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Differentiation of the Mitochondrial Subhaplogroup U4 in the Populations of Eastern Europe, Ural, and Western Siberia: Implication to the Genetic History of the Uralic Populations

B. A. Malyarchuk

*Institute of the Biological Problems of the North, Russian Academy of Sciences, Magadan, 685000 Russia;
fax: 41322-34463; e-mail: malyar@ibpn.kolyma.ru*

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Abstract—Phylogenetic relationships between the sequences of the mitochondrial DNA (mtDNA) hypervariable segment 1, belonging to subhaplogroup U4, were examined in the populations of Eastern Europe, Ural, and Northwest Siberia. It was shown that the frequency of subhaplogroup U4, as well as its proportion in the U-component of the gene pools, increased eastwards, reaching maximum values in the populations of Northwest Siberia. Phylogenetic analysis it was showed that the appearance of specific U4-lineage (16113C–16356–16362) in the ancestors of Mansi was most likely caused by its divergence from the East European cluster 16356–16362 in the Late Upper Paleolithic (18566 ± 12915 years before present). Other U4 mtDNA lineages (16189–16356 and 16311–16356), typical mostly of the indigenous populations of Northwest Siberia (Mansi, Nganasans, and Kets) may have formed during the Neolithic–early Bronze Age (6055 ± 3599 years before present, on average). It seems likely that the isolation of ancient populations inhabiting the region between the Ob' and Yenisei rivers was the key factor, providing the appearance of the unique Caucasoid mtDNA lineages in their gene pools. These results were consistent with the traditional point of view on the mixed origin of the Finno-Ugric populations of the Volga–Ural region and West Siberia, resulted from the genetic relationships between the populations of Europe and Asia.

INTRODUCTION

One of the first phylogenetic analysis of the mitochondrial DNA (mtDNA) variation in the populations of Western Europe showed that the most ancient in Europe mitochondrial haplogroup U (of the age that exceeds 50 000 years) was represented by a number of subhaplogroups differing by the time and place of their origin [1]. One of these was subhaplogroup U4, with an evolutionary age of more than 25 000 years [2]. Based on the level and time of the U4 mtDNA types divergence in the populations of Near East and Europe ($25\,650 \pm 9350$ and $20\,400 \pm 4300$ years, respectively), the Near Eastern (Anatolian) origin of this mtDNA subhaplogroup is suggested. The highest prevalence of the subhaplogroup, however, was detected in Europe and in particular in its northwestern part [2, 3]. The study of the geographic frequency distribution of subhaplogroup U4 in the European populations showed that its highest frequency (5.5%) was typical of Baltic–Finish populations of Northeastern Europe (Finns, Karelians, and Estonians), while in the populations of Central and Northwestern Europe, the frequency of U4 did not exceed 3% [3, 4].

The study of the populations of Eastern Europe showed that subhaplogroup U4 belonged to the mitochondrial lineages mostly prevalent among the populations of the Volga–Ural region [5]. The frequency of this subhaplogroup among the Finno–Ugric and Turkic

populations from the Volga and Cis-Ural regions varied from 2 to more than 20%, and the highest frequencies were observed among Komi-Zyryans, Chuvashes, and Bashkirs (24.2, 16.4, and 12.7%, respectively) [5]. Analysis of the more eastern, Trans-Ural and Siberian, populations showed that subhaplogroup U4 was widely distributed (with the frequency of 16 to 29%) among the indigenous populations of Northwest Siberia, Mansi, Nganasans, and Kets [6, 7]. This observation served as a basis for the suggestion that the high frequency of the U4 mtDNA types in the gene pools of the populations from the Eastern Cis-Ural and the adjacent Siberian regions can be considered as a genetic trace of the Upper Paleolithic proto-Eurasian population (“an independent Eurasian structure,” according to Bunak [8]), currently preserved only to the east of the Ural Mountains, but initially formed in the Middle East [6, 7]. The study of the indigenous populations of South Siberia also pointed to the presence of the U4 mtDNA types in the gene pools of some Altai–Sayan populations. In particular, subhaplogroup U4 with the frequency of about 6% was found in Altai-Kizhi and Khakassians [9]. Thus, reviewing the data on the prevalence of the U4 mtDNA types in the populations of Europe and the adjacent territories of Ural and West Siberia, it becomes evident that the frequency of this subhaplogroup increases eastwards, reaching maximum in the populations inhabiting the territories between the Ob' and Yenisei rivers. However, the pattern of phylogenetic relationships

