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Variability of the 3′ApoB Minisatellite Locus in Eastern Slavonic Populations

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Key Words
Population genetics · Human evolution · Genomics · Apolipoprotein B · Allele frequency distribution

Abstract
Objective: To describe and compare the 3′ apolipoprotein (Apo) B minisatellite allele frequency distributions of Eastern Slavonic populations and their Uralic, Altaic, and Caucasian speaking neighbors. ***Methods:*** Healthy individuals of 10 populations among Russians, Byelorussians, Komis and Bashkirs were studied for variable number tandem repeats (VNTRs) in the 3′ApoB minisatellite region. Data were analyzed with other results reported for this polymorphism in eastern Europeans and Siberians. ***Results:*** Allele frequency spectra in Eastern Slavonic, Northern Caucasian and Finno-Ugric speaking populations are bimodal with the main peak in alleles 34–36 and a secondary mode around allele 48, whereas Altaic speaking populations have a unimodal allele frequency distribution with a peak of around 34–36 VNTRs. Population relationships were revealed using both multidimensional scaling analysis (based on Nei's genetic distance estimate) and testing for genetic heterogeneity. Eastern Slavonic populations (Russians, Ukrainians, Byelorussians) were most closely related to each other and formed a separate tight cluster when plotted. Testing for genetic heterogeneity among the Eastern Slavonic ethnic groups revealed maximum diversity among Byelorussians, followed by Russians, then Ukrainians. The 3′ApoB minisatellite variability reveals little heterogeneity among the Eastern Slavonic ethnic groups, whereas there was significant heterogeneity for Northern Caucasian and Altaic speakers. ***Conclusion:*** For this 3′ApoB polymorphism the Eastern Slavonic populations, despite their wide geographical distribution, appear to be much more homogenous than other ethnic groups of the region. Multidimensional scaling analysis of these data allowed for differentiation between individual populations from an ethnic group even if there is little heterogeneity.

Introduction

Human population genetics is expanding rapidly, using different kinds of novel approaches based on peculiarities and comparisons among DNA markers [1–3]. The combination of particular loci allows one to track the evolution of a population with high accuracy. Here, we analyzed one such locus, the minisatellite 3′ apolipoprotein (Apo) B region with variable number tandem repeats (VNTRs), for a number of eastern European populations with differing ethnic affiliations. The 3′ApoB structure shows tandemly repeated sequences that are 14–16 nu-

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cleotide pairs long and rich in A and T; alleles usually differ from each other by 30 nucleotide pairs or by two repeats [4]. Allele frequencies of this locus vary between populations and have been widely used in investigations of the population history and diversity of humans [4–9].

Eastern Slavonic ethnic groups, forming the majority of the eastern European population, are the focus of this article. Archaeological and anthropological studies indicate that the colonization of the Eastern European Plain by Slavonic peoples from the central part of Europe began in the early Middle Ages [10, 11]. Theories about the origin and ethnogenesis of Eastern Slavonic ethnic groups (Russians, Ukrainians, and Byelorussians) are based on their common lineage [12], and are of two main types: hybridization and transformation. Hybridization theories argue that modern Russians, Ukrainians, and Byelorussians are the result of an admixture between Slavonic tribes, whose homeland was probably in central Europe, and pre-Slavonic populations of eastern Europe, such as Finno-Ugric (on the north-west and east of Russian Plain), Baltic (on the west) and Iranic tribes (on the south) [10]. Transformation theory assumes that Eastern Slavonic ethnic groups gradually evolved from ancient populations of eastern Europe, at least from the Late Bronze Age [13]. Studies of mitochondrial (mt) DNA sequence polymorphisms [14–17], Y-chromosome short tandem repeat (STR) haplotypes [18, 19], and autosomal STR diversity [7, 20] support the hybridization theory of the origin of Eastern Slavs, which implies their central European origin and subsequent mixture with and assimilation of pre-Slavonic populations of eastern Europe.

