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Mitochondrial DNA Variation in Russian Populations of Stavropol Krai, Orel and Saratov Oblasts

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Abstract—Mitochondrial DNA (mtDNA) polymorphism was examined in three Russian populations from the European part of Russia (Stavropol krai, Orel oblast, and Saratov oblast). This analysis showed that mitochondrial gene pool of Russians was represented by the mtDNA types belonging to haplogroups H, V, HV*, J, T, U, K, I, W, and X. A mongoloid admixture (1.5%) was revealed in the form of mtDNA types of macrohaplogroup M. Comparative analysis of the mtDNA haplogroup frequency distribution patterns in six Russian populations from the European part of Russia indicated the absence of substantial genetic differences between them. However, in Russian populations from the southern and central regions the frequency of haplogroup V (average frequency 8%) was higher than in the populations from more northern regions. Based on the data on mtDNA HVS1 sequence variation, it was shown that the diversity of haplogroup V in Russians ($h = 0.742$) corresponded to the highest h values observed in Europe. The reasons for genetic differentiation of the Russian population (historical, ecological, and adaptive) are discussed.

INTRODUCTION

The ethnogeny of Eastern Slavs is a complex process which, beginning from the early Middle Ages, involved ancient autochthonous population of Eastern Europe and migrant, proper Slavic populations [1, 2]. The lack of written documentation testifying to an extensive population expansion from the central European pre-homeland of Eastern Slavs to the territory of Eastern Europe along with anthropological data indicating that medieval eastern Slavic tribes were less similar to western European populations of the same time than contemporary groups of Eastern Slavs fit the hypothesis that the formation of eastern Slavic tribes was accompanied by the processes of slow demic diffusion from the different parts of central European area of Slavs [3]. According to anthropological data, admixture played a crucial role in the formation eastern Slavic tribes [4]. It is hypothesized that a substantial part of ancient populations of southern Russian steppe (till the middle of the 2 millennium B.C.E.) were the ancestors of eastern Slavic populations [3]. Application of integral cartographical analysis to anthropological investigations showed that at the background of pre-Slavic features, modern Russians contain some features typical to annalistic Slavs [5]. This similarity is most vivid in the western part of the Russian area.

The studies of geographic variations of the HLA allele and genotype frequencies along with the examination of allozyme polymorphism provided ample information on genetic structure of different eastern

Slavic populations. These investigations also offered an opportunity to determine genetic relationships between Slavs and their neighbors [6–8]. The evidence on gene-geographic position of Eastern Slavs among the ethnic groups of Eastern Europe, obtained by Balanovskaya and Nurbaev using the method of principal components to analyze the data on biochemical polymorphism, deserve special interest [9]. In this study an effect of close overlap between the “ethnic clouds” of three ethnic populations of Eastern Slavs was revealed, indicating that the gene pool of the right eastern Slavic community can be reproduced in most details in the region of the population overlap for the three ethnic groups. In the meantime, it was found that the “center of gravity” of Russian populations was located in one cluster with Finno-Ugric, but not Slavic ethnic groups. Moreover, Finno-Ugric populations were found to be located within the ethnic cloud of Russian populations, pointing to intense genetic relationships between Russian and Finno-Ugric populations of Eastern Europe. Gene cartographic analysis of allele frequency distribution patterns performed for several DNA loci in 28 populations representing eastern Slavic, Finno-Ugric, Turkic, and North Caucasian ethnic groups gave similar results [10]. These findings, however, do not permit unambiguous conclusions on the presence of substantial Finno-Ugric component in the gene pool of Russians.

Methods of analysis of variability in genetic systems characterized by the lack of recombinations and the inheritance in one of the parental lineages, represent a

promising modern approach to the investigation of the ethnic processes [11]. Maternally inherited mitochondrial DNA (mtDNA) is one of these highly polymorphic genetic systems [12]. Today, ample information on mtDNA variation in human population has been obtained. In eastern Slavic populations of Russia these issues, however, remain poorly studied. The data on mtDNA variation in a number of Russian [13] populations were in agreement with anthropological data testifying to homogeneity of anthropological features in Russians [1–4]. It was shown, however, that in ethnic territorial groups of Russians local variability prevailed over the typological one [1]. Because of this, it is reasonable to increase the number of population examined by means of molecular genetic methods.

