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HUMAN GENETICS

Gene Pool Structure of Eastern Ukrainians as Inferred from the Y-Chromosome Haplogroups

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Abstract—Y chromosomes from representative sample of Eastern Ukrainians (94 individuals) were analyzed for composition and frequencies of haplogroups, defined by 11 biallelic loci located in non-recombining part of the chromosome (*SRY1532*, *YAP*, *92R7*, *DYF155S2*, *12f2*, *Tat*, *M9*, *M17*, *M25*, *M89*, and *M56*). In the Ukrainian gene, pool six haplogroups were revealed: E, F (including G and I), J, N3, P, and R1a1. These haplogroups were earlier detected in a study of Y-chromosome diversity on the territory of Europe as a whole. The major haplogroup in the Ukrainian gene pool, haplogroup R1a1 (earlier designated HG3), accounted for about 44% of all Y chromosomes in the sample examined. This haplogroup is thought to mark the migration patterns of the early Indo-Europeans and is associated with the distribution of the Kurgan archaeological culture. The second major haplogroup is haplogroup F (21.3%), which is a combination of the lineages differing by the time of appearance. Haplogroup P found with the frequency of 9.6%, represents the genetic contribution of the population originating from the ancient autochthonous population of Europe. Haplogroups J and E (11.7 and 4.2%, respectively) mark the migration patterns of the Middle-Eastern agriculturists during the Neolithic. The presence of the N3 lineage (9.6%) is likely explained by a contribution of the assimilated Finno–Ugric tribes. The data on the composition and frequencies of Y-chromosome haplogroups in the sample studied substantially supplement the existing picture of the male lineage distribution in the Eastern Slav population.

INTRODUCTION

The problem of the origin and ethnic history of Slavs has been attracting attention of many generations of researcher working in different fields of science. Despite the currently available ample set of ethnographic, linguistic, and archaeological data, there is no unambiguous opinion on the problem of Slavic nations in general and on the ethnogeny of Eastern Slavs in particular [1]. The settling territory of Eastern Slavs was located in the zone of the contacts between northern and southern Caucasoids [2, 3]. This was the place of the interactions between the linguistically and anthropologically different ethnic groups. Eastern Slavs were formed as the result of complex ethnogenetic processes with the participation of the groups of forest and forest-steppe tribes of Eastern and Central Europe along with the tribes of the steppe zone of Eurasia. One of the major migration routes of Eastern Slavs passed through the territory corresponding to the present-day Ukraine, and then along a vast territory of the present-day European part of Russia [4]. Investigation of the population inhabiting the territory of the present-day Ukraine is of special interest since northern Black Sea coastal zone is believed to be the primary or secondary area of the distribution of the carriers of pre-Indo-European language [5, 6].

At present, an ample data set on the protein marker systems in Slavs is available [7]. Since the mid-1990s, the studies aimed at the analysis of the composition and the frequencies of uniparentally inherited molecular genetic markers have been dynamically developed. The data on the genetic polymorphism of mtDNA in Eastern Slavs, mostly in Russians, have been published [8–11]. In these populations the distribution of the Y-chromosome STR markers was also established [12].

The current description of the Y-chromosome molecular phylogeny (consecutive haplotype appearance) is based on the typing of the allelic state of a standard set of the SNP loci. Male lineages, i.e., Y-chromosomal haplotypes, have been well studied worldwide with respect to this SNP marker set [13–15]. Similar data on Slavic populations is being accumulated [16–20]. It should be noted in this respect that in this data set the Ukraine is so far represented by a single sample collected in the central part of the country. Compared to other populations, Slavs are more widely distributed over Europe. Because of this, estimates of the contributions of Y chromosomes from different ancestral groups to the gene pool of contemporary Slavs require

substantial increase of the total sample size. In this respect, the formation of each individual sample based on the groups compactly living in certain territories is even more important. Furthermore, it is also required that the samples examined should be randomly distributed over the whole area of Slavic settlement.

In this study distribution of the haplogroups, defined by 11 biallelic loci located in nonrecombining part of Y chromosome [13, 15, 18] was examined in the sample of Eastern Ukrainians.

