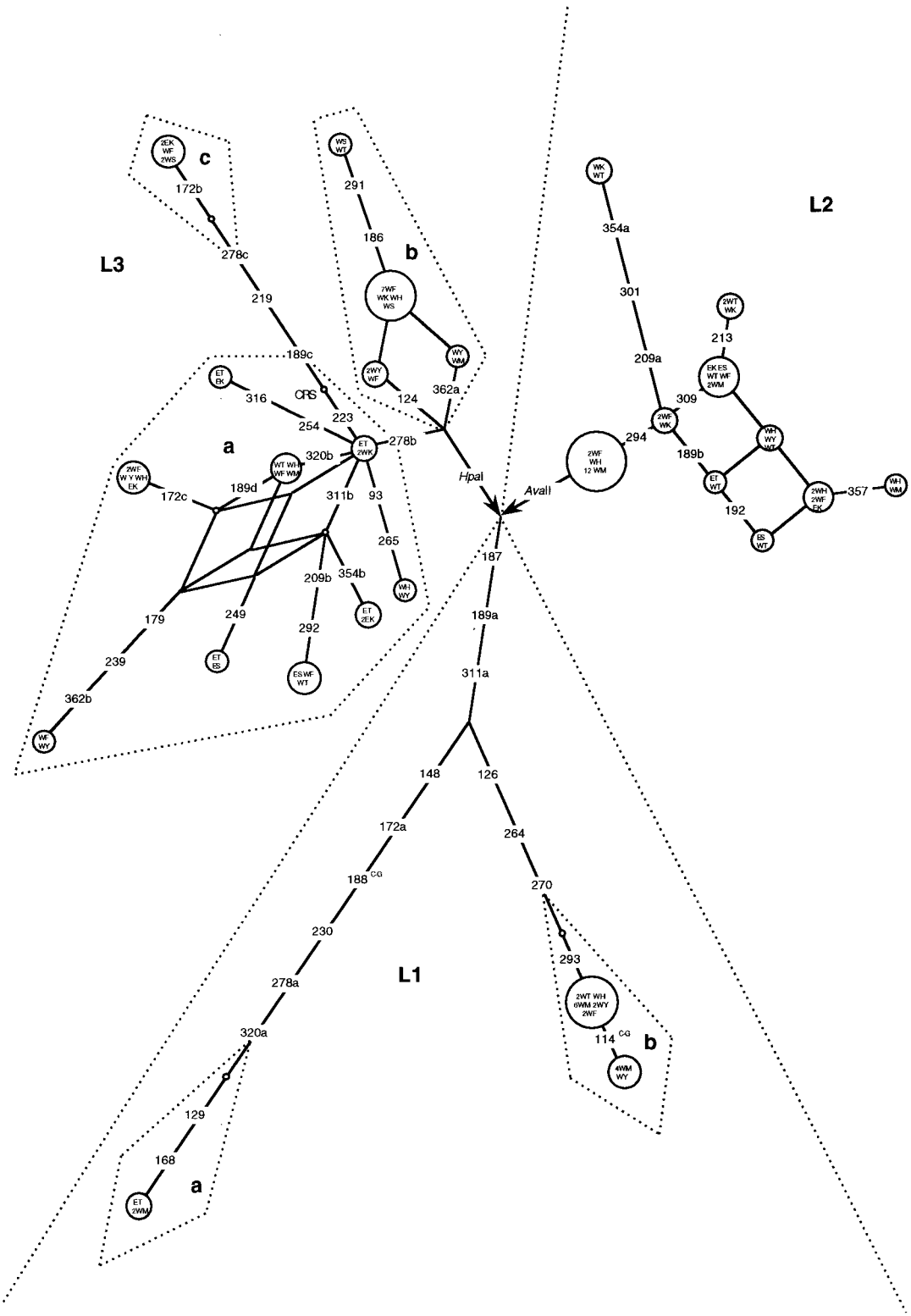

Figure 1 Interpopulation network composed of all sequences that occur in more than one African population. In all analyses, only np 16090–16365 (numbering is according to Anderson et al. 1981) were considered. Links are labeled according to np, with the "16" prefix omitted, and transversions are specified by superscript. Arrows indicate restriction-site gains. Parallel lines in a reticulation indicate that the np is identical. The order of the mutations on a path not interrupted by any branching or distinguished nodes is arbitrary. Suffixes "a," "b," etc. denote recurrent mutations. Sequences are represented by circles, with area proportional to frequency; the smallest circles (which include no designation) represent ancestral sequences confirmed by the data set. Two Tuareg individuals are at the node marked "CRS" (Anderson et al. 1981). The network is derived from the reduced median network (not shown), by resolution of one link at np 16189, leading to L3c. The reversal at np 16189 is confirmed both by additional northern-African data (Côrte-Real et al. 1996) and by results in trees that are one step longer than the maximum-parsimony trees. The reconstructed ancestral nodes of each cluster deviate from the CRS at the following positions: L1a—16129, 16148, 16172, 16187, 16188 C–G, 16189, 16223, 16230, 16311, and 16320; L1b—16126, 16187, 16189, 16223, 16264, 16270, 16278, 16293, and 16311; L2—16223, 16278, and 16390 (*Ava*II); L3—16223 and 16278; L3a—16223; L3b—16124, 16223, and 16278; L3c—16172 and 16219.