In order to obtain more information on the structure and diversity of the Russian gene pool, we examined the distribution of mtDNA haplogroups in the populations of Stavropol krai, Orel oblast, and Saratov oblast. According to anthropological data [1], Russian population from the southern regions of the European part of Russia was formed under the influence of ancient populations of the steppe zone. The effect of North Caucasian populations also cannot be excluded. Russian population of the Middle Volga region, which by its origin is thought to be associated with the annalistic Krivichi tribes from Vladimir–Ryazan and Novgorod groups, was formed under the influence of Finno-Ugric (presumptive ancestors of Mordovians) and Turkic ethnic populations. Russian population of Orel oblast is ethnogenetically associated with the tribes of Severyans and Early Vyatiches mentioned in the chronicles.

MATERIALS AND METHODS

Biological material (whole blood samples) was obtained from oblast and raion clinical hospitals and blood transfusion centers. Population samples from Stavropol krai ($N = 62$), Orel oblast ($N = 76$), and Saratov oblast ($N = 63$) were examined. Judging by questionnaire data and analysis of case records, all individuals examined were unrelated Russians at least in two generations down the maternal lineage. The attribution of an individual to a certain territory was performed according to the birthplaces of the individuals tested and their mothers. Thus, Russians from Stavropol krai were represented by the natives of Mineral'nye Vody raion. The Orel sample was comprised by the natives of Orel, whose parents were the inhabitants of Orel oblast. Russians from Saratov oblast were represented by the natives of the oblast, who lived in the city of Saratov and Saratov oblast.

Genomic DNA from the blood spots on filter paper was extracted using standard techniques, including cell lysis by proteinase K (Sigma, United States) in the presence of 1% sodium dodecylsulphate, purification of DNA samples by use of phenol/chloroform, and precipitation of DNA with ethanol or ultrafiltration of

DNA on Microcon-100 columns (Amicon, United States).

Screening for polymorphic sites determining the main haplogroups of mtDNA types distributed in the populations of Eurasia (Table 1) was conducted through the analysis of mtDNA fragments amplified in polymerase chain reaction with the primers described in [15, 16]. Restriction fragments were separated by electrophoresis in 8% polyacrylamide gel. Gels were stained with ethidium bromide and DNA fragments were visualized in the UV light.

Polymorphism was scored by the presence (+) or absence (–) of restriction endonuclease recognition sites. Similarly to our previous studies [13], mtDNA types were identified based on classification of the haplogroups of mtDNA types in the populations of Eurasia [14, 15]. According to this classification, the haplogroups of mtDNA types are denoted by single Roman letters (excluding haplogroup HV), and subhaplogroups within the haplogroups, by digits added to the letter code of the group (Table 1). The mtDNA types that belong to a particular group but cannot be attributed to any of the known subhaplogroups, were designated by asterisks (e.g., T = T* + T1 in the present work).

Sequences for both strands of mtDNA control region hypervariable segment 1 (HVS1) between nucleotide positions 16024 and 16400 were determined by use of the Sanger method as described earlier [17]. Numbering of variable nucleotide positions was performed in accordance with the Cambridge Reference Sequence of human mtDNA [12].

Diversity of mtDNA types (h) was calculated according to Nei and Tajima [18]:

$$h = (1 - \sum x^2)N/(N - 1),$$

where x is the population frequency of each mtDNA type and N is the sample size.

Statistical significance of interpopulation differences with respect to the frequencies of mtDNA haplogroups was evaluated using the similarity index r , and the identity index I , [19].

RESULTS AND DISCUSSION

Analysis of the structure of mitochondrial gene pools of Russian populations from Stavropol krai, Orel oblast, and Saratov oblast showed that the Russian populations were characterized by similar haplogroups of mtDNA types (Table 2). Russian mitochondrial gene pool is represented by macrohaplogroups R, N, and M. Macrohaplogroup R is comprised of haplogroups H, V, HV*, J, T, U, and K. Of these, haplogroups H, J, T, and U, accounting for the overwhelming majority of mtDNA types (more than 65%) in the populations, are most common. Macrohaplogroup N in Russians is represented by phylogenetically related haplogroups I, W, and X, characterized by low prevalence in European populations [20]. Macrogroup M is comprised of haplo-