between the U4 mtDNA types present in different East European and Siberian populations remains unclear. In this study, the diversity of subhaplogroup U4 and its individual clusters in different populations of Eastern Europe, Ural, and Siberia was examined. In our study, we used a phylogenetic approach that considers both the frequency and diversity of monophyletic DNA clusters, thus providing the most adequate conclusions on the evolutionary history of the gene pools and their individual components [1, 2].

MATERIALS AND METHODS

The phylogenetic analysis was based on the data on mtDNA polymorphism in western Finnish populations of the Baltic region ($n = 373$), represented in the studies [10, 11] by Finns ($n = 242$), Estonians ($n = 48$), and Karelians ($n = 83$); in eastern Finnish and Turkic populations of the Volga–Ural region ($n = 979$), represented in the study [5] by Mordovians ($n = 102$), Maris ($n = 136$), Komi-Zyryans ($n = 62$), Komi-Permyaks ($n = 74$), Tatars ($n = 228$), Chuvashes ($n = 55$), Udmurts ($n = 101$), and Bashkirs ($n = 221$); in the populations of Northwest Siberia ($n = 218$), represented by Nentsi ($n = 58$), Mansi ($n = 98$), Nganasans ($n = 24$), and Kets ($n = 38$) [6, 7, 12]; in the populations of South Siberia ($n = 480$), represented in the study [13] by Altaians ($n = 110$), Khakassians ($n = 53$), Buryats ($n = 91$), Sojots ($n = 30$), Tuvinians ($n = 90$), Tadjins ($n = 48$), and Tofalars ($n = 58$); in Russian populations of Stavropol krai, Krasnodar krai, Orel oblast, Belgorod oblast, Saratov oblast, and Nizhni Novgorod oblast ($n = 391$, elicited from the study [14]). The summarized sample size constituted 2441 individuals.

In almost all samples, the attribution of the mtDNA HVS1 types to subhaplogroup U4 was determined based on the data on the distribution of the markers, distinguishing haplogroup U (variant +12308*Hinf*I, mutation 12308AG) and its subhaplogroup U4 (variant +4643*Rsa*I, mutation 4646TC), presented in the studies mentioned above. The exceptions were the samples of Finns, Estonians, and Karelians (data taken from [10]), for which the data on the prevalence of the U4 mtDNA HVS1 types were presented in accordance with the database described in [2].

Evolutionary relationships between the U4 mtDNA HVS1 types were examined using RM (reduced-median) algorithm of the median network method [15] as implemented in the Network 3.1.1.1 software package (www.fluxus-engineering.com). Similarly to the other maximum parsimony methods, the median network method is based on the principle of minimization of the number of evolutionary events, leading to the DNA changes. The results of the analysis are presented graphically as phylogenetic nets, combining several plausible dendrogram topologies. Topology combination results in the appearance of n -dimensional cycles, the number of which can be reduced by decreasing the weight of the hot-spot nucleotide positions. Analyzing

U4 sequences of mtDNA, we reduced the hot-spot weights at positions 16093, 16129, 16189, and 16362 (according to [16]) to 1/10 relative to the other HVS1 positions. The hot-spot weight reduction leads to more fanlike branching of the mtDNA types within the clusters, providing far more precise evaluation of the nucleotide sequences divergence levels [2, 17].