MATERIALS AND METHODS

In the present study variability of 11 biallelic loci located in non-recombining part of the chromosome (*SRY1532*, *YAP*, *92R7*, *DYF155S2*, *12f2*, *Tat*, *M9*, *M17*, *M25*, *M89*, and *M56*) was examined in 94 individuals representing indigenous population of Eastern Ukraine (predominantly Kharkov oblast, Poltava oblst, Sumy oblast, and Chernigov oblast). The sample examined was comprised of individuals unrelated at least in three generations down the paternal lineage. Experimental material was collected from the military personnel volunteers after obtaining their informed consent and the data on the birthplaces and national affiliation of the ancestors in two pedigree generations. Only the individuals, whose ancestors (judging by the questionnaire data) were Ukrainians, were included in the study.

Total DNA was extracted from the peripheral blood lymphocytes by use of standard methods [21].

Genotyping was performed by polymerase chain reaction (PCR) in automated DNA-Tekhnologia Tertsik thermal cycler, followed by analysis of the PCR product sizes after digestion with appropriate restriction endonucleases (for (*SRY1532*, *92R7*, *Tat*, *M9*, and *M25*), or without digestion (for *YAP*, *DYF155S2*, *12f2*, *M17*, *M89*, and *M56*). Electrophoresis was performed in 3% (for *Tat* and *M25*) or 2% (for all other markers) agarose gels.

Amplification of the *SRY1532* locus containing the A–G transition [22] was performed using the primers and the reaction conditions described earlier [23]. Allele A was represented by one fragment (167 bp), while allele G gave rise to two fragments (55 and 112 bp), which were formed on the digestion of the PCR product with the *Ade*I restriction endonuclease (Fermentas, Lithuania).

Insertion *Alu* polymorphism at the *DYS287* (*YAP*) locus was typed using the procedure described in [24]. The 150-bp PCR product corresponded to the *Alu* repeat loss, while the 455-bp product corresponded to the *Alu* insertion gain.

The C–T transition at the *92R7* locus [25] was analyzed according to [26]. C allele was detected by the presence of the recognition site for the *Hin*dIII restriction endonuclease (SibEnzim, Novosibirsk), which cleaved the 709-bp PCR product into the fragments of 197 and 512 bp.

Deletion polymorphism at the *DYF155S2* locus was genotyped according to [13]. Amplification with the locus template without the deletion yielded the PCR product of 196 bp, while in case of the deletion this fragment was absent. The quality of the PCR reaction was controlled by the presence of the amplification product of the *DYF155S1* locus, overlapping with the *DYF155S2*.

Deletion polymorphism at the *12f2* locus was typed as in [27]. The presence of the 500-bp amplification product corresponds to the ancestral DNA state. The quality of the PCR reaction was controlled by the presence of the product (820-bp), which was amplified with the additional pair of primers [18].

The *Tat* mutation, which is a T–C transition, was typed by amplification of the 112-bp fragment according to [28]. Allele T generated two fragments (83 and 29 bp) upon the *Hsp*92II restriction endonuclease (Promega) digestion.

The *M9* C–G transversion [29, 30] was genotyped according to [31]. In case of allele C the amplified 341-bp fragment contained two recognition sites for the *Hin*fI endonuclease (Sibenzim), which on digestion generated the fragments of 182, 93, and 6 bp. Allele G is determined by the presence of one restriction endonuclease recognition site in the PCR product, cleavage at which generates two fragments of 248 and 93 bp.

The *M25* G–C transversion was genotyped as described in [30]. In the case of allele G, the 340-bp amplification product contains a single site for the *Eco*RI restriction endonuclease (SibEnzim), and the digestion results in the appearance of the 180 and 160-bp fragments. The mutant C allele forms an additional site, leading to the appearance of 160, 116, and 64-bp fragments on digestion.

Genotyping of the *M17*, *M56*, and *M89* markers [30] was performed using allele-specific PCR. The *M17* mutation is a single-nucleotide G deletion. The reverse PCR primer used was the primer described in the appendix to [30], and two forward primers were different from that described in the original reference by one nucleotide at the 3' end. M17F1: 5'-TGTGGTTGCTGGTTGTTACGGGG-3', M17F2: 5'-TGTGGTTGCTGGTTGTTACGGG-3'. Both primers successfully annealed (at 58°C) to normal nondeleted allele sequence, generating the products of 288 and 287 bp, respectively. In the case of a deletion specific binding of primer F1 practically did not occur, while the PCR quality with primer F2 remained unchanged.

