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African DNA Lineages in the Mitochondrial Gene Pool of Europeans

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Abstract—Mitochondrial DNA (mtDNA) nucleotide sequences of African origin are found in various European populations at a low frequency (on average, less than 1%). Data on mtDNA variation in Eurasian and African populations have been analyzed, and African mtDNA lineages have been found in Europeans. It has been demonstrated that, despite the high diversity of mtDNA haplotypes of African origin in Europeans, few monophyletic clusters of African lineages are characterized by long-term diversity formed in Europe. Only two such mtDNA clusters (from haplogroups L1b and L3b) have been found, their evolutionary age not exceeding 6500 years. European and African populations have been compared with respect to the frequency distributions of the alleles of autosomal microsatellite loci found in Russian carriers of African mtDNA haplotypes. It has been demonstrated that alleles typical of Europeans are characteristic of the autosomal genotypes of these Russian individuals.

Key words: mitochondrial DNA, autosomal microsatellite loci, human populations, genetic diversity, outbreeding

INTRODUCTION

To date, it has been determined that mitochondrial DNA (mtDNA) types of African origin are present in the Eurasian gene pool; their average frequency is approximately 1% [1, 2]. They are represented by nucleotide sequences belonging to different mtDNA haplogroups that were formed in Africa. African mtDNA lineages are the most frequent in populations of the Iberian Peninsula and Middle East, which have experienced the strongest influence of northern African populations during their history [2–4]. For example, almost all Eurasian U6 lineages of African origin have been found in western Iberian and southwestern Asian populations [3]. The African lineages L0–L3A have accumulated in Middle Eastern and southern European populations. Judging from the distribution pattern of various mtDNA groups in Africa, L1b types may have come to Eurasia from northern or western Africa and L2a types, from southeastern or western Africa [2]. However, it is difficult to determine the precise origin of an mtDNA type, much less the time of its appearance in Eurasia; the results of studying this problem indicate that most African mtDNA lineages spread to Eurasia and America because of the slave trade. It is known that approximately 13×10^6 Africans were brought as slaves to America alone from the 15th to the 19th centuries [2]. It is assumed that eastern Africa was the donor of maternal mtDNA lineages found in the Middle East, and western and southeastern Africa were donors of African mtDNA lineages found in Europe [2, 3].

Data on the mtDNA variation in eastern European populations indicate that their gene pools contain practically no African mtDNA lineages [5–7]. Only in Caucasian populations have mtDNA lineages belonging to haplogroup M1 been found at a low frequency (about 1%); however, this haplogroup is characteristic not only of northern African populations, but also of Middle Eastern and Anatolian populations; therefore, the M1 haplogroup in this case cannot be considered a marker of African–Caucasian genetic relations [3, 8]. African mtDNA L-types have been found, at a very low frequency, only in Russians. For example, we found a few mtDNA types of the African haplogroups L1b and L3b in the Tula and Kaluga regions [6]. Taking into account all data on the mtDNA variation of hypervariable segment 1 (HVS1) in Russian populations [5, 6, 9–11], the frequency of African mtDNA lineages in Russians is only 0.2%. The origin of these mitochondrial lineages remains unknown. To elucidate this problem, we analyzed the distribution of mtDNA lineages of African origin in other European populations and studied the phylogenetic relationships between African mtDNA lineages in European and African populations. To determine the origin of nuclear genotypes in the Russian carriers of African

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Table 1. Nucleotide motifs of HVS1 of African mtDNA lineages

mtDNA cluster	HVS1 nucleotide sequence (-16000)
L1*	187-189-223-278-311
L0a*	129-148-172-187-188G-189-223-230-311-320
L0a1	129-148-168-172-187-188G-189-223-230-311-320
L0a2	148-172-187-188G-189-223-230-311-320
L0d	129-187-189-223-230-243-311
L1b	126-187-189-223-264-270-278-311
L1c*	129-187-189-223-278-294-311-360
L1c1	129-187-189-223-278-293-294-311-360
L1c2	129-187-189-223-265C-278-286G-294-311-360
L1c3	129-189-215-223-278-294-311-360
L1e	129-148-166-187-189-223-311
L2a	223-278-294-390
L2b	114A-129-213-223-278-390
L2c	223-278-390
L2d	223-278-390-399
L3*	223
L3b	124-223-278-362
L3d	124-223
L3e1*	223-327
L3e1a	185-223-327
L3e1b	223-325D-327
L3e2*	223-320
L3e2b	172-189-223-320
L3e3	223-265T
L3e4	223-264
L3f	209-223-311
L3g	223-293T-311-355-362

Note: Transitions relative to the Cambridge Reference Sequence of mtDNA [15] are shown; the transversion types are indicated additionally; D is a nucleotide deletion. The clusters are designated according to the mtDNA classification [1, 12, 13].

mtDNAs, we compared them with European and African populations with respect to the distribution of the alleles of autosomal microsatellite loci.