Table 1. Polymorphic restriction variants determining haplogroups of mtDNA types in the population of Eurasia

mtDNA haplogroup	Haplogroup-specific restriction variants
H	-14766 <i>MseI</i> , -7025 <i>AluI</i>
V	-14766 <i>MseI</i> , +15904 <i>MseI</i> , -16297 <i>MseI</i>
HV*	-14766 <i>MseI</i>
U	+12308 <i>HinfI</i>
K	+12308 <i>HinfI</i> , -9052 <i>HaeII</i> , +10394 <i>DdeI</i>
J	-13704 <i>BstNI</i> , +10394 <i>DdeI</i>
T*	+13366 <i>BamHI</i> , +15606 <i>AluI</i>
T1	+13366 <i>BamHI</i> , +15606 <i>AluI</i> , -12629 <i>AvaII</i>
I	-4529 <i>HaeII</i> , +8249 <i>AvaII</i> , +16389 <i>BamHI</i> , +10032 <i>AluI</i>
W	+8249 <i>AvaII</i> , -8994 <i>HaeIII</i>
X	+14465 <i>AccI</i>
M:	+10394 <i>DdeI</i> , +10397 <i>AluI</i>
C	+10394 <i>DdeI</i> , +10397 <i>AluI</i> , -13259 <i>HincII</i> +13262 <i>AluI</i>
D	+10394 <i>DdeI</i> , +10397 <i>AluI</i> , -5176 <i>AluI</i>
E	+10394 <i>DdeI</i> , +10397 <i>AluI</i> , -7598 <i>HhaI</i>
G	+10394 <i>DdeI</i> , +10397 <i>AluI</i> , +4830 <i>HaeII</i> +4831 <i>HhaI</i>
A	+663 <i>HaeIII</i>
B	9-bp deletion
F	-12406 <i>HpaI/HincII</i>

Note: Haplogroups of mtDNA were designated according to classification proposed in [14]. Positions of polymorphic sites are indicated with respect to the Cambridge Reference Sequence of human mtDNA [12].

Table 2. Frequency distribution patterns of mtDNA haplogroups (%) in three Russian populations

Haplogroups/sub-haplogroups of mtDNA	Stavropol krai (N = 62)	Orel oblast (N = 76)	Saratov oblast (N = 63)
H	35.48	47.37	41.27
V	8.06	3.95	4.76
HV*	1.61	1.32	1.59
J	4.84	11.84	6.35
T*	4.84	7.89	12.70
T1	1.61	1.32	3.17
U	19.35	15.80	19.05
K	4.84	2.63	1.59
I	4.84	1.32	1.59
W	4.84	1.32	0
X	8.06	1.32	1.59
M	0	1.32	3.17
“Other”	1.63	2.61	3.17

groups C, Z, D, E, G, and M*, predominantly distributed among Asian Mongoloids [14, 20]. The frequency of the M haplogroup-specific mtDNA types in Russians is usually low. In the samples tested Mongoloid admixture with the frequency of 3.2% was found in the Saratov sample in the form of sporadic mtDNA types from haplogroups M* and G, and with the frequency of 1.3% in Orel sample, in the form of mtDNA type belonging to haplogroup D.

Table 3 demonstrates average frequencies of mtDNA haplogroups observed in three Russian population samples, examined in the present work and in the samples from Krasnodar krai, Belgorod, and Niznii Novgorod oblast, examined by us earlier [13]. Russian populations were characterized by similar mtDNA haplogroups frequency distribution patterns compared to the gene pools of the populations from the neighboring regions of Europe (Table 3). Low differentiation level of European population was reported in many studies. It probably reflects common genetic origin of the European populations [15]. Among genetic features distinguishing Russians from their neighbors, a low frequency of haplogroup K (1.8%) deserves special interest. This feature brings Russians somewhat closer to Finno-Ugric populations of Eastern Europe, which are also characterized by low averaged frequency of this mtDNA haplogroup (2.5%).