Genetic distances ρ between the mtDNA sequences were calculated as the mean number of mutations between the founder genes and the derivative mtDNA types belonging to the corresponding monophyletic clusters [18]. Determination of the evolutionary ages of the mtDNA clusters was based on the concept that for the HVS1, genetic distance $\rho = 1$ corresponds to the time interval of 20180 years [18]. This rate is close to the other mtDNA HVS1 mutation rates suggested earlier [19, 20]. Standard deviations for ρ were calculated according to [17] using Network 3.1.1.1 software program. It should be noted in this respect that statistical robustness of the timing data based on the mtDNA HVS1 sequence variation is doubtful, since there is still no agreement on the initial assumptions underlying the method of the mutation rate estimation (see, for example, [19]). In addition, some discrepancies between the mutation rate values determined based on the family (pedigree) and population data were observed [21]. Nevertheless, in the present study, similarly to most of the other phylogenetic works (including those, used here for comparison [2, 4, 5]), the mtDNA HVS1 mutation rate mentioned above was used.

RESULTS AND DISCUSSION

Analysis of haplogroup U4 frequency distribution patterns in the populations of Europe, Ural, and Siberia (table) showed that in Russian populations of Eastern Europe, the frequency of U4 is comparable to that observed in the populations of Central and Northwestern Europe (about 3% [3]). Among the Finno–Ugric populations the frequency of U4 gradually increases from 5.9% in Baltic–Finnish populations (Finns, Estonians, and Karelians) to 10% in Eastern-Finnish (and also Turkic) populations of the Volga–Ural region, reaching maximum values (17%, on average) in Ugro–Samoyedic populations of Western Siberia. Among the South Siberian populations examined (Altaians, Khakassians, Buryats, Sojots, Tuvinians, Tadjins, and Tofalars), subhaplogroup U4 was detected only in Altai-Kizhi (5.5%) and Khakassians (7%) [13]. Note that similar changes were observed for the proportion of the U4 types among all U mtDNA types in the populations tested. Specifically, in the populations of Northwestern and Central Europe, and also in Russians, the proportion of U4 within haplogroup U constitutes 13 to 17%, while in the indigenous populations of Eastern Europe, Ural, and West Siberia it gradually increases, reaching maximum value (67%) in the populations of Northwest Siberia (table). To the south of Siberia, the frequency of U4 decreases, although its

proportion in haplogroup U still remains high (33.3%). Thus, analysis of the subhaplogroup U4 frequency distribution indicates that this subhaplogroup mostly prevails in the populations of Northwest Siberia. This finding provides formulation of a hypothesis (as was done in [6, 7]) on the archaic nature of the U4 mtDNA types in the gene pools of Mansi, Kets, and Nganasans, and also that these mtDNA types can be considered as the genetic trace of proto-Eurasian population, preserved to the east of the Ural Mountains from Upper Paleolithic. Investigation of this issue requires the analysis of phylogenetic relationships between U4 mtDNA types, observed within wider geographical range, including analysis of the mtDNA lineages found in Finnish and Turkic-speaking populations of the Volga region.