Typing of the A–T transversion (mutation *M56*) was performed using reverse primer described earlier [30]. In this case, each of the two forward primers was strictly complementary to only one allelic variant and differed from another one by one nucleotide at the 3' end. M56F1: 5'-ATGCAATGGGAGGATTACGAA-3', complementary to allele A and M56F2: 5'-ATGCAATGGGAGGATTACGAT-3', complementary to

Distribution of the Y-chromosome haplogroups among the Ukrainians

Haplogroup	Frequency, % (*N*)		
	present study	[19]	[18]
E	4.2(4)	4.0(2)	4.0(1)
F	21.3(20)	26.0(13)*	48.0(13)
J	11.7(11)	6.0(3)	0.0(0)
N3	9.6(9)	6.0(3)	11.0(4)
P	9.6(9)	4.0(2)	4.0(1)
R1a1	43.6(41)	54.0(27)	30.0(8)
Total	100(94)	100(50)	100(27)

* Nine of these individuals (18.0%) belong to haplogroup I, and two individuals belong to haplogroup G (4%).

allele T. The 381-bp fragment was generated only in one PCR variant, at the annealing temperature of 62°C.

Allelic state in the case of the *M89* C–T transition was determined using a similar approach. Forward primer is described in [30], and each of the two reverse primers was strictly complementary to only one of the alleles. M89R1: 5'-TCAGGCAAAGTGAGAGATG-3', complementary to allele C, and M89R2: 5'-TCAGGCAAAGTGAGAGATA-3', complementary to allele T. The annealing procedure was carried out at 60°C. The 365-bp fragment was present only in one PCR variant.

In some samples all biallelic markers were genotyped, while in most of the cases genotyping was performed according to a hierarchical scheme, based on the established order of the accumulation of Y-specific mutations [32]. For instance, nucleotide substitution at the *SRY1532* locus was predominantly typed in the individuals carrying T allele at the *92R7* locus.

Y-chromosome haplotypes were classified in accordance with a nomenclature system suggested by the Y-Chromosome Consortium [32].

For visualization of the amplified products and gel video filming, the Advanced American Biotechnology system for gel documentation and analysis was used with Video Studio v.1.0 (Ulead Systems Inc.), Video Packer Plus v.1.2p (Aura Corp.&VIC Hi Tech Corp.), and Adobe Photoshop v.6.0 (Adobe Systems Inc.) software packages.

RESULTS AND DISCUSSION

Analysis of the allelic distribution at 11 loci from the non-recombining part of Y chromosome (*SRY1532*, *YAP*, *92R7*, *DYF155S2*, *12f2*, *Tat*, *M9*, *M17*, *M25*, *M89*, and *M56*) carried out in 94 individuals representing ethnic Ukrainians revealed the presence of six haplogroups (table). The same lineages were described earlier in small samples of the Ukrainians in the studies focused on the analysis of the Y-chromosome diversity on the territory of Europe [18, 19]. The table presents Y-chromosome haplogroup frequencies in the Ukrainians determined in the present study along with those reported elsewhere. In general, all three samples demonstrated similar main haplogroup distribution patterns.

The differences in the frequencies of individual lineages observed could have been associated either with actually existing differences between the population samples examined, or with the small sample sizes examined in the previous studies (27 individuals in [18] and 50 individuals in [19]). Unfortunately, the authors did not indicate the parts of the Ukraine territory, where the samples were collected.

The most common Y-chromosome variant among the Ukrainians was haplogroup R1a1 (designated earlier in accordance with the previous haplogroup nomenclature version as HG3 [14]). The frequency of R1a1 observed in the present study was 43.6%. The area of the haplogroup distribution is restricted to the territory of Eurasia. In Europe similar to the Ukrainians R1a1 frequency was observed among Balto-Slavic populations belonging to the Indo-European linguistic family: 40 to 50% in Russians, 39% in Belarusians, 37% in Czechs and Slovenians, 47% in Slovaks, 55% in Poles, 41% in Latvians; and 34% in Lithuanians [17, 18, 20]. Somewhat lower values were observed among the Finno-Ugric populations, constituting 29% in Maris, 27% in Estonians, 22% in Hungarians, 20% in Karelians, 3% in Finns, and 3 to 5% in Saami [18, 33]. Thus, the proportion of haplogroup R1a1 is the highest in Central and Eastern Europe, and in Western European populations it is substantially lower.