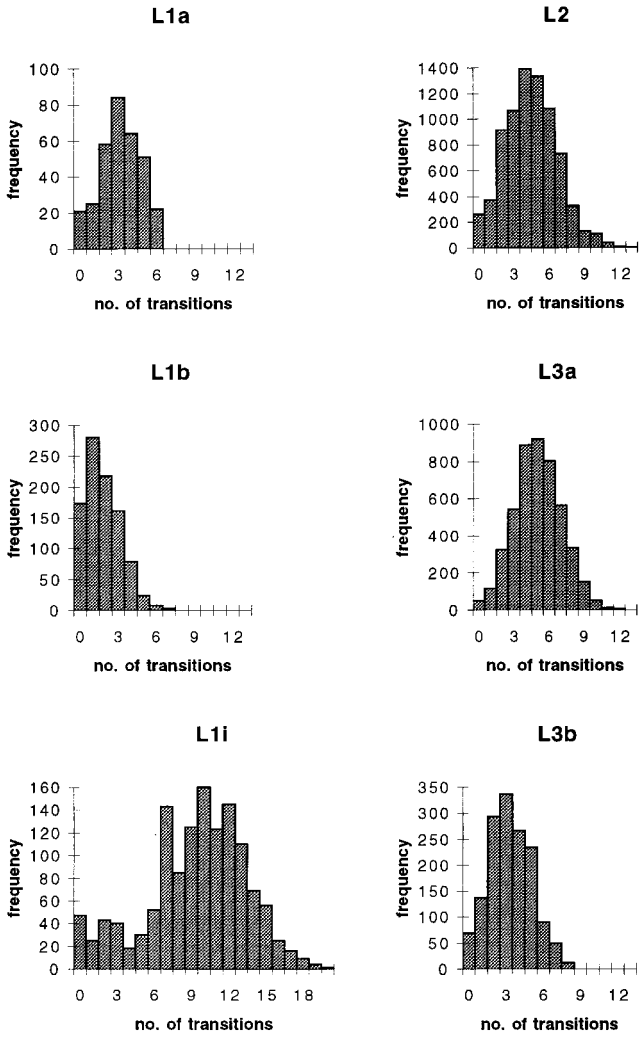

Figure 2 Pairwise-difference distribution of expansion clusters (L1a, L1b, L2, L3a, and L3b) and isolated lineages (L1i). The latter should be interpreted with particular caution, since the high degree of geographic structure among the isolated lineages may increase the sensitivity of the pairwise distribution to relative samples sizes in different populations. Cluster L3c lacks sufficient data to allow a meaningful pairwise analysis.

of the sequences fell into four major clusters (L1a, L1b, L2, and L3), one of which (L3) was further subdivided into subclusters. The clusters are labeled as in the study by Chen et al. (1995) (but note that the rooting in their fig. 2 is incorrect, since an Asian and a European were chosen as outgroups—this is remedied in their fig. 3 by midpoint rooting), with L3 corresponding to the group lacking the *Hpa*I site at np 3592 (see below). All clusters are starlike, with smooth unimodal pairwise distributions (fig. 2), and are geographically widespread, suggesting both demographic and geographic expansion. The remaining 13% of the sequences, which are not shared between populations and are thus termed "isolated lineages" (L1i), are not clearly starlike or unimodal in the pairwise analysis (fig. 2), although the pairwise distribution is nevertheless approximately bell shaped, possibly suggesting that these lineages are the relics of a less dramatic and more ancient expansion event across Africa. The network in figure 3 presents the phylogenetic relationships of the isolated African lineages to the four major African expansion clusters.

The Most Recent Common Ancestor of Human mtDNA

Outgroup rooting of the network in figure 3, by use of the recently published nuclear fragment of mtDNA, which is believed to have integrated chromosomally at a time before the most recent common ancestor (MRCA) of human mtDNA (Zischler et al. 1995), indicated that the node marked by an asterisk (*) is a probable candidate for the sequence of the human mitochondrial MRCA ("mitochondrial Eve"). It was therefore possible to use the average transition distance ρ from this sequence as an estimator of the time to the MRCA. Since subsequent expansions have unbalanced the mtDNA gene pool, we present two estimates: one is taken as the age of the group, L1i, of isolated lineages (111,000 years), and the other is the estimated coalescence time for the tree of the four major clusters L1a + [L1b+(L2+L3)]; for the latter estimate we take the weighted average of the cluster ages plus 101,000 years (corresponding to five transitions separating each cluster root from the MRCA): $(\frac{1}{2} \times 153{,}000) + (\frac{1}{4} \times 120{,}000) + (\frac{1}{8} \times 157{,}000) + (\frac{1}{8} \times 178{,}000) \approx 148{,}000$ years. We then regard 111,000–148,000 years as a realistic range for the age of the human mitochondrial MRCA, which overlaps with the estimates of 143,000 years, based on an interspecific calibration using complete mtDNA sequences (Horai et al. 1995), and 101,000–133,000 years, using African RFLP data (Chen et al. 1995).

Early Expansions within Africa

The two largest African clusters (L2 and L3, constituting 70% of the sample) are closely related to each other, in comparison with the complete African phylogeny (fig. 3), and coalesce on a peripheral sequence characterized by transitions at np 16223 and 16278, relative to the CRS. The age of this expansion can be given an approximate lower bound by dating the oldest starlike subcluster, L3a (fig. 2) within L3, and can be given an approximate upper bound by assuming a single founder for the expansion of L3. This yields, for the founder sequence, a coalescence-age range of 60,000 ± 3,200 to 77,000 ± 2,400 years ago, making this the oldest detectable major expansion event in Africa (table 2). The phylogeny predicts that L2 should have a similar age, and the MRCA of L2 in fact also dates to 56,000 ± 3,000 years ago (table 2). The expansion of L2/L3 affected all sampled African popula-