The median network of the U4 mtDNA types distributed among the populations of Europe, Ural, and Siberia is presented in the figure. The central position of the U4 phylogeny is occupied by the HVS1 type, differing from the Cambridge reference sequence [22] by the variant 16356C. Within subhaplogroup U4 three major clusters, 16134–16356, 16356–16362, and 16356–310, were distinguished. The latter cluster, marked by the variant 310C in HVS2, mostly prevailed in Slavic populations (in Russians and Poles), but its individual lineages were also found among the neighboring German and Finno-Ugric populations of Europe [14, 23]. The most abundant in the number of the mtDNA types were clusters 16134–16356 and 16356–16362 (figure). The mtDNA types belonging to these clusters are distributed among different populations of the Eurasian region examined and are characterized by high evolutionary age. Specifically, the evolutionary age of the whole subhaplogroup U4 constitutes $28\,252 \pm 9\,289$ years ($\rho = 1.40 \pm 0.46$), while its clusters, marked by the variants 16134 and 16362, have diverged about 23 000 years ago ($22\,602 \pm 13\,722$ for $\rho = 1.12 \pm 0.68$ and $22\,803 \pm 11\,704$ years for $\rho = 1.13 \pm 0.58$, respectively). Thus, judging by the level of the mtDNA divergence, it can be suggested that both of these clusters arose rather synchronously during Upper Paleolithic. It should be noted that, if the age of cluster 16134–16356 is estimated only from the data on sequence variation of these mtDNA lineages, the divergence time of this mtDNA cluster would be $17\,800 \pm 2\,900$ years [5]. Evolutionary age of the total subhaplogroup U4 evaluated in the present study from the data of the mtDNA HVS1 sequence variation in the populations of Eastern Europe, Ural, and West Siberia (~28 000 years) was somewhat higher than the U4 age estimate (~26 000 years), based on which the Near Eastern origin of this mtDNA haplogroup was suggested [2]. In this connection, the East European origin of subhaplogroup U4 can be suggested. Testing of this hypothesis, however, requires special investigation of the phylogenetic relationships between the U4 mtDNA types in broader geographical context.

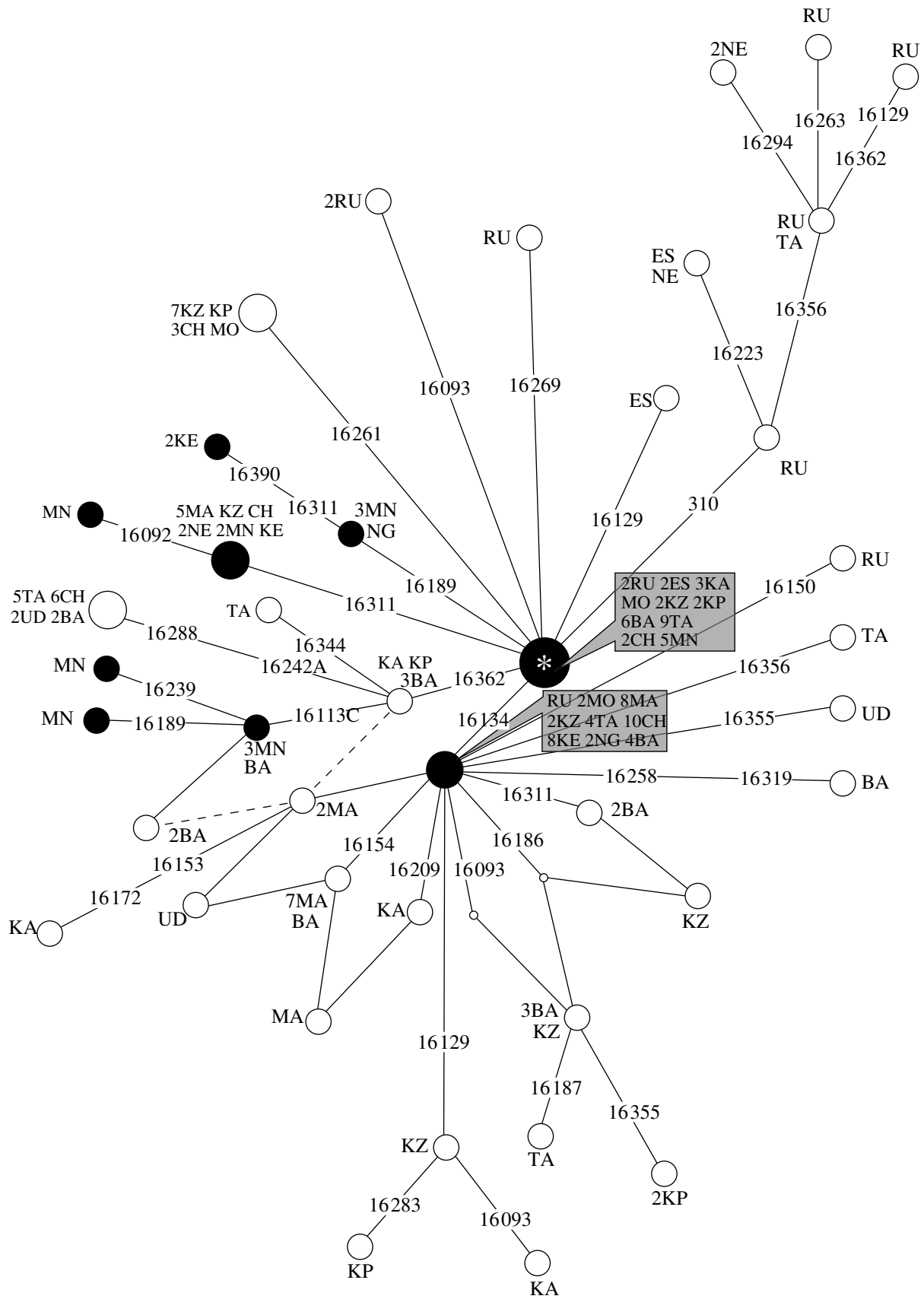
The frequency of subhaplogroup U4 in the populations of Eastern Europe, Ural, and Siberia