Semino *et al.* [19] have suggested that the modern distribution pattern of this haplogroup reflects the expansion of the population, which was isolated during the Ice Age on the territory of the present-day Ukraine [19]. This hypothesis is supported by the distribution of the Neolithic–early Bronze Age Kurgan archaeological culture. In respect of linguistics, the correlation can be found in the distribution of the Indo-European languages from the north of the Black Sea in the 5th century B.C. [5, 34]. Analysis of the linkage between the *SRY1532* and *M17* markers shows that they are, probably, the phylogenetic analogs. Age estimates for the *SRY1532* mutation, defining haplogroup R1a, are either 7500 years before present (YBP) [35], or 5400 ± 810 YBP [17]. These data are in good agreement with the suggestion on the archaeological correlation of this haplogroup with the carriers of the Kurgan culture.

Eastern part of the distribution area of haplogroup R1a1 is in Central Asia [20, 36] and on the territory of Altai and Sayans [17, 37]. Note that haplogroup R1a1 prevails among Southern Siberian and Central Asian populations, whose early ethnogeny is associated with the steppe Bronze culture. Among these populations, the frequency of haplogroup R1a1 constitutes 21% in Uzbeks, 24% in Tadjiks, from 41 to 57% in Kyrgyzes, from 52 to 58% in Southern Altaians, 40% in Northern

Altaians, and about 15% in Tuvinians [17, 37]. In East Asia, haplogroup R1a1 is very rare. In Pakistan and India haplogroup R1a1 accounts for about 30% of all Y chromosomes [38, 39]. Furthermore, in India the proportion of this haplogroup is remarkably higher among the representative of upper castes (Brahmans, Kshatriyas, and Vaishyas). This finding may reflect the contribution of the dominating Aryan elite to the gene pool of these groups. Though haplogroup R1a1 was also observed among some tribes of Southern India (up to 26%), this observation is most likely associated with intensive gene flow through the caste and tribal barriers, as it was demonstrated by Ramana *et al.* [40].

Rosser *et al.* [18] showed that haplogroup R1a1 chromosomes, which are presented in both Europe and Asia, coalesce to the common ancestor about 2500 to 3800 YBP, which corresponds to the distribution of the Andronov culture of the Bronze Age. In respect to its linguistic features, the population of the Andronov culture belonged to the Indo-Iranian linguistic family [5] and was distributed throughout that part of Asia, where the carriers of haplogroup R1a1 currently reside. Thereby, early Indo-European migrations are, probably, marked by this haplogroup.

Macrohaplogroup F (21.3%) is the second most frequent in Ukrainians. The haplogroup defining mutation at the *M89* locus is considered to be the ancestral relative to haplogroups J, N, and P found in the present study (see below) and to haplogroup R1a1 [19]. Macrogroup F also includes haplogroup H, distributed in Asia and not detected in the Europeans, along with haplogroups G (defined by the *M201* mutation) and I (mutation in *M170*). It is suggested that haplogroup G originates from the Middle East [19], and its distribution in Europe is associated with rather recent migrations. The frequency of haplogroup G decreases from the southeast to northwest, from 30% in the Caucasus to 2 to 5% in Central Europe. On the territory of Europe haplogroup I has been dated at 22 000 YBP, among the early migrants from the Middle East. it is suggested that the distribution of this haplogroup occurred in parallel with the mitochondrial haplogroup H. At present, the proportion of haplogroup I is maximal in the populations of central and eastern Europe, constituting 45% in Croatians, 41% in Saami, 37% in Germans, 23% in Poles, and 15% in Czechs. Thereby, it can be suggested that the proportion of haplogroup I not identified in the present study in the Ukrainian gene pool constitutes about 60 to 70% of all F lineages.

