

Population Structure of Volga Tatars Inferred from the Mitochondrial DNA Diversity Data

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Abstract—The data on mitochondrial DNA (mtDNA) variation in two populations of Volga Tatars, representing the population of Buinsk and Aznakaevo districts of the Republic of Tatarstan are presented. Comparative analysis of the data on mtDNA variation in the populations of Eastern Europe showed that Volga Tatars were characterized by low interpopulation differentiation ($F_{ST} = 0.33\%$), while the level of interethnic differentiation in Eastern Europe is 1.8%. Genetic similarity of Tatars from the eastern regions of Tatarstan to Bashkirs, as well as of Tatars from western regions to Chuvashes, with whom they share territorial borders, was revealed. Positive correlation between population genetic structure in Eastern Europe and linguistic affiliation of the ethnic groups studied was observed.

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INTRODUCTION

It is thought that Volga Tatars originating from Turkic-speaking tribes, who in the early middle age spread across the territory of middle Volga and lower Kama region assimilating more ancient, probably Finno-Ugric and Scythian-Sarmat population of that part of Eastern Europe [1, 2]. The position of Volga region at the junction between Europe and Asia, between the steppe of the South and forests of the North, from the ancient times provided interethnic contacts. This geographic position has become the main reason for extremely complex ethnic history of the population of this region. Anthropologically, about 80% of Volga Tatars are characterized by Caucasoid traits, and only about 20%, by Mongoloid traits. In general, Volga Tatars are representatives of the Sub-Uralic type [3], while different territorial groups of Volga Tatars can have specific anthropological features due to polymorphism of anthropological characters [4]. Despite the fact that Tatars is the second largest population of the Russian Federation, they belong to the group of populations poorly studied in terms of genetics [5–7].

Analysis of the maternally inherited mitochondrial DNA (mtDNA) variation showed that among the populations of Volga–Ural region, Volga Tatars were characterized by rather high genetic diversity along with the intermediate frequencies (about 12%) of mtDNA haplogroups specific to the gene pools of the populations of East Eurasia (Siberia and Central, and East Asia) [5]. At the same time, it should be noted that the data on nucleotide variation of the mtDNA

control region hypervariable segment 1 (HVS1) available from literature were obtained from the population of only two districts of the Republic of Tatarstan, Almetyevsk district and Elabuga district [5, 6]. For these reasons, further investigation of the mtDNA polymorphism in Volga Tatar populations seems quite reasonable. This study presents the data on the mtDNA variation (at the level of HVS1 nucleotides and single nucleotide substitutions in the coding region, determining the mtDNA haplogroups) in two populations of Volga Tatars from the Buinsk and Aznakaevo districts of the Republic of Tatarstan. Interpopulation relationships were analyzed taking into consideration the data on the mtDNA HVS1 sequence variation in the populations of Eastern Europe.

MATERIALS AND METHODS

Genomic DNA was isolated from the blood samples obtained from unrelated individuals representing two ethnogeographic groups of Tatars, Kazan Tatars and Mishari Tatars. The sample of Kazan Tatars was collected in the Azanakovo district of the Republic of Tatarstan ($N = 71$). Mishari Tatars were represented by a dispersed sample from the Buinsk district of the Republic of Tatarstan ($N = 126$). The material was collected during expeditions in 2004 through 2005. Ethnic affiliation of the individuals was determined using individual questionnaires and taking into consideration the data down to the third generation.

Sequences of the mtDNA HVS1 were determined using the method of capillary DNA sequencing and an

Table 1. Populations of Eastern Europe used in comparative analysis of the mtDNA HVS1 sequence variation

Populations	<i>N</i>	Sampling locality	Literature source
Tatars-1	71	Aznakaevo district of Tatarstan	This work
Tatars-2	126	Buinsk district	This work
Tatars-3	223	Almetyevsk and Elabuga districts of Tatarstan	[5]
Tatars-4	45	Almetyevsk and Elabuga districts of Tatarstan	[6]
Bashkirs	209	Different districts of Bashkortostan	[5]
Chuvashes	56	Morgaushi district of Chuvashia	[5]
Mordovians	99	Staroe Shaigovo district of Mordovia	[5]
Maris-1	136	Zvenigovo district Republic of Mari El	[5]
Maris-2	60	Morkinsk district Republic of Mari El	[6]
Udmurts	112	Malaya Purga district of Udmurtia	[5]
Komi-Permyaks	68	Perm' Krai	[5]
Komi-Zyryans	61	Sysol'skii district of Komi Republic	[5]
Estonians	47	Tallinn, Estonia	[13]
Karelians	83	Petrozavodsk, Karelia	[13]
Russians-1	68	Belgorod oblast	[14]
Russians-2	74	Nizhnii Novgorod oblast	[14]
Russians-3	79	Novgorod oblast	[15]

Note: *N*, sample size

ABI 3130 genetic analyzer (Applied Biosystems, Foster City, United States). The sequencing data were analyzed with the help of the SeqScape v. 2.5 software package (Applied Biosystems, Foster City, United States). Single nucleotide polymorphisms determining the mtDNA haplogroups were examined with the help of restriction analysis [8, 9].