EXPERIMENTAL

According to the current classification, African mtDNA lineages belong to several paragroups (paraphyletic clusters of mtDNA lineages designated by an asterisk, e.g., L3*) and monophyletic groups (Table 1) [1, 12–14]. We used for analysis a database (in the form of median networks) containing African mtDNA HVS1 nucleotide sequences found in African and Eurasian populations [1, 2]. This database represented the diversity of HVS1 nucleotide sequences in African and Eurasian populations (a total of more than 17,000 sequences between positions 16,090 and 16,365) [2]. The HVS1 nucleotide positions were numbered according to the Cambridge Reference Sequence of mtDNA [15]. We also used databases on mtDNA variation in Portuguese [4], Spanish [16], and western African [17] populations.

The evolutionary relationships between mtDNA HVS1 types were analyzed by the median network method [18]. The genetic distances (ρ) between mtDNAs were calculated as the mean number of mutations in which the founder genotypes differed from derivative genotypes included into the respective monophyletic clusters [19]. When estimating the evolutionary ages of mtDNA clusters, were assumed that, in the case of HVS1, a genetic distance of $\rho = 1$ corresponds to a time period of 20,180 yr [19].

Data on the variation of 15 autosomal microsatellite loci (short tandem repeats or STRs) were obtained: *D3S1358, vWA, FGA, TH01, TPOX, CSF1PO, D5S818, D13S317, D7S820, D16S539, D2S1338, D8S1179, D21S11, D18S51*, and *D19S433*) from panel CODIS used for molecular genetic identification of Russian carriers of African mtDNA lineages. The STR polymorphism was analyzed by means of an ABI 377 sequencer (PE Applied Biosystems, United States) using the AmpF1STR Profiler PCR Amplification Kit and AmpF1STR SGM Plus PCR Amplification Kit (PE Applied Biosystems). For comparative analysis, we used data on the distribution of STR allele frequencies in Russian populations [20] (see also unpublished data of the authors) and in European and African populations (the ALFRED database [21]).

RESULTS AND DISCUSSION

Analysis of the diversity of mtDNA HVS1 nucleotide sequences showed that African mtDNA lineages were present in different European populations both from southern Europe (the Portuguese, Italians (Sicilians and Tuscans), Albanians, Spaniards, and Bosnians) and from northern Europe (the French, Swiss, Germans, Poles, Russians, Norwegians, and Icelanders) (Table 2). The highest frequencies of mtDNA L types (5.8%) were found in the Portuguese. Table 2 shows the nucleotide sequences of the African HVS1 variants found in Europeans. These types of mtDNA were represented by two groups; one of them comprised mitochondrial lineages identical to those found in African populations (i.e., they had already been found in Africa), and the other one, the sequences homologous (not identical) to African lineages (Table 2). Since mtDNA lineages identical to African lineages are likely to have appeared in Europe recently, the second group of mtDNAs differing from African ones in