The frequency of haplogroup P in the Ukrainians is 9.6%. According to literature, the highest frequency of haplogroup P (70 to 80%) is observed in Western Europe: in Scotland, Ireland, and in Spaniards of Pyrenean Peninsula. In Basques, the frequency of haplogroup P is about 85%. The frequency of haplogroup P gradually decreases eastwards, constituting 5 to 10% in Baltic States and in Eastern Slavs [18, 19]. It is suggested that the distribution of haplogroup P is associated with the carriers of the Orinyak archaeological culture, which in Europe is dated at 35 000 to 40 000 YBP [19]. The present-day distribution pattern of haplogroup P can be formed similarly to that of haplogroup I, i.e., post-glacial settling of its carriers from the long-term geographical isolates [19].

Haplogroups J and E, comprising 11.7 and 4.2% of the chromosomes in the Ukrainian gene pool, respectively, are thought to be associated with the settling of the Middle Eastern agriculturists during the Neolithic. At present maximum frequency of haplogroup J was observed in Middle East, constituting 49.5% in Syrians, 39% in Palestinians, and 36% in Israeli Jews and Lebanese [41]. The frequency of this haplogroup is also high in the Caucasus and Anatolia (25 to 30%) [18]. The pattern of the haplogroup J (marked by the *12f2* deletion) frequency change indicates that it could have arisen in the Middle East in Upper Paleolithic, and then has spread westward and eastward with the migrants, who brought to Europe not only the new methods of making stone tools and ceramics, agriculture, and cattle-breeding, but also haplogroups E and G. It is possible, that Y-chromosomal haplogroup J was brought to Europe together with mitochondrial haplogroup J, which had arisen during the Paleolithic, but appeared in Europe also during the Neolithic [42, 43]. In case that haplogroup J was distributed by Phoenicians, who colonized the Mediterranean during the first millennium B.C., more recent appearance of the haplogroup J carriers in the in this region cannot be excluded.

The last genetic component of the Ukrainian male gene pool is represented by haplogroup N3. The area of this haplogroup is restricted to Northern Eurasia. Haplogroup N3 is widely distributed among Finno-Ugric populations, and also among the ethnic groups belonging to Balto-Slavic branch of the Indo-European family. In Finno-Ugric populations haplogroup N3 accounts for 30 to 60% of all Y chromosomes, constituting 42% in Saami, 61% in Finns, 39% in Karelians, 37% in Estonians, 62% in Komis, 51% in Maris, and 30% in Udmurts [16, 18, 19, 33]. Uralian populations of Northern Asia are also characterized by the high N3 frequency, constituting 62% in Khanty, 20% in Mansi, and 25 to 40% in Nentsi. The proportion of haplogroup N3 in the male lineages of Balto-Slavic populations is slightly lower, constituting 47% in Lithuanians, 32% in Latvians, 15% in Russians, 2.5% in Belarussians, and 3% in Slovaks and Poles [17, 18]. The frequency of haplogroup N3 in Central and Northern Europe is substantially lower. Age estimates of this haplogroup vary from 4200 [44] and 6100 ± 940 [17] to 8400 ± 700 years [35]. Geographic distribution pattern and timing of haplogroup N3 suggest that it has appeared of Northern Eurasia after the Last Glacial Maximum and distributed among the ancestors of the present-day Finno-Ugric and Altaic ethnic groups.

The presence of the N3 lineage in Eastern Slavs can be most likely explained by the assimilation of Finno-

Ugric tribes in the course of Slavic migrations from central Europe to the east. In this case, the frequency of haplogroup N3 in Slavs marks the contribution of Finno-Ugric populations to the present-day gene pool of Slavs.

Thus, multicomponent structure of the male portion of the Ukrainian gene pool has been described. Haplogroups P and I accounting for about 25% of all the lineages represent the heritage of the autochthonous population, which peopled Europe as early as in the Paleolithic. Haplogroup R1a1, probably, is the marker of the Indo-European contribution. Genetic contribution of the Neolithic migrants from the Middle East is marked by haplogroups J, G, and D, accounting for about 25% of the gene pool.

Further detailed analysis of the structure described requires the use of the additional biallelic markers and performance of the haplotype analysis using microsatellite repeats. This work is currently in progress.

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