The Russians, Ukrainians and Byelorussians – the main modern ethnic groups of Eastern Slavs – consist of numerous populations, inhabiting huge geographic regions. The widespread distribution and admixture during the ethnogenesis of Eastern Slavs may have resulted in heterogeneity among these peoples, as was revealed during anthropological studies [21]. Recent studies of DNA diversity among Eastern Slavonic populations have resulted in differing views of their gene pool heterogeneity. Studies of mtDNA sequence polymorphisms revealed little [17] or high heterogeneity [14–16] of such populations, whereas studies of Y chromosome STR haplotypes [18, 19], autosomal STR polymorphisms [8, 20, 22, 23], and phage M13 minisatellite DNA fingerprinting [24] revealed homogeneity among these populations. Most of these papers found that comparisons of Slavonic samples from distant geographic regions of eastern Europe reveals the complicated structure of the gene pool in eastern Europe, caused by admixture between Slavonic and neighboring ethnic groups. One of the possible reasons for the contradictory conclusions about the heterogeneity in these studies is the low number of population samples from within any given ethnic group.

Here, we studied 3′ApoB minisatellite polymorphisms in healthy individuals from 10 different populations (four Russian, four Byelorussian, the Komi, and the Bashkir) living in the Russian Federation and the Republic of Belarus. For a detailed comparison, data from our previous studies of 3′ApoB variability in other eastern European populations [8, 25, 26] have been combined with those reported here.

Methods

DNA samples were obtained with informed consent from donors of 10 populations from four ethnic groups: two Eastern Slavonic (Russians and Byelorussians), one Altaic (Bashkirs), and one from Uralic (Komi-Permyats) linguistic families. To be included, all individuals needed to belong to the native ethnic group of the regions studied (to belong to at least the third generation living in the region), to be unrelated to each other, and to be healthy.

The Eastern Slavonic linguistic group (Indo-European linguistic family) was represented by samples from four Russian populations from the European (northwestern) part of Russia (the Belaia Sluda, the Kholmogory, the Puchej, and the Velij), and four Byelorussian populations (the Grodno, the Pinsk, the Nesvij and the Khoiniki) from different regions of the Republic of Belarus (for a detailed description of Byelorussians see Popova et al. [27]). The Belaia Sluda group is an isolated Russian population, living at the border of the Arkhangelsk region of north Russia and the Republic of Komi. From ethnohistorical and anthropological points of view, this group might carry an admixture of ancient Vepsian [12] or Saami lineages [10, 11]. The Kholmogory are based in a town near Arkhangelsk city, representing Russian north coast dwellers. The Puchej group (living in a town of the Ivanovo administrative district) is from the northeastern European part of Russia, and is derived from Russians who settled on the Volga River as traders before the sixteenth century. The Velij group is a northwestern Russian population from the border between Russia and the Belarus republic, with a complex history of population movements.

Populations from the south Ural region were represented by Finno-Ugric speakers (Uralic linguistic family, the Komi-Permyats from the Perm district of Russia), and by Turkic speakers (Altaic linguistic family, the Bashkirs, from the Beloretsky region of the Republic of Bashkiria; for a detailed description of these groups see Bermisheva et al. [28]). As these two groups inhabit nearby regions at the border between Europe and Asia, they have been considered as mixed populations with different levels of European and Asian origin [29].