Region	U fre- quency	U4 fre- quency	Propor- tion of U4 in U
	%		
Eastern Europe (Russians; <i>n</i> = 391) ¹	19.9	3.3	16.7
Baltic region (<i>n</i> = 373) ²	25.7	5.9	22.9
Volga–Ural region (<i>n</i> = 979) ³	28.4	9.7	34.2
Northwest Siberia (<i>n</i> = 218) ⁴	25.2	17.0	67.3
South Siberia (<i>n</i> = 480) ⁵	6.9	2.3	33.3

Note: Data from: ¹, Russians [14]; ², Finns, Estonians, and Karelians [10, 11]; ³, Mordovians, Maris, Komi-Zyryans, Komi-Permyaks, Tatars, Chuvashes, Udmurts, and Bashkirs [5]; ⁴, Nentsi, Mansi, Kets, and Nganasans [6, 7, 12]; ⁵, Altaians, Khakassians, Buryats, Sojots, Tuvinians, Tadjins, and Tofalars [13].

For the present study, of principal importance is the conclusion that unique mitochondrial lineage, marked by the A–C transversion in position 16113 of HVS1 and distributed predominantly in the gene pool of Mansi, belongs to cluster 16356–16362 and is the only representative of this cluster in Trans-Ural populations (figure). Based on the level of divergence between the mtDNA types 16113C–16356–16362, it can be hypothesized that the radiation of this “Uralic” lineage from the East European cluster 16356–16362 occurred about 19 000 years ago ($18\,566 \pm 12\,915$ years for $\rho = 0.92 \pm 0.64$), i.e., during the period of maximum glaciation. Thus, one of the unusual U4 components of the gene pool of the population of Yenisei North is of Upper Paleolithic descent. It is, however, associated with the East European populations of Upper Paleolithic rather than with the populations of Near East (as suggested in [6, 7]).

Another rare U4 mtDNA lineage, determined by motif 16311–16356, was found in Mansi, Kets, and Nensi, as well as in some East European populations, including Maris, Chuvashes, and Komi-Zyryans. The divergence time of this U4 branch constitutes about 6500 years. Somewhat later (~5600 years) another lineage, 16189–16356, prevalent among Mansi, Kets, and Nganasans, appeared. Among East European lineages synchronous to that mentioned above (~5200 years ago), lineage 16261–16362, typical of the gene pools of Komi, Mordovians, and Chuvashes deserves special consideration. Thus, judging by the time and the divergence level of lineages 16311–16356 and 16189–16356 (6055 ± 3599 on average, for $\rho = 0.3 \pm 0.18$), the appearance of these unusual mtDNA lineages in the



gene pools of Mansi, Nganasans, and Kets resulted from further development of the gene pools of Finno-Ugric populations from Volga region and Ural in later time, during the Neolithic and early Bronze Age.