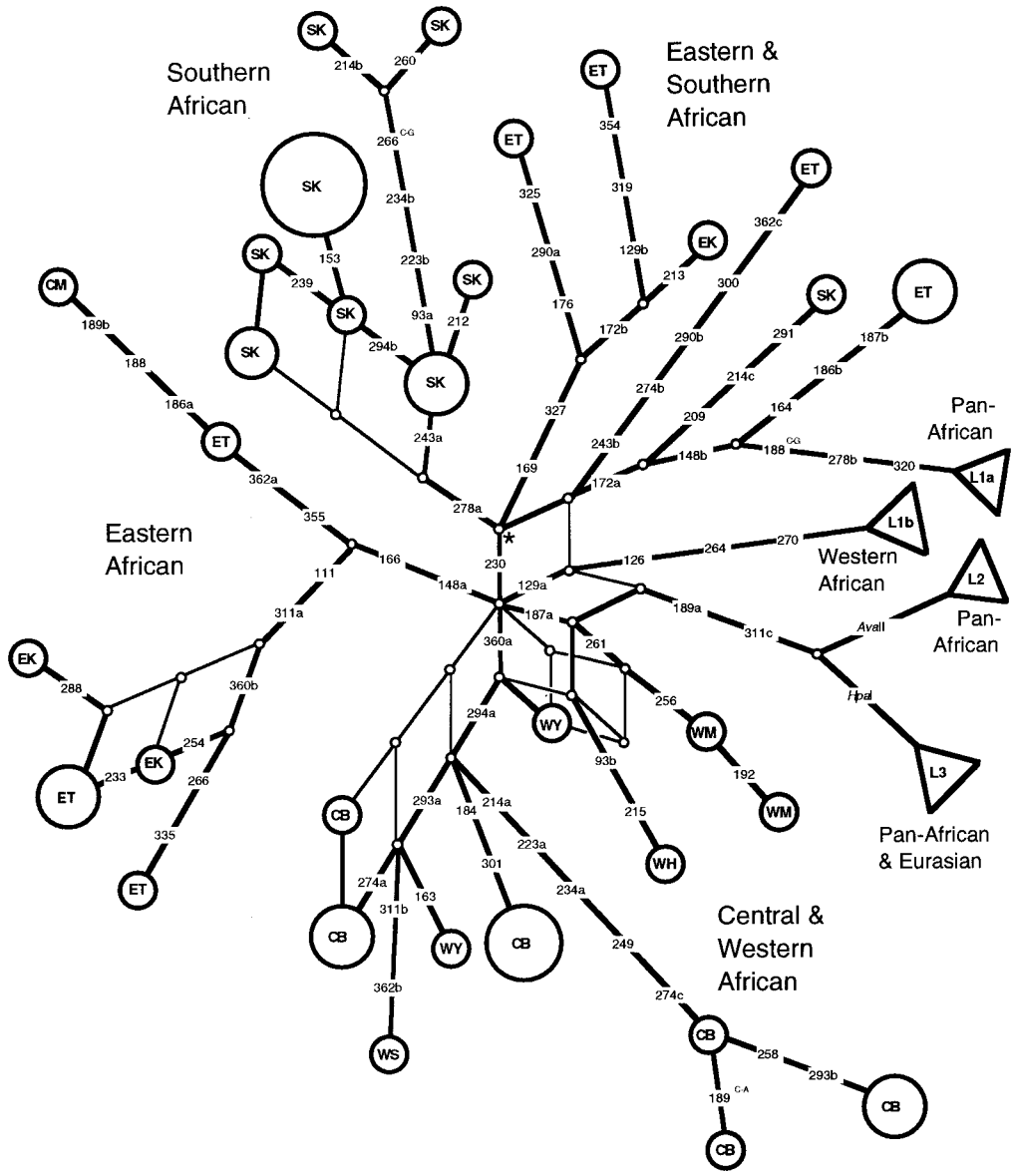

Figure 3 Reduced median network of isolated African lineages (L1i). For the reduction procedure, a mitochondrial sequence frequency of 8 (which is the maximum frequency of any isolated lineage) was assigned to clusters L1a, L1b, L2, and L3. The thicker lines indicate a plausible tree that is congruent with the African RFLP tree (Chen et al. 1995). The putative root of the network is indicated by an asterisk (*) and was determined by use of the recently discovered nuclear-mtDNA insert as an outgroup (Zischler et al. 1995). The sequence at this node differs from the CRS by transitions at np 16129, 16187, 16189, 16223, 16230, 16278, and 16311. This network contains trees that are one step longer than the unique maximum-parsimony tree (not shown). Compared with the network, the maximum-parsimony tree has several implausible features, both in that it is incongruent with the African RFLP tree published by Chen et al. (1995) and in that it separates two Turkana sequences by 18 mutations, although they differ at only 10 positions.

tions, with the exception of the !Kung of Botswana. The oldest subcluster of this expansion, L3a (fig. 1), consists mainly of eastern-African sequences, suggesting a possible eastern-African origin for the L2/L3 expansion. A lower bound can be set for the arrival of the L3 expansion in western Africa, because of the occurrence of a western African–specific subcluster of L3b, coalescing in a lineage with transitions at np 16124 and 16223 (but not at np 16278), relative to the CRS. Its coalescence time indicates that the expansion of cluster L3 reached western Africa by 30,000 years ago.

Expansion out of Africa

A single African subcluster, L3a (which lacks the *Hpa*I site at np 3592 and has the control-region sequence defined by a single transition, relative to the CRS, at np

Table 2

Age Estimates of African Sequence Clusters, by Use of the Estimator ρ

Group	Sample Size	ρ ± SE[a]	Time to MRCA
L1i	53	5.49 ± .28	111,000 ± 5,700
L1a	26	2.58 ± .20	52,000 ± 4,000
L1b	44	.95 ± .15	19,000 ± 3,000
L2	124	2.78 ± .16	56,000 ± 3,000
L3	160	3.80 ± .12	77,000 ± 2,400
L3a	98	2.97 ± .16	60,000 ± 3,200
L3b	55	2.18 ± .15	44,000 ± 3,000
L3c	7	2.29 ± .17	46,000 ± 3,400

[a] SE (Standard error) values are appropriate to a perfectly starlike phylogeny and should otherwise be taken as indicating a lower bound.