Analysis of the mtDNA haplogroups frequency distribution patterns in Russian populations showed that the population samples examined were statistically very close to each other (Table 4). Only the population sample from Stavropol krai was statistically significantly different from the populations of Krasnodar krai and Niznii Novgorod oblast ($P < 0.01$). The differences between the populations of Stavropol krai and Saratov oblast were also statistically significant ($P = 0.08$). It was suggested that the differences between the populations of Stavropol and Krasnodar krai observed reflected high population heterogeneity of the southern part of Russia. In the meantime, the populations of Belgorod, Orel, and Saratov oblasts were most similar to each other. Generally, our findings showed that only Russians from Stavropol krai differed from the main bulk of Russian populations examined. It can be suggested that genetic peculiarity of Russians from Stavropol krai is the result of the influence from the side of North Caucasian populations. However, comparative analysis of mtDNA haplogroups frequency distribution patterns in Russian population from Stavropol krai and in North Caucasian population sample, represented by Adygeis, Kabardinians, northern Ossetians, and Chechens ($N = 199$; [20]) showed the presence of statistically significant differences between the samples tested ($I = 31.39$; $P = 0.002$). Moreover, populations of the southern part of Russia were substantially different from the North Caucasian populations with respect to the haplogroup V frequency (Table 5.). In the populations of North Caucasus studied (a sample of 510 individuals, representing Kabardinians, Adygeis, Circassians,

Table 3. Frequency distribution patterns of mtDNA haplogroups (%) in the regional haplogroups of the population of Europe

Haplogroups of mtDNA	Eastern Europe (Russians; N = 397)	Central Europe (N = 314)	Northern and Eastern Europe (N = 398)	Southeastern Europe (N = 233)
H	41.31	47.8	42.7	38.2
V	5.79	5.1	4.5	3.9
HV*	2.52	1.3	0.3	2.6
J	10.08	9.9	8.0	8.2
T	9.32	10.8	7.8	11.2
U	18.14	13.4	22.9	20.1
K	1.76	3.5	2.5	5.2
I	2.27	2.2	2.8	1.7
W	1.51	1.6	4.5	3.0
X	2.02	2.2	0.8	1.3
M	1.26	0.3	1.3	1.3
“Other”	4.02	1.9	1.9	3.3

Note: Average regional frequencies of mtDNA types are taken from [20]: Northern and Eastern Europe, Finns, Estonians, Karelians, Chuvashes, and Mordovians; Central Europe, Poles, Czechs, Germans, and Danes; Southeastern Europe, Bulgarians and Romanians.

Ingushes, and Ossetians; [21, 23]) the frequency of haplogroup V was 0.78%. This haplogroup was found only in the population sample of northern Ossetians (3.8%; $N = 106$) in the form of mtDNA types belonging to subhaplogroup pre*V [24]. At the same time, Russian populations inhabiting the territories from Stavropol krai to Kursk oblast are distinguished for rather high frequency of haplogroup V (average frequency 8%). The frequency of haplogroup V in Russian populations decreases northward reaching the values comparable to those in Finno-Ugric populations (2.53% in Mordovians and 0.68% in Estonians [24]).

The origin and distribution of mitochondrial haplogroup V in European populations deserves considerable interest, since it is hypothesized that geographical distribution of haplogroup V reflects the process of recolonization of Northern Europe, which began about 15 000 years ago from the region of glacial refugium located at the southwest of Europe [24–27]. It is also suggested that later, with the climate improvement (about 8.500 years ago), haplogroup V dispersed in Europe in the direction from west to east [24].

Maximum frequencies of haplogroup V are typical of Basques (12.4%) and Saami (52%). Analysis of mtDNA for sequence variation at HVS1, however, showed that in Saami this mitochondrial haplogroup was characterized by extremely low diversity ($h = 0.074$), while in Sicilians ($h = 0.755$), Germans ($h = 0.666$), and the Scotch ($h = 0.701$) maximum diversity values were observed [24]. It should be noted, however, that in the cited study Eastern European populations were represented only by Estonians, Mordovians, and Russians. Furthermore, judging by relatively low frequency of haplogroup V (4.9%), Russians in this study were of rather “northern” descent (see also Table 5).