The reconstruction of phylogenetic relationships between U4 mtDNA types in the present-day populations of Eastern Europe, Ural and Northwest Siberia indicates that the divergence of this subhaplogroup in Eastern Europe has begun as early as in Upper Paleolithic (23 000 years ago), resulting in the appearance of its major mtDNA clusters (16 134–16 356 and 16 356–16 362). According to Okladnikov [24], exactly at this time, in the arctic conditions of Eastern Europe, the culture of the Upper Paleolithic hunters appeared. They “at the close of the Ice Age inhabited the territories east to the Ural Mountains, and being confined, have created there their own culture, which was different from that observed at the initial territory at the west” [25]. The isolation mechanism, explaining the specificity of the anthropological characteristics of Finno-Ugric populations is supported by data on the appearance in Mansi of U4-specific lineage 16 113C–16 356–16 362, radiated from the East European cluster 16 356–16 362 at the close of the Ice Age. The hypothesis on rather isolated development of the gene pools of Trans-Ural populations in later time (during the Neolithic and early Bronze Age) is supported by the data on the appearance in their gene pools of specific “Neolithic” U4 lineages, 16 189–16 356 and 16 311–16 356. Interestingly, lineage 16 311–16 356 as a component of subhaplogroup U4 with low frequencies was also observed at the north (in Nentsi) and south of Siberia (in Altaians and Khakasians), suggesting that the carriers of this lineage participated in the migrations which took place in the 4th to 3rd millennium before present and resulted in the distribution of the Uralic populations along the vast territories from the north of Europe to the south of Siberia [25].

Analysis of the mtDNA polymorphism in Mansi, Kets, and Nganasans demonstrated that Caucasoid component of their gene pools was at most represented by the mtDNA types distributed in the East European populations (the data are not shown, but this conclusion can be easily achieved by comparison of the literature data on mtDNA polymorphism in different Finno-Ugric populations [5, 10–12]).

It should be noted in this respect that only Mansi haplogroup H at a frequency of 5% contains a unique subhaplogroup characterized by motif 16 169–16 184 [6]. This subhaplogroup was not found in the populations of the Volga-Ural region, but was detected at a

low frequency (about 2%) in the Southern Siberia in Altaians [13]. These results suggest the following. First, not only subhaplogroup U4, but also haplogroup H was influenced by the isolation, which resulted in the appearance of its Ural-specific subhaplogroup. Second, the Caucasoid component of the eastern Uralic populations could be involved in the formation of the gene pools of South Siberian populations. At the same time, analysis of the gene pools of Mansi, Kets, and Nganasans still has not revealed other examples of locally arisen mtDNA lineages, indicating that the gene pools of the Upper Paleolithic hunters, isolated at the east to the Ural Mountains, were characterized by low number of founder mitochondrial lineages, or, alternatively, the number of these lineages was gradually reduced by gene drift at the stages of low population size.

Derbeneva *et al.* [6] suggested that the presence of subhaplogroup U7 along with subhaplogroup U4 in the gene pool of Mansi could be considered as a proto-Eurasian trace of the initial expansion of the Upper Paleolithic Near Eastern migrants to the territory between the Ob' and Yenisei rivers. The Mansi gene pool is also characterized by the high frequency (10%) of subhaplogroup J2, which is rare in Finno-Ugric populations of Eastern Europe [5]. According to [6], the presence of this subhaplogroup in Mansi marks the Neolithic stage in the peopling of the Ural region. It should be noted, however, that the high frequency and along with the absence of diversity characteristic of mitochondrial lineages U7 and J2, observed in Mansi disagree with the idea on the long-term presence of these mtDNA lineages in the gene pool of Mansi and their ancestors. At the same time, archaeological and ethnographic data indicate that at the close of the 1st Millennium before present there was an expansion of the carriers of Andronov culture, or may be of some other southern tribes (probably, the Sarmat), from the southern steppe of Western Siberia and Northern Kazakhstan to the Ob' River region. These were the tribes that left the “southern” mark in the Northern Ob'-Ugric culture [26]. Anthropological data also indicate that Mansi have unambiguously accumulated southern Caucasoid Mediterranean anthropological type [27]. The highest frequencies of subhaplogroup U7 (up to 1.5%) were observed in the populations of Near East, Southeastern Europe, and Central Mediterranean regions [3]. Similarly, the highest frequencies of subhaplogroup J2 (2 to 3%) were detected in the populations of Anatolia, Transcaucasia, and Central Mediterranean region [3]. It should be noted that the unusual W* mtDNA variant described