Table 2. African mtDNA lineages found in different European populations

mtDNA cluster	HVS1 nucleotide sequence	Identical to African mtDNA	Homologous to African mtDNA
L0a1#	129-148-168-172-187-188G-189-223-230-311-320	Germans (3), portuguese (1)	
L0a1	129-148-**166**-168-172-187-188G-189-223-230-311-320		Albanians (1)
L1b#	126-187-189-223-264-270-278-311	Spaniards (1)	
L1b	126-**175**-189-223-264-270-278-311		Germans (1), russians (1)
L1b	126-**145**-187-189-223-264-270-278-**293**-311	Portuguese (1)	
L1b	126-187-189-223-264-270-278-**293**-311-**362**		Portuguese (1)
L1b	**114CA**-126-187-189-223-264-270-278-**293**-311-**362**		Portuguese (1)
L1b	126-187-189-223-264-270-**274**-278-**293**-311-**362**		Bosnians (1)
L1b	126-223-264-270-278-311		Spaniards (1)
L1b	126-187-189-223-264-278-311	Spaniards (1)	
L1c3	129-189-215-223-278-**284**-294-311-360		English (1)
L2aα3#	189-192-223-278-294-390	Portuguese (1), italians (1)	
L2aα3	189-192-223-278-294-**309**-390	Portuguese (1)	
L2aα3	189-192-223-**260**-278-294-390		Portuguese (1)
L2aα3	189-192-223-**260**-278-294-**309**-390		Portuguese (1)
L2aβ1#	223-278-294-309-390	Portuguese (1)	
L2aβ1	223-278-294-309-**357**-390		Portuguese (1)
L2aβ1	**93**-223-278-294-309-**311**-**320**-390		Portuguese (1)
L2aβ1	**169**-**188**-223-**239**-278-294-309-390		Portuguese (1)
L2aβ2	**111A**-189-223-278-294-309-390		Portuguese (1)
L2aβ2	189-223-278-294-309-**317T**-390		Portuguese (1)
L2aβ2	189-223-278-294-309-**311A**-390		Portuguese (1)
L2a1bγ2	189-223-278-290-**292**-294-309-390		Portuguese (1)
L2a1bγ2	**86**-189-223-278-290-294-309-390		Norwegians (1)
L2b	114A-129-213-223-**234**-278-390		Spaniards (1)
L2b	**93**-114A-129-213-223-**271**-278-390		Portuguese (1)
L3b	**111**-124-223-**245**-278-362		Portuguese (1)
L3b	**93**-124-223-278-362	Spaniards (1)	
L3b	223-278-362	Norwegians (1)	
L3b	124-223-278-**294**-362		Russians (1)
L3b	223-278-**294**-362		Italians (1)
L3d#	124-223	Poles (1)	
L3d1#	124-223-319	Germans (2)	
L3d2	**93**-124-223-256		Portuguese (1)
L3d*	**111**-124-223-**311**		Portuguese (1)
L3e1a	**169**-223-327		Portuguese (1)
L3e1b	**145**-223-**256**-325D-330		Portuguese (1)
L3e2b#	172-189-223-320	Portuguese (1)	
L3e2b	172-189-223-**248**-320		Portuguese (1)
L3e3#	223-265T	Portuguese (1)	
L3e3	**189**-223-265T	Portuguese (1)	
L3e3	**93**-223-265T-**278**		French (1)
L3f #	209-223-311		Portuguese (1)
L3f	**167**-209-223-311		Portuguese (1)
L3f	209-223		Icelanders (1)

Note: # indicates the ancestral variants of mtDNA monophyletic clusters, i.e., the central (root) haplotypes from which all other (derivative) mtDNA haplotypes have originated. Transitions relative to the Cambridge Reference Sequence of mtDNA [15] are shown; the transversion types are indicated additionally. Positions at which HVS1 nucleotide sequences differ from the ancestral mtDNA variants are boldfaced. The number of subjects with the given mtDNA type is indicated in parentheses.

Table 3. Europe-specific clusters of mtDNA of African origin

mtDNA cluster	HVS1 nucleotide sequence	Population
I (L1b)	126-187-189-223-264-270-278-**293**-311-**362**	Portuguese (1)
I (L1b)	**114CA**-126-187-189-223-264-270-278-**293**-311-**362**	Portuguese (1)
I (L1b)	126-187-189-223-264-270-**274**-278-**293**-311-**362**	Bosnians (1)
II (L3b)	124-223-278-**294**-362	Russians (1)
II (L3b)	223-278-**294**-362	Italians (1)

Note: Positions at which HVS1 nucleotide sequences differ from the ancestral mtDNA variants are boldfaced. The number of subjects with the given mtDNA type is indicated in parentheses.