16223 at its root), defines almost all Eurasians (Excoffier and Langaney 1989; for rare exceptions in the Near East and southern Europe, see the low-resolution but large-sample-size RFLP studies by Bonné-Tamir et al. [1986], Brega et al. [1986], De Benedictis et al. [1989], and Ritte et al. [1993]). It is also common in Africa, where it displays a clear frequency gradient from east to west (fig. 4). The oldest subcluster within L3a (characterized by transitions at np 16223 and 16311) is eastern African specific, suggesting an eastern-African origin for L3a and thus also for Eurasians. A possible alternative, the Middle East (Stringer 1988; Di Rienzo and Wilson 1991), is less likely to be the origin of L3a, since L2, the sister cluster of L3 (fig. 1), is virtually African specific. Taken together, these findings suggest that one or a small set of closely related lineages expanded in Africa and founded the L2/L3 cluster, an eastern-African subset of which spread into Eurasia some time <60,000 years ago. This correlates well with both a proposed out-of-Africa expansion date of 65,000 years ago, when mainly non-African mtDNA (Mountain et al. 1995) is used, and the peak in the distribution of pairwise differences among Africans that was identified by Sherry et al. (1994). An eastern-African origin for Eurasians is strongly supported by results from nuclear-DNA variation (Tishkoff et al. 1996), whereas the genetic date of ~60,000 years ago for the major Eurasian founding sequence is more recent than the paleontological date of ~100,000 years for the oldest anatomically modern human remains in the Middle East (Grün and Stringer 1991; Mercier et al. 1993). This discrepancy may be due to inaccuracies inherent to both paleontological and genetic dating, or the Middle Eastern human remains may represent a minor, earlier expansion out of Africa (Stringer et al. 1989).

Subsequent Expansions in Eastern and Western Africa

Only two additional lineages have experienced detectable expansions. One is the founder of cluster L1a (fig.

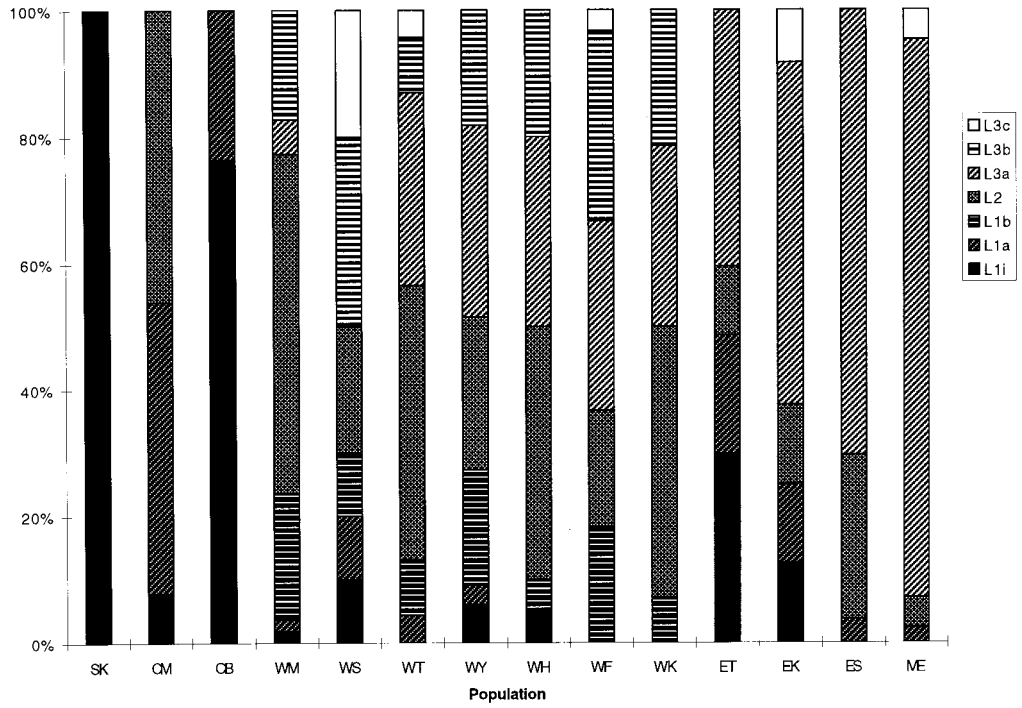

Figure 4 Frequencies of clusters in African populations and Middle Easterners (ME) (Di Rienzo and Wilson 1991). Other populations are as coded in table 1.

3), which coalesces at ~52,000 years ago and is found mainly in eastern, central, and (Soodyall 1993) southern Africa, although single examples are present as outliers in the Mandenka (Graven et al. 1995), the Middle East, and Sardinia (Di Rienzo and Wilson 1991) and Turkey (Calafell et al. 1996). It has been suggested that a subset of cluster L1a, defined by a 9-bp deletion at np 8272–8289 (Vigilant 1990), may represent an expansion of Bantu-speakers (Bandelt et al. 1995; Chen et al. 1995; Soodyall et al. 1996). Another possible marker for Bantu expansions that merits investigation is the sequence motif np 16124-16223-16278 found in southwestern Africa (among the Herero, Nama, and Dama in the data of Vigilant [1990] and Soodyall [1993]). This motif is a subset of L3b, which is widespread in western Africans who mainly speak languages of the Niger-Kordofanian family, of which Bantu is a member.