Taking into consideration relatively high prevalence of haplogroup V (8% on average) in Russian populations from the southern and central parts of European Russia, we estimated the diversity of this mtDNA haplogroup based on sequence variation of HVS1. For these purposes, the data obtained in the present study for the populations of Stavropol krai, Orel oblast, and Saratov oblast (Table 6), as well as the data on mtDNA HVS1 polymorphism in the populations from Kursk and Rostov oblasts [20, 22] were used. Sixteen samples from the total number of 260 mtDNA examined belonged to haplogroup V and were represented by seven different mtDNA types. The analysis showed that mtDNA haplogroup V in Russians was characterized by high diversity level ($h = 0.72$), which corresponded to the highest h values observed in Europe. Our findings thus suggest that the distribution of haplogroup V in Eastern Europe could be associated with the recolonization of northern European regions from the eastern European refugium located in the Middle Don

Table 4. Genetic differences between Russian populations from the European part of Russia

Populations	1	2	3	4	5	6
1. Krasnodar krai		29.83***	11.18	13.58	14.31	13.91
2. Stavropol krai	0.864		10.80	14.39	19.28*	34.69***
3. Belgorod oblast	0.951	0.959		<u>3.68</u>	<u>6.44</u>	14.99
4. Orel oblast	0.943	0.947	0.987		<u>5.65</u>	13.63
5. Saratov oblast	0.935	0.923	0.976	0.980		15.99
6. Nizhnii Novgorod oblast	0.942	0.874	0.949	0.956	0.943	

Note: Above diagonal, identity indices I ; below diagonal, similarity indices r [19]. Minimum values of the identity index are underlined.

* $P < 0.1$.
*** $P < 0.01$.

Table 5. Frequencies (%) of mitochondrial haplogroups V, I, W and X in Russian populations

Populations	V	I	W	X	$\Sigma(I, W, X)$
Stavropol krai ¹ (62)	8.06	4.84	4.84	8.06	17.72
Krasnodar krai ² (49)	8.16	2.04	0	0	2.04
Rostov oblast ³ (25)	8.00	4.0	8.0	4.0	16.0
Belgorod oblast ² (69)	7.25	4.35	1.45	1.45	7.25
Kursk oblast ⁴ (34)	8.82	2.94	8.82	0	11.76
Orel oblast ¹ (76)	3.95	1.32	1.32	1.32	3.96
Saratov oblast ¹ (63)	4.76	1.59	0	1.59	3.18
Niznii Novgorod oblast ² (78)	3.85	0	1.28	0	1.28
Kostroma oblast ⁴ (55)	1.82	0	0	0	0
North Caucasian population ⁵ (199)	2.0	2.0	2.5	5.5	10.0

Note: Frequencies of mitochondrial haplogroups were taken from: ¹ present study; ² [13]; ³ [20]; ⁴ [22]; ⁵ [21]. In brackets are the sizes of the samples examined.

River/Middle Dneestr River region [26, 27]. It is hypothesized that during the glacial period most of the East European populations were concentrated in this particular area [27].

High total frequency of haplogroups I, W, and X, belonging to macrohaplogroup N, the ancient cluster of human mtDNA evolutionary tree, does not conflict with this scenario (Table 5). The frequency of macrohaplogroup N among the population of the southern regions of Russia (excluding population sample of Krasnodar krai) is similar to total frequencies of haplogroups I, W, and X recorded in Europe, in Balkan Peninsula (more than 10% in Greeks and Albanians [21]).

A model of recolonization of Europe by the populations inhabiting the glacial refugia has become popular in recent years. It can explain some gene geographic trends in the distribution of mtDNA haplogroups in European populations [20, 24, 25]. It cannot be excluded, however, that more recent migrations could have had substantial effect on the gene marker distribution patterns observed in the present-day European populations. Regarding Eastern Slavic populations, it should be taken into consideration that, judging by

anthropological data [1], Slavonization of Eastern European populations was accompanied by the interactions between the Slavs and autochthonous European inhabitants of early Middle Ages. This interaction probably had an influence on the genetic structure of the populations formed. At the same time, the distribution of haplogroup V among Russians demonstrated in Table 5, pointed to the existence of genetic differentiation observed in the ethnically homogenous medium. The reasons causing this phenomenon are still unclear since, apart from the Europe recolonization model, some other explanations can be suggested. For example, in the populations inhabiting southern part of Russia more features specific to pre-Slavic population could have been preserved, while population of the central and more northern regions of Russia to a greater extent exhibit genetic features of proper Slavs. Adaptive changes occurred in the gene pools of the populations living in different ecological conditions also cannot be excluded. Though in case of mtDNA the later proposal seems less probable compared to historical interpretations, it should be noted that the effect of ecological factors on the gene pool and morbidity of the population of the European part of Russia has been already described in the studies on biochemical polymorphism [28, 29].