some nucleotide substitutions is the most interesting. As evident from Table 2, these mtDNA types are highly prevalent in European populations: about 70% of mitochondrial lineages found in Europe are not identical to those found in Africa. The origin of these mtDNA lineages is still unclear and may be explained in two ways, depending on whether or not African mtDNA lineages are presumed to have spread to Europe long ago and have evolved independently due to mutation process. The existence of European variants of African mtDNA types may be explained by the insufficient size of the African sample analyzed. Therefore, we may assume that European variants of African mtDNA lineages are also present in African populations, but they have not been found in population studies. This implies that the evolution of African mtDNA lineages has occurred exclusively in Africa. This hypothesis also agrees with the assumption that African mtDNA lineages found in Europe are very rare in Africa or even have disappeared there altogether, but have been preserved in Europe. Although the analyzed database contained more than 3000 nucleotide sequences of HVS1 of the African populations of Africa and America [1, 2, 17], this does not prove that European variants of African mtDNA lineages appeared in Europe independently. Some African lineages may have spread to Europe so long ago that mutations have already accumulated in them. Therefore, analysis of European variants of African mtDNA lineages aimed at searching phylogenetic branches whose evolution occurred only in Europe seems more reliable. These branches must be represented by monophyletic clusters of mtDNA types, rather than single mitochondrial lineages. The analysis demonstrated that, despite the diversity of African mtDNA lineages in European populations (especially in the Portuguese), Europe-specific clusters of mtDNA of African origin but which formed in Europe are very few. We found only two such clusters (Table 3). The European variant of cluster L1b (designated I-L1b in Table 3) differs from African clusters by a mutation at position 16,362 and some additional mutations found in southern European populations (in Portuguese, Spaniards, and Bosnians). In addition, L3b mtDNA sequences were found in Europeans (Russians and Italians) (this cluster is designated II-L3b in Table 3). They differed from African L3b lineages in a mutation at position 16,294 and from one another in a mutation at position 16,124. The divergence between HVS1 types included in both clusters was small (0.11–0.2). No more than 6500 yr was necessary to achieve this level (2215 ± 806 and 4028 ± 2417 yr for $\rho = 0.11$ and $\rho = 0.2$, respectively).

The mtDNA lineage found in the Tula sample of Russians (sequence 126–175–189–223–264–270–278–311 in Table 3) belongs to haplogroup L1b. Interestingly, the same mtDNA lineage was found in Germans. Analysis of mtDNA variation demonstrated that this L1b type of HVS1 differed from African variants in a mutation at position 16 175. As can be seen in Table 3, the gene pools of European populations contained many individual mtDNA types differing from their ancestral African variants of mtDNA in mutations at only one or two nucleotide positions. However, they did not form any monophyletic clusters of haplotypes and were not characterized by an old evolutionary age, because no more than 10,000 yr are necessary for the appearance of one difference in mutation between two HVS1 nucleotide sequences [19]. Thus, irrespective of whether the observed single European variants of African mtDNA lineages were formed in Europe or whether they will yet be found in African populations, analysis of mtDNA variation in Eurasian populations shows that there are no "branched" monophyletic clusters that have African origin but have formed in Eurasia. This is surprising, taking into account the long history of contact between races.

Table 4 shows the comparison of the frequencies of alleles of the autosomal microsatellite loci found in Russians with mitochondrial haplotypes of African origin in European, African, and Russian populations. We found that the autosomal haplotypes of the Russians carrying African mtDNA haplotypes were mainly characterized by alleles common to European and African populations. However, Russians had alleles that are characteristic of Europeans but are extremely rare in Africans (e.g., *D13S317*8*, *D13S17*9*, *D81179*10*, and *D19S433*15* in an L1b

Table 4. Autosomal STR genotypes in Russian carriers of African mtDNA haplotypes (L3b and L1b) and STR allele frequencies in African, European, and Russian populations