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The median network for the mitochondrial subhaplogroup U4 in the populations of Eastern Europe, Ural, and West Siberia. The position of the central U4 type, which differs from the Cambridge reference sequence [22] by a transition at position 16356 is marked by *. The numbers of the nucleotide positions denote transitions; the transversion types are additionally indicated. The circle sizes are proportional to the mtDNA type frequencies. The populations are designated as follows: MN, Mansi; NG, Nganasans; KE, Kets; NE, Nentsi; ES, Estonians; KA, Karelians; RU, Russians; BA, Bashkirs; TA, Tatars; CH, Chuvashes; MA, Maris; MO, Mordovians; KZ, Komi-Zyryans; KP, Komi-Permyaks; UD, Udmurts. Darkened circles correspond to the mtDNA types, found in Western Siberian populations (in Mansi, Nganasans, and Kets).

in Kets, was also found in Transcaucasian populations (Armenians [2]). Hence, the presence of “southern” mtDNA variants in the gene pools of Mansi and Kets can be explained in terms of relatively recent participation of the groups of a southern descent in the ethnogeny of Western Siberian populations.

Our findings indicate that the gene pools of Northwest Siberian populations are characterized by composite structure, the specificity of which resulted from the recurrent isolation of the populations in the North, as well as due to their relationships with other ethnic groups, including those the southern ones. It was also demonstrated that the gene pools of Finno-Ugric populations contained no traces of any archaic mtDNA lineages, occupying isolated positions on the mitochondrial phylogenetic tree. If this was the case, then the existence of ancient Eurasian race with the characters intermediate between the Caucasoids and Mongoloids, to the west and east of the Ural Mountains could be suggested. On the contrary, our findings show that the some unique mitochondrial lineages present in the gene pools of Mansi, Nganasans, and Kets resulted from the local evolution of mtDNA variants, characterized by East European descent and still distributed in the Finno-Ugric populations of Eastern Europe.

At the same time, according to Bunak [8], the ancient Uralic race could be the variant of proto-Asian race, which have diverged from the common Mongoloid stem long before the formation of typical Mongoloid characters. Analysis of the mtDNA polymorphism in the Finno-Ugric populations from the Volga–Ural region and Northwest Siberia [5–7, 10, 12] showed the gene pools of these populations really contained differentially expressed Mongoloid component, represented by the mtDNA types, prevalent in the populations of East Siberia and Central Asia. In this case, however, the Mongoloid component of Finno-Ugric populations also did not display the presence of any specific “archaic” haplogroups, subhaplogroups, or individual mtDNA lineages. All mtDNA types detected in Mansi, Kets, and Nganasans belonged to the known East European mtDNA haplogroups (A, F, C, Z, D, G, M*) with definite ideas on their origin [13, 28–30]. It can be thus concluded that the data on the structure of the mitochondrial gene pools of the Finno-Ugric populations of the Volga region and West Siberia are consistent with the traditional point of view on their mixed origin, resulted from the genetic relationships between the populations of Europe and Asia [31]. In addition, the data obtained suggested that the isolation of ancient populations inhabiting the region between the Ob and Yenisei rivers has led to the appearance of the unique Caucasoid mtDNA lineages in their gene pools, which emphasize genetic specificity of these populations.

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