Computation of the genetic diversity indices and analysis of interpopulation differentiation (AMOVA) were carried out using the ARLEQUIN 3.11 software package [10]. The correlation between the matrices of genetic, geographic, and linguistic distances was evaluated using Mantel test [11] (1000 permutations) implemented in the ARLEQUIN 3.11 package. The matrix of pairwise genetic differentiation index (F_{ST}) values between the populations was used as a genetic distance. The matrix of linguistic distances was constructed using the approach suggested by V.A. Stepanov [12]. Specifically, the distance between the populations belonging to different linguistic families was taken as 1.00; in case that pair of populations belonged to one linguistic family, 0.50; and in case that populations belonged to one group within the linguistic family, 0.25. The distances (in km) between the settlements were determined with the help of the Calculator for Distances between Geographical Locations (<http://www.go.ednet.ns.ca/~larry/bsc/jslatng.html>). The matrix of pairwise genetic differentiation index (F_{ST}) values was used for the reconstruction of phylogenetic relationships between the populations of Volga Tatars, as well as between them and the populations of

Volga–Ural region. For these purposes, factor analysis (the method of principle components), realized within the STATISTICA 6.0 software package, was used.

For comparative analysis, literature data on polymorphism of the mtDNA HVS1 in Volga–Ural populations (Tatars, Bashkirs, Chuvashes, Maris, Mordovians, Komi-Permyaks, Komi-Zyryans, and Udmurts) [5, 6], in Estonians and Karelians [13], as well as in three population samples of Russians from Belgorod oblast, Nizhnii Novgorod oblast, and Novgorod oblast [14, 15], were used (Table 1).

RESULTS AND DISCUSSION

Based on the HVS1 variation and polymorphism of the restriction endonuclease recognition sites, determining the mtDNA haplogroups, mitochondrial gene pools of the two populations of Volga Tatars, from Buinsk and Aznakaevo districts of the Republic of Tatarstan were characterized (Table 2). A total of 27 mtDNA haplogroups were identified. Among these, the most frequent in Tatars were the haplogroups widespread in the populations of Western Eurasia (Europe and West Asia). The frequency of Eastern Eurasian component was 24% in the population of Aznakaevo district and 12% in the population from Buinsk district (Table 2). According to the data of Bermisheva et al. [5], the frequency of Eastern Eurasian mtDNA variants in Tatars from Almetyevsk and Elabuga districts was 12.8%. Thus, Volga Tatars occupy the intermediate position among the ethnic groups of

Table 2. Frequency of mtDNA haplogroups in Volga Tatars

Haplogroup	Kazan Tatars Tatars-1 (<i>N</i> = 71)	Mishari-Tatars Tatars-2 (<i>N</i> = 126)
A	4.2 (3)	3.2 (4)
C	5.6 (4)	0
D	9.9 (7)	4.8 (6)
G	0	1.6 (2)
M10	0	0.8 (1)
M7b	0	0.8 (1)
N9a	1.4 (1)	0
Y	0	0.8 (1)
Z	2.8 (2)	0
East Eurasian component	23.9 (17)	11.9 (15)
H	32.4 (23)	34.1 (43)
I	5.6 (4)	1.6 (2)
J	7.0 (5)	7.1 (9)
K	0	4.8 (6)
M1	0	1.6 (2)
N1a, b, c	0	2.4 (3)
R2	1.4 (1)	0
T	2.8 (2)	4.8 (6)
T1	5.6 (4)	0.8 (1)
U1	0	0.8 (1)
U2	1.4 (1)	0
U3	0	1.6 (2)
U4	5.6 (4)	8.7 (11)
U5	2.8 (2)	4.0 (5)
U8a	0	4.0 (5)
HV0	2.8 (2)	6.3 (8)
W	7.0 (5)	5.6 (7)
X	1.4 (1)	0
West Eurasian component	76.1 (54)	88.1 (111)

Volga–Ural region, characterized by high (more than 20% in Bashkirs and Udmurts) and moderate frequencies (less than 10% in Chuvashes, Maris, and Mordoviants) of Eastern Eurasian variants of mtDNA [5].