The second cluster (L1b) that has expanded outside the twin cluster L2/L3 is younger and, accordingly, has had less time to spread. L1b coalesces at 19,000 years ago and is restricted to western Africa.

Discussion

The existence of expansion clusters in western Africa is contrary to the interpretation of previous workers, who have suggested that there either were no demographic expansions within western Africa (Graven et al. 1995) or that, at least, stationarity could not be rejected (Eller and Harpending 1996). This disagreement is readily explained by the different analytic approach taken here, which does not rely, as does much previous work using mtDNA, on the population-based analysis of distributions of pairwise distances (i.e., mismatch distributions). Such an analysis, in the absence of a prior phylogenetic dissection of the sequences, will tend to conflate different expansion events, which we would expect to have taken place long before the emergence of the modern ethnic groups on which the populations in such studies are usually based. This is evident in the example of Watson et al. (1996), in which the population-coalescence times are frequently the result of the fusion of several of the ancient phylogenetic clusters discussed above and therefore, in themselves, are not related to the age of the individual populations—indeed, the individual population phylogenies frequently coalesce on the mitochondrial Eve sequence itself (Bandelt and Forster, in press).

The present work suggests that the starlike phylogenies previously discovered by use of pairwise distributions (Harpending et al. 1993; Sherry et al. 1994) and phylogenetic analysis (Mountain et al. 1995) were generated in eastern Africa 60,000–80,000 years ago by the expansion of a small, closely knit subset of a diverse ancestral mtDNA pool. This implies that the low diversity of modern humans, in comparison with other hominoids (Ruvolo et al. 1994), both within and outside Africa, can be at least partly accounted for by a founder effect that occurred long after the origin of anatomically modern humans. Our sample of isolated lineages is, at present, still too small to allow firm conclusions concerning the period before these major expansions. Nevertheless, they show promising avenues for future research. The age of mitochondrial Eve may coincide with the paleontologically dated transition from archaic *Homo sapiens* (*Homo heidelbergensis*) to anatomically modern *Homo sapiens* at ~120,000–130,000 years ago (Day and Stringer 1982; Rightmire 1989; Bräuer 1992), suggesting that there may have been a population bottleneck at this time, foreshortening the coalescence tree—although, given the deeper coalescences of some nuclear genes, a protracted period of approximately constant small population size at approximately this time may also account for the absence of earlier lineages (Penny et al. 1995; Ruvolo 1996). Furthermore, the pairwise distribution and the structure of the network may also suggest a moderate range expansion, >~100,000 years ago, of anatomically modern humans within Africa, prior to the major expansions. This would coincide with the appearance of modern human remains in the fossil record of southern Africa (Deacon and Shuurman 1992; Bräuer et al. 1992; Bräuer and Singer 1996).

It is curious that only one mitochondrial sequence or, at most, a set of very closely related lineages (the ancestors of L3—and, possibly, of L2) should have participated in the earliest major expansion, given that all parts of Africa today harbor diverse, phylogenetically isolated lineages from the earlier period. Since a general environmental change in one area is unlikely to have directly triggered population expansion in only a single mitochondrial lineage, it is possible that a small subpopulation carrying it acquired some advantage, perhaps in response to environmental change, such as the onset of the Last Glacial. It seems reasonable to speculate that a behavioral innovation appeared some 60,000–80,000 years ago in a subpopulation of anatomically modern humans, containing the ancestors of L3 (and possibly also L2), who had previously been living with a Middle Paleolithic/Middle Stone Age technology—and that this small subpopulation subsequently expanded as a result. This change may well correspond with the evidence for the dramatic increase in communicative activity that is associated with either the Later Stone Age or an even earlier period in Africa (Klein 1989; Mellars 1989; Deacon and Shuurman 1992; Brooks et al. 1995; Yellen et al. 1995; Power and Watts 1996) and the Upper Palaeolithic in Eurasia (Gamble 1986, 1993; Mellars 1992). Whatever this change involved (Mellars and Stringer 1989; Knight et al. 1995; Mithen 1996; Noble and Davidson 1996), it seems likely that it originated in Africa and that this was the decisive event in the spread of modern humans from Africa into Eurasia.

Note added in proof.—The recently published Neanderthal sequence (Krings et al. 1997) offers a unique opportunity to test our rooting of the African mtDNA network. The Neanderthal sequence does indeed share with the proposed root for figure 3 (marked by an asterisk [*]) the nucleotides at the seven characteristic positions, except for the fast site 16187. In addition, the Neanderthal sequence matches cluster L1a sequences at two of the signature positions (np 16148 and 16320). If the Neanderthal sequence were given greater weight, as an outgroup, than the more distant nuclear insert, then the mitochondrial Eve would differ from the CRS within np 16090–16365 by transitions at np 16129, 16148, 16187, 16189, 16223, 16230, 16278, 16311, and, possibly, 16320. As a consequence, one would infer that transitions at np 16129 and 16172 are even more frequent than is apparent in our network, so that the single !Kung outlier, together with one Turkana sequence, would be separated from the branch connecting L1a with the node marked by an asterisk in figure 3.