Table 6. Nucleotide sequences of HVS1 from haplogroup V mtDNA types in Russians

MtDNA types	Stavropol krai	Orel oblast	Saratov oblast
CRS	1	0	0
16 298C	3	2	1
16 153A 16 298C	1	1	0
16 126C 16 298C	0	0	2

Note: CRS, Cambridge Reference Sequence of mtDNA HVS1 according to [12]. The listed nucleotide positions of mtDNA HVS1 are those differing from the CRS by transitions. The figures indicate the numbers of individuals with certain mtDNA types.

Investigations of mtDNA polymorphism in Russian populations show that application of the method of comparative analysis for the studies of genetic structures of the populations, represented by the compositions of mtDNA type haplogroups usually does not provide determination of genetic differentiation of the populations. At the same time, phylogeographic analysis, i.e., analysis of the distribution and diversity of certain monophyletic clusters (mtDNA haplogroups and sub-haplogroups) [14, 20] proved to be a highly informative approach for the investigation of interpopulation differentiation of the Russian population. Further increase of the number of populations examined and extension of

the data on the mtDNA sequence diversity within the monophyletic clusters are the necessary requirements for the investigation of the genetic history of Eastern Slavs.

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REFERENCES

- Alekseeva, T.I., *Etnogenez vostochnykh slavyan* (Ethnogenesis of Eastern Slavs), Moscow: Mosk. Gos. Univ., 1973.
- Alekseeva, T.I. and Alekseev, V.P., Anthropological Data on the Origin of Slavs, *Priroda*, 1989, no. 1, pp. 60–69.
- Alekseev, V.P., *Istoricheskaya antropologiya i etnogenez* (Historical Anthropology and Ethnogenesis), Moscow: Nauka, 1989.
- Alekseeva, T.I., Anthropological Portrait of Ethnic Russians, *Voprosy antropologii, dialektologii i etnografii russkogo naroda* (The Problems of Anthropology, Dialectology, and Ethnography of the Russian People), Moscow: Inst. Etnol. Antropol., 1998, pp. 3–27.
- Rychkov, Yu.G. and Balanovskaya, E.V., General Cartographic Analysis in Anthropology: A Reflection of Slavonic Tribes Known from Chronicles in Anthropological Geography of the Modern Russian Population, *Vopr. Antropol.*, 1988, no. 80, pp. 3–37.
- Bunak, V.V., Gene Geographic Regions Revealed in Eastern Europe by the ABO Blood Groups, *Vopr. Antropol.*, 1969, no. 32, pp. 6–27.
- Spitsyn, V.A., Kukhkhoezer, V., Makarov, S.V., *et al.*, The Russian Gene Pool: Frequencies of Genetic Markers, *Genetika* (Moscow), 2001, vol. 37, no. 3, pp. 386–401.
- Rychkov, Yu.G., Zhukova, O.V., Sheremet'eva, V.A., *et al.*, *Genofond i genogeografiya narodonaseleniya* (The Gene Pool and Gene Geography of Human Populations), Rychkov, Yu.G., Ed., St. Petersburg: Nauka, 2000, vol. 1.
- Balanovskaya, E.V. and Nurbaev, S.D., A Computer Technology of Gene Geographic Studies of the Gene Pool: IV. Populations in the Space of Principal Components, *Genetika* (Moscow), 1997, vol. 33, no. 12, pp. 1703–1718.
- Limborskaya, S.A., Human Molecular Genetics: Medical Genetic and Population Studies, *Mol. Biol.* (Moscow), 1999, vol. 33, no. 1, pp. 63–73.
- Lell, J.T. and Wallace, D.C., The Peopling of Europe from the Maternal and Paternal Perspectives, *Am. J. Hum. Genet.*, 2000, vol. 67, pp. 1376–1381.