DNA isolation and purification, polymerase chain reaction (PCR) analysis, gel electrophoresis, and multidimensional statistical analyses were carried out as described [8]. Calculations of population characteristics, Nei's pairwise genetic distances [30], and

Table 1. Allele frequencies of 3′ApoB minisatellite locus in Russian, Byelorussian, Bashkir, and Komi populations

Number of tandem repeats*	Russians				Byelorussians				Bashkirs	Komis
	Velij	Puchej	Kholmogory	Belaia Sluda	Khoiniki	Nesvij	Grodno	Pinsk	Beloretsky	Permyats
24					0.011				0.008	
27	0.005									
29				0.007			0.011			
30	0.068	0.064	0.086	0.054	0.065	0.032	0.034	0.086	0.025	0.092
31				0.007	0.011		0.023			
32	0.050	0.064	0.052	0.054	0.011	0.064	0.034	0.07	0.100	0.026
34	0.198	0.234	0.241	0.250	0.239	0.191	0.261	0.180	0.375	0.342
35	0.009	0.005	0.009							0.020
36	0.428	0.404	0.405	0.385	0.380	0.381	0.409	0.391	0.392	0.368
37		0.005							0.017	0.013
38	0.045	0.037	0.043	0.041	0.054	0.056	0.034	0.023	0.033	0.040
39					0.011					0.007
40	0.023	0.027		0.034	0.044	0.040	0.023	0.008		
41										0.007
42	0.005	0.005								
43		0.005								
44	0.018	0.027	0.043	0.027		0.040	0.034	0.016		0.020
45	0.032	0.027	0.009	0.007	0.033	0.024	0.023	0.008	0.008	
46	0.045	0.043	0.017	0.027	0.076	0.064	0.011	0.133	0.017	0.007
48	0.059	0.053	0.095	0.081	0.054	0.111	0.102	0.086		0.040
49										0.013
50	0.018			0.020	0.011				0.017	0.007
52				0.007					0.008	
Sample size (chromosomes)	222	188	116	148	92	126	88	128	120	152
Observed heterozygosity	0.757	0.766	0.862	0.784	0.717	0.841	0.727	0.859	0.667	0.710
Expected heterozygosity (Nei, 1973)	0.761	0.765	0.754	0.767	0.779	0.79	0.747	0.777	0.693	0.734
Number of distinct genotypes	36	33	19	27	21	26	20	22	15	22
Number of distinct alleles	14	14	10	14	13	10	12	10	11	14
χ^2 test for Hardy-Weinberg equilibrium	Hi2 = 64.27	76.69	30.24	52.37	150.89	31.18	51.2	31.02	35.81	179.33
	p = 0.985	0.858	0.955	0.989	0.001	0.941	0.91	0.944	0.979	0
	DF = 91	91	45	78	78	45	66	45	55	91
Likelihood ratio test for Hardy-Weinberg equilibrium	G2 = 53.12	50.17	32.23	45.17	50.77	32.65	28.97	30.53	27.31	57.6
	p = 0.999	0.999	0.923	0.998	0.993	0.915	1.000	0.951	0.999	0.998
	DF = 91	91	45	78	78	45	66	45	55	91

* Designations according to Ludwig et al. [4].

molecular variances were carried out using POPGENE version 1.32 [31] and GDA software [32]. Fisher's exact testing of contingency tables was performed using R × C software [33].

Results and Discussion

The allele frequency distributions (AFDs) obtained are shown in table 1. We detected 23 alleles with 24–52 repeats out of 1,380 chromosomes typed. The allele spectra in Eastern Slavonic populations were bimodal, with the main peak in alleles 34–36 and a secondary mode around alleles 48, which coincided with allele frequency profiles of other Indo-European populations for this locus [6–9]. A high degree of similarity was found among the allele profiles for the Eastern Slavonic populations studied. Most frequent in these samples was allele 36 (frequencies ranged from 38 to 43%), followed by allele 34 (range 18–25%).