Analysis of the mtDNA HVS1 sequence diversity in the populations of Eastern Europe indicated that the indices of genetic diversity in Tatars from Aznakaevo and Buinsk districts were generally consistent with those for other populations of Volga–Ural region (Table 3). Compared to the other two samples of Volga Tatars examined earlier [5, 6], it should be noted that the sample from the westernmost Buinsk district was characterized by the lowest values of genetic diversity indices. This finding can be partly explained by lower frequency of Eastern

Eurasian mtDNA lineages, providing the increase of within-population heterogeneity.

To analyze the population structure of Tatars, using the mtDNA haplogroup and individual HVS1 haplotype distributions, the interpopulation differentiation was examined. The analysis showed that in Eastern Europe the degree of interethnic differentiation (F_{ST}) over the mtDNA haplogroups constituted 2.6%. At the same time, interpopulation differentiation in Volga Tatars was an order of magnitude lower, 0.26%. Moreover, all pairwise F_{ST} differences between the Tatar samples were not statistically significant. In case of the analysis of differentiation at the level of mtDNA HVS1 haplotypes, the value of interpopulation differences for the four samples of Volga Tatars constituted 0.33% ($P = 0.04$). In some cases of pairwise comparisons, statistically significant F_{ST} differences between individual Tatar samples were observed (Table 4). It was also demonstrated that Tatars from Aznakaevo district were statistically significantly indifferent from Bashkirs, while Tatars from Binsk district were statistically significantly indifferent from Chuvashes. These findings can be explained by geographical closeness of Aznakaevo district (eastern Tatarstan) to Bashkortostan and of Buinsk district (west of Tatarstan) to Chuvashia (Table 4).

Based on analysis of pairwise nucleotide differences between the mtDNA HVS1 haplotypes, interethnic differentiation of the populations of Eastern Europe constituted 1.8% ($P < 0.001$). This value was much higher than that for ethnic groups of Central Europe ($F_{ST} = 0.1\%$; $P = 0.1$, for Slovaks, Czechs, Poles, Austrians, southern Germans, Bosnians, and Slovenians [16]), but substantially lower than that for the populations of Central Asia ($F_{ST} = 2.34\%$; $P < 0.0001$) [17], and South Siberia ($F_{ST} = 2.86\%$; $P < 0.001$) [18]. At the same time, the degree of interpopulation differentiation of Volga Tatars ($F_{ST} = 0.33\%$; $P = 0.04$) fits that in Russian population of Eastern Europe ($F_{ST} = 0.35\%$; $P = 0.009$) [19].

To identify the factors determining patterns of genetic relationships between the populations of Eastern Europe, a principal components factor analysis was carried out (figure). The first three principle components account for 92.3% of total variation. Furthermore, 58% of total variation is explained by the first component; 26.5%, the second component and 7.8%, the third component. In the space of the first two components, two large population clusters can be identified. The first cluster joins the populations of Komi-Zyryans, Mordoviants, Karelians, Estonians, and three Russian population samples. All populations of this cluster were characterized by statistically significant loadings on the first factor (the loadings with absolute values higher than 0.7 were considered as statistically significant). The second cluster was formed by three Tatar samples (Tatars-1, Tatars-2, and Tatars-4), Bashkirs, and Komi-Permyaks, characterized by statistically significant loadings on the second factor. The

Table 3. Genetic diversity indices in the populations of Eastern Europe inferred from the mtDNA HVS1 variation data