Locus	Allele	Genotype of the sample with mtDNA haplotype		Allele frequencies in populations of		
		L3b	L1b	africans	europeans	russians
D3S1358				2N = 4242	2N = 4042	2N = 1170
	14	+		0.097[1]	0.117	0.109
	15		+	0.286[1]	0.253	0.268
	16		+	0.35[1]	0.244[3]	0.309[2]
	17	+		0.209	0.204	0.198
VWA				2N = 1562	2N = 7968	2N = 1170
	16		+	0.258[1]	0.222	0.213[2]
	18		+	0.142[1]	0.192[3]	0.223[2]
	19	++		0.06	0.074[3]	0.092[2]
FGA				2N = 634	2N = 7286	2N = 1170
	20	+		0.061[1]	0.14	0.15[2]
	22		+	0.125[1]	0.196	0.215[2]
	23.2		+	0	0.005	0.003
	24	+		0.194[1]	0.131	0.126[2]
TH01				2N = 1766	2N = 7968	2N = 366
	6		++	0.097[1]	0.237	0.221[2]
	9	+		0.152[1]	0.187[3]	0.23[2]
	10	+		0.013[1]	0.081[3]	0.003
TPOX				2N = 966	2N = 7968	2N = 366
	7	+		0.02[1]	0.001	0[2]
	8	+	+	0.396[1]	0.533	0.566[2]
	11		+	0.203[1]	0.261	0.249
CSF1PO				2N = 284	2N = 7286	2N = 366
	10	+	+	0.27	0.283	0.257
	11		+	0.22[1]	0.324[3]	0.273
	12	+		0.24	0.276	0.243
D5S818				2N = 5048	2N = 2254	2N = 1170
	11	+	++	0.245[1]	0.33	0.346[2]
	13	+		0.232[1]	0.169	0.153[2]
D13S317				2N = 5048	2N = 2254	2N = 1170
	8		+	0.011[1]	0.129	0.146[2]
	9		+	0.011[1]	0.081	0.091[2]
	11	++		0.301	0.291[3]	0.355[2]
D7S820				2N = 5048	2N = 2254	2N = 1170
	9	+		0.133	0.149	0.152
	10	+	+	0.335[1]	0.277	0.272[2]
	12		+	0.098[1]	0.157	0.153[2]
D16S539				2N = 216	2N = 1386	2N = 366
	11	+	++	0.255	0.296	0.298
	13	+		0.139	0.177	0.191
D2S1338				2N = 216	2N = 860	2N = 366
	20		+	0.13	0.141	0.134
	22	+		0.097[1]	0.026	0.014[2]
	24	+		0.065	0.106	0.085
	25		+	0.079	0.10	0.096

Table 4. (Contd.)

Locus	Allele	Genotype of the sample with mtDNA haplotype		Allele frequencies in populations of		
		L3b	L1b	africans	europeans	russians
D8S1179				2N = 5802	2N = 2254	2N = 1170
	10		+	0.001[1]	0.084[3]	0.055[2]
	12	+		0.121	0.134[3]	0.177[2]
	14		+	0.341[1]	0.224	0.231[2]
	15	+		0.215[1]	0.126	0.105[2]
D21S11				2N = 4242	2N = 4042	2N = 1170
	28	+		0.269[1]	0.156	0.149[2]
	29	+	++	0.151[1]	0.217	0.207[2]
D18S51				2N = 5048	2N = 2254	2N = 1170
	11	+		0.001[1]	0.014	0.015[2]
	15		+	0.153	0.158	0.18[2]
	17		+	0.176[1]	0.111	0.126[2]
	20	+		0.052[1]	0.023	0.022[2]
D19S433				2N = 216	2N = 872	2N = 366
	13	++		0.241	0.233	0.213
	14		+	0.166[1]	0.333	0.372[2]
	15		+	0.028[1]	0.151	0.156[2]

Note: (+) indicates the alleles found only in Russian carriers of African mtDNA variants; (++) indicates homozygous genotypes of the corresponding locus. The mean STR allele frequencies in European and African populations are indicated according to the ALFRED database [21]; the allele frequencies in Russians, according to [20] (2N = 804) and unpublished data of the same authors (2N = 366). 2N is the total number of alleles in the sample. Superscripts indicate the pairs of allele frequencies significantly ($P < 0.05$) differing in the following populations: [1]African versus Europeans, [2]Africans versus Russians, and [3]Europeans versus Russians.

subject and *D18S51*17* in an L3b subject), which indicates their European origin. Only two alleles found in an L3b Russian subject (*D2S1338*22* and *TPOX*7*) were frequent in Africans but extremely rare or absent in Russians. Apparently, these alleles are a genetic trace of a past mixing of races. Thus, the results indicate that the mtDNA lineages of African origin found in Russians were not a recent African admixture. In general, analysis of mtDNA variation in Eurasian populations has demonstrated that, despite long contact between European and African populations (especially in southern Europe) and the possibility of independent evolution of African mtDNA lineages in the European gene pool, there are no monophyletic clusters of African origin that could have formed during a long mutation process in Europe.

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