- Anderson, S., Bankier, A.T., Barrell, B.G., *et al.*, Sequence and Organization of the Human Mitochondrial Genome, *Nature*, 1981, vol. 290, pp. 457–465.
- Malyarchuk, B.A., Denisova, G.A., Derenko, M.V., *et al.*, Mitochondrial DNA Variation in Ethnic Russian Populations of the Krasnodar Krai and Belgorod and Nizhnii Novgorod Oblasts, *Genetika* (Moscow), 2001, vol. 37, no. 10, pp. 1411–1416.
- Macaulay, V., Richards, M., Hickey, E., *et al.*, The Emerging Tree of West Eurasian mtDNAs: A Synthesis of Control-Region Sequences and RFLPs, *Am. J. Hum. Genet.*, 1999, vol. 64, pp. 232–249.
- Torrioni, A., Huoponen, K., Francalacci, P., *et al.*, Classification of European mtDNAs from an Analysis of Three European Populations, *Genetics*, 1996, vol. 144, pp. 1835–1850.
- Finnila, S., Hassinen, I., Ala-Kokko, L., and Majamaa, K., Phylogenetic Network of the mtDNA Haplogroup U in Northern Finland Based on Sequence Analysis of the Complete Coding Region by Conformation-Sensitive Gel Electrophoresis, *Am. J. Hum. Genet.*, 2000, vol. 66, pp. 1017–1026.
- Grzybowski, T., Extremely High Levels of Human Mitochondrial DNA Heteroplasmy in Single Hair Roots, *Electrophoresis*, 2000, vol. 21, pp. 548–553.
- Nei, M. and Tajima, F., DNA Polymorphism Detectable by Restriction Endonucleases, *Genetics*, 1981, vol. 97, pp. 145–163.
- Zhivotovsky, L.A., Statistical Methods for Analyzing Gene Frequencies in Natural Populations, *Itogi Nauki Tekhn., Ser.: Obshch. Genet.*, 1983, vol. 8, pp. 76–104.
- Richards, M., Macaulay, V., Hickey, E., *et al.*, Tracing European Founder Lineages in the Near Eastern mtDNA Pool, *Am. J. Hum. Genet.*, 2000, vol. 67, pp. 1251–1276.
- Tolk, H.V., Pericic, M., Barac, L., *et al.*, MtDNA Haplogroups in the Populations of Croatian Adriatic Islands, *Coll. Anthropol.*, 2000, vol. 2, pp. 267–279.
- Orekhov, V., Poltoraus, A., Zhivotovsky, L.A., *et al.*, Mitochondrial DNA Sequence Diversity in Russians, *FEBS Lett.*, 1999, vol. 445, pp. 197–201.
- Nasidze, I. and Stoneking, M., Mitochondrial DNA Variation and Language Replacements in the Caucasus, *Proc. R. Soc. London, B*, 2001, vol. 268, pp. 1197–1206.
- Torrioni, A., Bandelt, H.-J., Macaulay, V., *et al.*, A Signal, from Human mtDNA, of Postglacial Recolonization in Europe, *Am. J. Hum. Genet.*, 2001, vol. 69, pp. 844–852.
- Torrioni, A., Bandelt, H.-J., D'Urbano, L., *et al.*, MtDNA Analysis Reveals a Major Late Paleolithic Population Expansion from Southwestern to Northeastern Europe, *Am. J. Hum. Genet.*, 1998, vol. 62, pp. 1137–1152.
- Housley, R.A., Gamble, C.S., Street, M., and Pettitt, P., Radiocarbon Evidence for the Late Glacial Human Recolonization of Northern Europe, *Proc. Prehist. Soc.*, 1997, vol. 63, pp. 25–54.
- Dolukhanov, P., "Prehistoric Revolutions" and Languages in Europe, *The Roots of Peoples and Languages of Northern Eurasia*, Kunnapp, A., Ed., Tartu: Univ. Tartu, 2000, pp. 71–78.
- Rychkov, Yu.G., Zhukova, O.V., Ogryzko, E.V., and Shneider, Yu.V., The East European Gene Pool and Diseases of the Rural Population of European Russia, *Genetika* (Moscow), 1998, vol. 34, no. 8, pp. 1138–1150.
- Rychkov, Yu.G., Zhukova, O.V., and Shneider, Yu.V., The Ecological Component of the Geographic Variation of the North Eurasian Gene Pool and Its Archeological Age, *Genetika* (Moscow), 1998, vol. 34, no. 7, pp. 953–962.