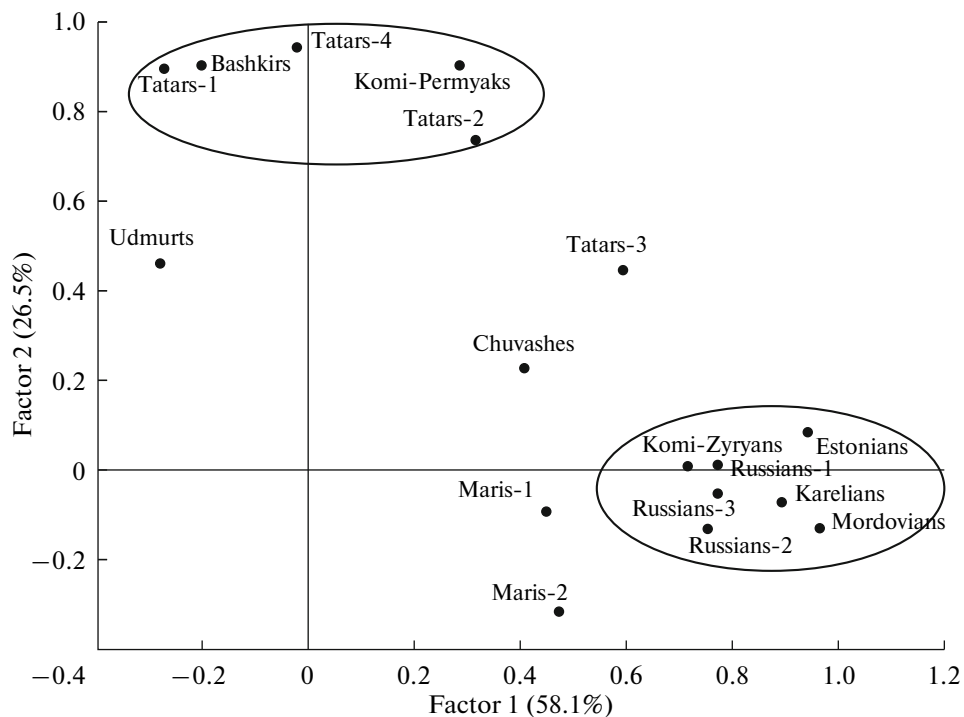
Populations	<i>N</i>	<i>H</i> (SE)	<i>K</i>	<i>Pi</i> (SE)	π (SE)
Tatars-1	71	0.958 (0.014)	35	4.841 (2.391)	0.012 (0.007)
Tatars-2	126	0.957 (0.011)	66	4.162 (2.082)	0.010 (0.006)
Tatars-3	223	0.977 (0.005)	112	4.957 (2.421)	0.012 (0.007)
Tatars-4	45	0.986 (0.009)	35	5.360 (2.634)	0.013 (0.007)
Bashkirs	209	0.988 (0.002)	101	6.057 (2.896)	0.015 (0.008)
Chuvashes	56	0.982 (0.008)	39	4.684 (2.329)	0.012 (0.006)
Mordovians	99	0.973 (0.009)	59	4.625 (2.288)	0.012 (0.006)
Maris-1	136	0.928 (0.012)	35	3.565 (1.823)	0.009 (0.005)
Maris-2	60	0.924 (0.018)	21	3.981 (2.019)	0.010 (0.006)
Udmurts	112	0.963 (0.006)	39	6.320 (3.020)	0.016 (0.008)
Komi-Permyaks	68	0.963 (0.012)	35	5.388 (2.629)	0.013 (0.007)
Komi-Zyryans	61	0.954 (0.012)	29	4.104 (2.073)	0.010 (0.006)
Estonians	47	0.983 (0.009)	35	4.056 (2.060)	0.010 (0.006)
Karelians	83	0.964 (0.011)	45	3.958 (2.002)	0.010 (0.006)
Russians-1	68	0.969 (0.012)	47	4.282 (2.148)	0.011 (0.006)
Russians-2	74	0.961 (0.016)	50	4.224 (2.120)	0.011 (0.006)
Russians-3	79	0.980 (0.008)	54	5.091 (2.496)	0.0127 (0.007)

Note: *N*, sample size; *H*, genetic diversity; *K*, the number of genotypes identified; *Pi*, mean number of pairwise differences; π , nucleotide diversity; SE, standard errors (in brackets).

two Mari samples and Chuvashes grouped together by the third component.

To determine the factors mostly responsible for the genetic diversity pattern, populations of Eastern Europe were grouped in accordance to ethnolinguistic classification, or with respect to geographic locality

(Table 5). Maximum values of interpopulation variation were obtained if the populations were grouped in accordance to their affiliation to linguistic groups (0.71%). However, in none of the grouping variants the proportion of differences between the groups was higher than the differences between the populations



Distribution of the populations in the space of the two principle components based on factor analysis of the matrix of F_{ST} values between the populations. In ovals are the populations having statistically significant loadings on the first and second components.