Acknowledgments

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Appendix

Table A1

African Mitochondrial Sequence Haplotypes and their Distributions

Group	Sequence Types[a]	Distribution in Population[b]													
		SK	CM	CB	WM	WS	WT	WY	WH	WF	WK	ET	EK	ES	Total
L1a	093 129 148 172 187 188C–G 189 223 230 311 320	·	·	1	·	·	·	·	·	·	·	·	·	·	1
L1a	093 148 172 187 188C–G 189 223 230 311 320	·	·	3	·	·	·	·	·	·	·	·	·	·	3
L1a	111 129 148 168 172 187 188C–G 189 223 230 278 293 311 320	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L1a	111 129 148 168 172 187 188C–G 189 223 230 311 320	·	·	·	·	1	·	·	·	·	·	·	·	·	1
L1a	129 148 168 172 187 188C–G 189 223 230 278 293 311 320	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L1a	129 148 168 172 187 188C–G 189 223 230 284 293 311	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L1a	129 148 168 172 187 188C–G 189 223 230 290 311 320	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L1a	129 148 168 172 187 188C–G 189 223 230 293 311	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1a	129 148 168 172 187 188C–G 189 223 230 311 320	·	·	·	2	·	·	·	·	·	·	1	·	·	3
L1a	129 148 168 172 187 188C–G 189 223 230 311 320 362	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L1a	129 148 168 172 188C–A 189 223 230 289 311 320	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1a	129 148 168 172 188C–G 189 223 230 311	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1a	129 148 172 187 188C–G 189 217 223 230 311 320	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L1a	129 148 172 188C–A 189 223 230 289 311 320	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1a	148 172 184 187 188C–G 189 223 230 311 320	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1a	148 172 187 188C–A 189 223 230 242 311 320	·	6	·	·	·	·	·	·	·	·	·	·	·	6
L1a	148 172 187 188C–G 189 223 230 311 320	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1b	093 126 187 189 223 264 270 278 293 311	·	·	·	·	·	·	·	·	5	·	·	·	·	5
L1b	114C–G/A 126 187 189 223 264 270 274 278 293 311	·	·	·	3	·	·	·	·	·	·	·	·	·	3
L1b	114C–G/A 126 187 189 223 264 270 278 293 311	·	·	·	4	·	·	1	·	·	·	·	·	·	5
L1b	126 145 187 189 223 264 270 278 293 311	·	·	·	3	·	·	·	·	·	·	·	·	·	3
L1b	126 145 187 189 223 264 270 278 311	·	·	·	3	·	·	·	·	·	·	·	·	·	3
L1b	126 166del 172 187 189 223 264 270 278 293 311 318	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L1b	126 172 187 189 223 270 278 311	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L1b	126 187 189 213 223 260 264 270 278 293 311	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L1b	126 187 189 213 223 260 264 274 278 293 311	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L1b	126 187 189 214 223 264 265 270 278 293 311	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L1b	126 187 189 223 256 264 270 278 293 311	·	·	·	2	·	·	·	·	·	·	·	·	·	2
L1b	126 187 189 223 264 270 278 293 301 311	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L1b	126 187 189 223 264 270 278 293 311	·	·	·	6	·	2	2	1	2	·	·	·	·	13
L1b	126 187 189 223 270 278 311	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L1b	126 187 189 264 270 278 293 311	·	·	·	·	1	·	·	·	·	·	·	·	·	1
L1b	126 223 264 270 278 311	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L1b	186 187 189 223 264 270 278 293 311 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L1i	093 129 187 189 214 230 234 243 266C–G 311	1	·	·	·	·	·	·	·	·	·	·	·	·	1
L1i	093 129 187 189 230 234 243 260 266C–G 311	1	·	·	·	·	·	·	·	·	·	·	·	·	1
L1i	093 129 189 215 223 278 311 360	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L1i	111 129 148 166 187 189 223 233 254 278 288	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L1i	111 129 148 166 187 189 223 233 254 278 360	·	·	·	·	·	·	·	·	·	·	3	·	·	3

(*continued*)

Table A1 (continued)