Table 4. Matrix of the genetic differentiation index (F_{ST}) values inferred from the mtDNA HVSI variation data

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Tatars-1	0.000																
2 Tatars-2	0.008	0.000															
3 Tatars-3	0.013	0.001	0.000														
4 Tatars-4	-0.004	-0.004	-0.004	0.000													
5 Bashkirs	0.005	0.016	0.018	0.005	0.000												
6 Chuvashes	0.023	0.005	0.001	0.003	0.013	0.000											
7 Mordovians	0.030	0.020	0.010	0.016	0.029	0.015	0.000										
8 Maris-1	0.034	0.011	0.007	0.016	0.029	-0.002	0.017	0.000									
9 Maris-2	0.045	0.023	0.013	0.024	0.036	0.008	0.020	0.006	0.000								
10 Udmurts	0.016	0.040	0.034	0.017	0.031	0.042	0.034	0.054	0.055	0.000							
11 Komi-Permyaks	0.009	0.010	0.007	-0.001	0.008	0.011	0.016	0.028	0.036	0.024	0.000						
12 Komi-Zyryans	0.040	0.020	0.013	0.014	0.038	0.014	0.017	0.018	0.026	0.047	0.016	0.000					
13 Estonians	0.024	0.008	0.003	0.005	0.023	0.009	-0.003	0.015	0.019	0.035	0.005	0.007	0.000				
14 Karelians	0.032	0.015	0.009	0.016	0.025	0.007	0.000	0.012	0.016	0.043	0.016	0.018	-0.006	0.000			
15 Russians-1	0.020	0.006	-0.001	0.006	0.020	0.004	-0.001	0.005	0.007	0.035	0.011	0.017	0.000	0.002	0.000		
16 Russians-2	0.033	0.011	0.002	0.013	0.033	0.008	0.007	0.008	0.006	0.050	0.022	0.013	0.001	0.006	-0.001	0.000	
17 Russians-3	0.027	0.014	0.007	0.014	0.023	0.007	0.004	0.012	0.010	0.041	0.018	0.025	0.004	0.005	-0.004	0.004	0.000

Note: The F_{ST} index values statistically insignificant at $P \leq 0.05$ are in Italic type.

Table 5. Genetic differences among the populations of Eastern Europe, grouped in accordance to the linguistic and geographic data

Population groups	Number of populations	Number of groups	Differences, %		
			within the populations	among the populations within the groups	among the groups
Eastern Europe	17	1	98.20	1.8	—
Linguistic ¹	17	3	98.06	1.51	0.43
Linguistic ²	17	6	98.07	1.22	0.71
Geographic ³	16	3	97.88	1.46	0.66

Note: ¹, Populations grouped according to the linguistic group affiliation: Turkic group of Altaic linguistic family, Tatars, Bashkirs, Chuvashes; Finno-Ugric group of Uralic linguistic family, Mordovians, Maris, Udmurts, Komis, Estonians, Karelians; Slavic group of Indo-European linguistic family, Russians. ², Populations grouped in accordance to the linguistic subgroup affiliation: Northeastern subgroup, Tatars and Bashkirs; Bulgar subgroup, Chuvashes; Volga-Finnic subgroup, Mordovians and Maris; Perm' subgroup, Udmurts and Komis; Baltic-Finnic subgroup, Estonians and Karelians; eastern Slavic subgroup, Russians. ³, Geographic population groups: northwestern, Estonians, Karelians, and Russians-3; Volga region group, Tatars, Chuvashes, Mordovians, Maris, and Russians-2; Uralic group, Komis, Udmurts, and Bashkirs. The value in *italic type* is not statistically significant ($P = 0.06$), other differences are statistically significant ($P < 0.03$).

within the groups. These findings suggest the absence of correlation between the genetic diversity pattern typical of the populations of Eastern Europe examined and the geographic distribution. On the other hand, these data point to small influence of the linguistic factor on interpopulation genetic differentiation.

Analysis of correlation between the matrices of genetic, geographic, and linguistic distances, performed using Mantel's test, showed that in Eastern Europe there was statistically significant correlation between the genetic distance matrix and linguistic affiliation of the populations examined ($r = 0.147$; $P = 0.025$) (Table 6). Upon constant geographic distances, the value of partial correlation coefficient between genetic and linguistic distance matrices was high and statistically significant ($r = 0.155$; $P = 0.03$), confirming the existence of association between the gene pool structure of the populations examined and their linguistic affiliation. At the same time, even in this case, for the populations of Eastern Europe examined no direct correlation between genetic and geographic distances was observed.

Thus, analysis of mtDNA diversity performed made it possible to gain insight into the level and pattern of interpopulation differentiation in Volga Tatars, which is thought to be an important step in under-

standing molecular phylogeography of the population of Eastern Europe.

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Table 6. Correlation between genetic, geographic, and linguistic distance matrices analyzed with the help of Mantel test

Distance matrices	r	P
Genetic and geographic	−0.012	0.495
Genetic and linguistic	0.147	0.025
Geographic and linguistic	0.257	
Genetic and geographic (upon constant linguistic distances)	−0.052	0.604
Genetic and linguistic (upon constant geographic distances)	0.155	0.03

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