Group	Sequence Types[a]	Distribution in Population[b]													
		SK	CM	CB	WM	WS	WT	WY	WH	WF	WK	ET	EK	ES	Total
L1i	111 129 148 166 187 189 223 254 278 360	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L1i	111 129 148 166 187 189 223 266 278 335 360	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1i	129 148 166 186 187 188 223 278 311 355 362	·	1	·	·	·	·	·	·	·	·	·	·	·	1
L1i	129 148 166 187 189 223 278 311 355 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1i	129 153 187 189 223 230 243 294 311	8	·	·	·	·	·	·	·	·	·	·	·	·	8
L1i	129 163 187 189 223 278 293 294 311 360	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L1i	129 169 172 187 189 213 223 230 278 311 327	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L1i	129 169 176 187 189 223 230 278 290 311 325 327	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1i	129 184 187 189 223 278 294 301 311 360	·	·	4	·	·	·	·	·	·	·	·	·	·	4
L1i	129 187 189 212 223 230 243 311	1	·	·	·	·	·	·	·	·	·	·	·	·	1
L1i	129 187 189 214 234 249 258 274 278 293 294 311 360	·	·	3	·	·	·	·	·	·	·	·	·	·	3
L1i	129 187 189 214 234 249 274 278 294 311 360	·	·	1	·	·	·	·	·	·	·	·	·	·	1
L1i	129 187 189 223 230 239 243 294 311	1	·	·	·	·	·	·	·	·	·	·	·	·	1
L1i	129 187 189 223 230 239 294 311	2	·	·	·	·	·	·	·	·	·	·	·	·	2
L1i	129 187 189 223 230 243 294 311	1	·	·	·	·	·	·	·	·	·	·	·	·	1
L1i	129 187 189 223 230 243 311	3	·	·	·	·	·	·	·	·	·	·	·	·	3
L1i	129 187 189 223 261 278 311 360	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L1i	129 187 189 223 274 278 293 294 311	·	·	1	·	·	·	·	·	·	·	·	·	·	1
L1i	129 187 189 223 274 278 293 294 311 360	·	·	3	·	·	·	·	·	·	·	·	·	·	3
L1i	129 187 189 223 278 293 294 360 362	·	·	·	·	1	·	·	·	·	·	·	·	·	1
L1i	129 187 189T–A 214 234 249 274 278 294 311 360	·	·	1	·	·	·	·	·	·	·	·	·	·	1
L1i	129 189 192 223 256 261 278 311	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L1i	129 189 223 256 261 278 311	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L1i	148 164 172 186 189 223 230 278 311	·	·	·	·	·	·	·	·	·	·	3	·	·	3
L1i	169 172 187 189 223 230 278 311 319 327 354	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L1i	172 187 189 209 214 223 230 278 291 311	1	·	·	·	·	·	·	·	·	·	·	·	·	1
L1i	187 189 223 230 243 274 278 290 300 311 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L2	092 148 189 223 278 286 309	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L2	092 189 192 223 278 291 294	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L2	093 189 192 223 278 294 309	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L2	093 189 223 278 294	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L2	093 213 223 278 294 309	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L2	093 223 234 278	·	·	·	12	·	·	·	·	·	·	·	·	·	12
L2	095C–G 096G–C 172 189 223 229 278 291 294 311	·	1	·	·	·	·	·	·	·	·	·	·	·	1
L2	111C–A 145 171 184 189 223 239 278 292 311 355	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L2	114C–A 129 213 223 278 284 343 362	·	·	·	2	·	·	·	·	·	·	·	·	·	2
L2	114C–A 129 213 223 278 343 355 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L2	114C–A 129 213 223 278 355 362	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L2	126 189 278	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L2	129 189 278 300 354 362	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L2	129 223 278 294 309	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L2	145 213 223 274 278 294	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L2	148 150 223 278 294 355	·	·	·	6	·	·	·	·	·	·	·	·	·	6
L2	148 223 244 278 286 294 309	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L2	167 189 223 278	·	·	·	2	·	·	·	·	·	·	·	·	·	2
L2	170 189 223 229 264 278 294 311	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L2	170 189 223 229 278 294 311	·	2	·	·	·	·	·	·	·	·	·	·	·	2
L2	172 189 223 229 278 291 294 311	·	3	·	·	·	·	·	·	·	·	·	·	·	3
L2	181 223 278 294 309	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L2	187 189 192 223 278 294 309	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L2	187 223 278 362	·	·	·	3	·	·	·	·	·	·	·	·	·	3
L2	189 192 223 256 278 294 309	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L2	189 192 223 265A–C 278 294 309	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L2	189 192 223 274 278 294 309	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L2	189 192 223 278 291 294	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L2	189 192 223 278 294	·	·	·	·	·	1	·	·	·	·	·	·	1	2
L2	189 192 223 278 294 309	·	·	·	·	·	·	·	2	2	·	·	1	·	5
L2	189 192 223 278 294 309 357	·	·	·	1	·	·	·	1	·	·	·	·	·	2
L2	189 192 278	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L2	189 192 278 294 309	·	·	·	·	1	·	·	·	·	·	·	·	·	1
L2	189 223 278 291 294	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L2	189 223 278 294	·	·	·	·	·	1	·	·	·	·	1	·	·	2

(*continued*)

Table A1 (continued)

Group	Sequence Types[a]	Distribution in Population[b]													
		SK	CM	CB	WM	WS	WT	WY	WH	WF	WK	ET	EK	ES	Total
L2	189 223 278 294 309	·	·	·	·	·	1	1	1	·	·	·	·	·	3
L2	209 223 278	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L2	209 223 278 294 301 354	·	·	·	·	·	1	·	·	·	1	·	·	·	2
L2	213 223 274 278 294	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L2	213 223 278 294 309	·	·	·	1	·	1	·	·	·	·	·	·	·	2
L2	213 278 294 309	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L2	217 223 254 264 278	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L2	223 224 278 309	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L2	223 234 278	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L2	223 256 264 278 294	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L2	223 260 278 294	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L2	223 261 278 294 309	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L2	223 261 278 318	·	·	·	7	·	·	·	·	·	·	·	·	·	7
L2	223 264 278	·	·	·	2	·	·	·	·	·	·	·	·	·	2
L2	223 274 278	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L2	223 278	·	·	·	12	·	·	·	1	2	·	·	·	·	15
L2	223 278 286 294	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L2	223 278 286 294 301 309	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L2	223 278 286 294 309	·	·	·	·	1	·	·	·	·	·	·	·	·	1
L2	223 278 290 294 309	·	·	·	2	·	·	·	·	·	·	·	·	·	2
L2	223 278 292 294 309	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L2	223 278 294	·	·	·	·	·	·	·	·	2	1	·	·	·	3
L2	223 278 294 309	·	·	·	2	·	1	·	·	1	·	·	1	1	6
L2	223 278 294 309 356	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L2	223 278 300	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L2	223 278 318	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L3a	093 129 223 249 311 359	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	093 209 218 223 292 311	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	093 223 260 278 311	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	093 223 265	·	·	·	·	·	·	1	1	·	·	·	·	·	2
L3a	093 223 278	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L3a	111 223 311 327	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3a	111C–A 129 172 223 248 291 311	·	·	·	·	·	·	·	·	·	·	·	·	2	2
L3a	126 169 223 293A–T 311 355 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	126 172 209 223	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	126 305A–T 362	·	·	·	·	·	·	·	·	·	·	·	·	2	2
L3a	126 362	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	129 172 188 189 223 320	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	129 174 192 218 223 256C–A 311 362	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L3a	129 189	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L3a	129 189 223 249 311	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	129 209 223 234 292 295 311	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3a	129 209 223 292 295 311	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	129 209 292 295 311	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3a	129 223	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	136 169 223 278	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	145 222	·	·	·	·	·	·	·	·	4	·	·	·	·	4
L3a	145G–C 222	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	147C–G 172 213 223 248 355	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	153 223 265A–T	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	169 192 223 278	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	172 173 219 311 320	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	172 180A–C 189 223 320	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3a	172 184 223 260 311	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	172 189 223 278 320	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	172 189 223 311 320	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L3a	172 189 223 320	·	·	·	·	·	·	1	1	2	·	·	1	·	5
L3a	179 185 223 260 311	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	179 189 223 239 311 320 362	·	·	·	·	·	·	1	·	1	·	·	·	·	2
L3a	179 192 223 274 293A–T 311 320 355 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	185 223 311 327	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	186 209 223 311 327	·	·	·	·	·	·	·	·	·	·	·	1	·	1

(*continued*)

Table A1 (continued)

Group	Sequence Types[a]	Distribution in Population[b]													
		SK	CM	CB	WM	WS	WT	WY	WH	WF	WK	ET	EK	ES	Total
L3a	187 189 223 265A–T	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3a	189 192 223 293A–T 294 311 344 355 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	189 192 270 320	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	189 209 223 292 311 320	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L3a	189 218 223 303 360	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	189 223 249 311	·	·	·	·	·	·	·	·	·	·	1	·	1	2
L3a	189 223 265A–T	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L3a	189 223 287C–G 293A–T 311 355 362	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	189 223 320	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3a	209 213 223 234	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	209 223 235 292 311	·	·	·	·	·	·	·	·	2	·	·	·	·	2
L3a	209 223 261 292 311	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L3a	209 223 292 311	·	·	·	·	·	1	·	·	1	·	·	·	1	3
L3a	209 223 311	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	209 223 311 354	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	218 223 303 360	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	223	·	·	·	·	·	·	·	·	·	2	1	·	·	3
L3a	223 241A–C 311 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	223 248 327	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L3a	223 249 278 293A–T 294 311 355 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	223 254 316	·	·	·	·	·	·	·	·	·	·	1	1	·	2
L3a	223 260 311	·	·	·	·	·	·	·	·	·	·	·	·	2	2
L3a	223 264	·	·	·	4	·	·	·	·	·	·	·	·	·	4
L3a	223 274 293A–T 311 355 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	223 311	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	223 311 320	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3a	223 311 354	·	·	·	·	·	·	·	·	·	·	1	2	·	3
L3a	223 311 362	·	·	·	·	·	·	·	·	·	·	1	·	·	1
L3a	223 319	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	223 320	·	·	·	1	·	1	·	1	1	·	·	·	·	4
L3a	223 325del 327	·	·	·	·	·	·	·	·	·	·	·	1	·	1
L3a	224 311	·	·	·	·	·	·	·	·	·	·	·	·	1	1
L3a	261 298	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3a	264 311	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3a	CRS	·	·	·	·	·	2	·	·	·	·	·	·	·	2
L3b	093 223 278 362	·	·	·	·	·	·	·	·	4	·	·	·	·	4
L3b	111 124 223 319G–C	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3b	124 145G–C 223	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3b	124 148 223 278 293 311 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3b	124 162 223 278 311	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3b	124 166 215 223 325	·	·	·	3	·	·	·	·	·	·	·	·	·	3
L3b	124 166 223	·	·	·	·	·	·	1	·	·	·	·	·	·	1
L3b	124 169 209 223 278 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3b	124 172 223 304	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L3b	124 183 223 311	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3b	124 186 223 278 291 362	·	·	·	·	1	1	·	·	·	·	·	·	·	2
L3b	124 189 223 278 304 311 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3b	124 189 223 278 311	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L3b	124 223	·	·	·	2	·	·	·	·	·	·	·	·	·	2
L3b	124 223 238 263 309	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3b	124 223 256	·	·	·	4	·	·	·	·	·	·	·	·	·	4
L3b	124 223 261 278 362	·	·	·	2	·	·	·	·	·	·	·	·	·	2
L3b	124 223 278	·	·	·	·	·	·	2	·	1	·	·	·	·	3
L3b	124 223 278 304 311 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3b	124 223 278 311 362	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L3b	124 223 278 362	·	·	·	·	1	·	·	1	7	1	·	·	·	10
L3b	124 223 288	·	·	·	·	·	·	·	·	·	1	·	·	·	1
L3b	124 223 291	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3b	124 223 311	·	·	·	·	·	1	·	·	·	·	·	·	·	1
L3b	124 223 319	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3b	124 223 319 362	·	·	·	·	·	·	·	·	1	·	·	·	·	1
L3b	124 223 327	·	·	·	·	·	·	1	·	·	·	·	·	·	1

(*continued*)

Table A1 (continued)

Group	Sequence Types[a]	Distribution in Population[b]													
		SK	CM	CB	WM	WS	WT	WY	WH	WF	WK	ET	EK	ES	Total
L3b	145 223 270 278 362	·	·	·	·	1	·	·	·	·	·	·	·	·	1
L3b	209 278 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3b	213 223 278 362	·	·	·	1	·	·	·	·	·	·	·	·	·	1
L3b	223 278 318 362	·	·	·	·	·	·	·	1	·	·	·	·	·	1
L3b	223 278 362	·	·	·	1	·	·	1	·	·	·	·	·	·	2
L3c	172 189 219 278	·	·	·	·	2	·	·	·	1	·	·	2	·	5
L3c	172 189 219 278 311	·	·	·	·	·	1	·	·	·	·	·	·	·	1
Total		19	13	17	110	10	23	33	20	60	14	37	24	27	407

[a] Described in terms of variant positions, relative to CRS, in the region np 16090–16365 (position numbers are given without the prefix "16"). Unless otherwise indicated (as either transversions or deletions ["del"]), variants are transitions.

[b] Population codes are as in table 1.

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