Populations from the south Ural region showed a unimodal AFD with a peak around 34–36 repeats, which is similar to Asian populations. Previous studies demonstrated that Asian populations have allele 34 at the highest frequency, whereas allele 36 is most common among Indo-European speaking populations [5, 8, 9]. Both Bashkir and Komi populations from the south Ural had ap-

Fig. 1. The geographic location of populations analyzed. Numbers are decoded in table 2. Russians: 1, Velij; 2, Puchej; 3, Belaia Sluda; 4, Kholmogory; 5, Novgorod; 6, Kursk; 7, Smolensk; 8, Kostroma; 9, Oschevensk; 10, Kuban Cossaks; Byelorussians: 11, Grodno; 12, Nesvij; 13, Khoiniki; 14, Pinsk; 15, Bobruisk; 16, Mjadel'; Ukrainians: 17, Alchevsk; 18, Kiev; 19, L'vov; Adygeis: 20, Shapsugs; 21, Eastern Adygeis; 22, Western Adygeis; 23, Circassians; 24, Abkhazians; 25, Komis (Permyats); 26, Kalmyks (Elista); 27, Bashkirs (Beloretsky region, not shown here); 28, Yakuts (Tiungiuliu, not shown here).

Table 2. Classification of the populations studied

Linguistic family	Linguistic group	Ethnic group	Population	Geographic region	Map point	Reference
Indo-European	Eastern Slavonic	Russians	Velij	Russian plane	1	this study
			Puchej		2	this study
			Belaia Sluda		3	this study
			Kholmogory		4	this study
			Novgorod		5	8
			Kursk		6	8
			Smolensk		7	8
			Kostroma		8	8
			Oschevensk		9	8
			Kuban Cossaks	North Caucasus	10	25
		Byelorussians	Grodno	Russian plane	11	this study
			Nesvij		12	this study
			Khoiniki		13	this study
			Pinsk		14	this study
			Bobruisk		15	8
			Mjadel'		16	8
		Ukrainians	Alchevsk		17	26
			Kiev		18	26
			L'vov	Carpaty mountains	19	26
Northern Caucasian	Abkhaz-Adygei	Adygeis	Shapsugs (Coastal)	North Caucasus	20	25
			Eastern Adygeis (Coastal)		21	25
			Western Adygeis (Highlanders)		22	25
		Circassians	Circassians		23	25
			Abkhazians	Abkhazians	24	25
Uralic	Finno-Ugric	Komis	Permyats	South Urals	25	this study
Altaic	Mongolian	Kalmyks	Elista	Northwestern Caspian	26	8
	Turkic	Bashkirs	Beloretsky	South Urals	27	this study
		Yakuts	Tiungiuliu	Siberia	28	8

proximately equal frequencies of alleles 34 and 36, and this is in line with anthropological evidence of an Asian admixture among these ethnic groups [29].

High heterozygosity levels for this gene were observed for all populations investigated, (67–86%, table 1). There was also a high incidence of 3′ApoB minisatellite polymorphisms. The genotype distributions did not deviate from Hardy-Weinberg expectations, based on the likelihood ratio and Fisher's exact tests. The only exception is the Khoiniki population, where Fisher's exact test revealed deviation from Hardy-Weinberg expectations, whereas likelihood ratio test with Bonferroni correction showed no deviation. This can be explained by the small size of the sample from this group, which also showed a wide allele spectrum requiring multiallele correction during the test of the deviation from Hardy-Weinberg expectations [34].

Data from our previous studies of 3′ApoB variability in other eastern European populations [8, 25, 26] were combined with those reported here. These included Russians (the Kursk, the Novgorod, the Kostroma, the Smolensk, and the Oschevensk); Byelorussians (the Mjadel and the Bobruisk); Kalmyks, Yakuts, Abkhazians, Circassians, Shapsugs, eastern Adygeis (highlanders) and western (coastal) Adygeis (for a detailed description of these populations see Verbenko et al., 2003 [8] and Verbenko et al., 2004 [25]), and Ukrainians (the Kiev, the L'vov, the Alchevsk) (for a detailed description see Kravchenko et al., 1996 [26]). The populations involved in the study are shown on the map (fig. 1), and their linguistic and ethnic affiliations with map references are in table 2.

Multidimensional scaling analysis with Nei's pairwise distance matrix [30] was used to analyze the population

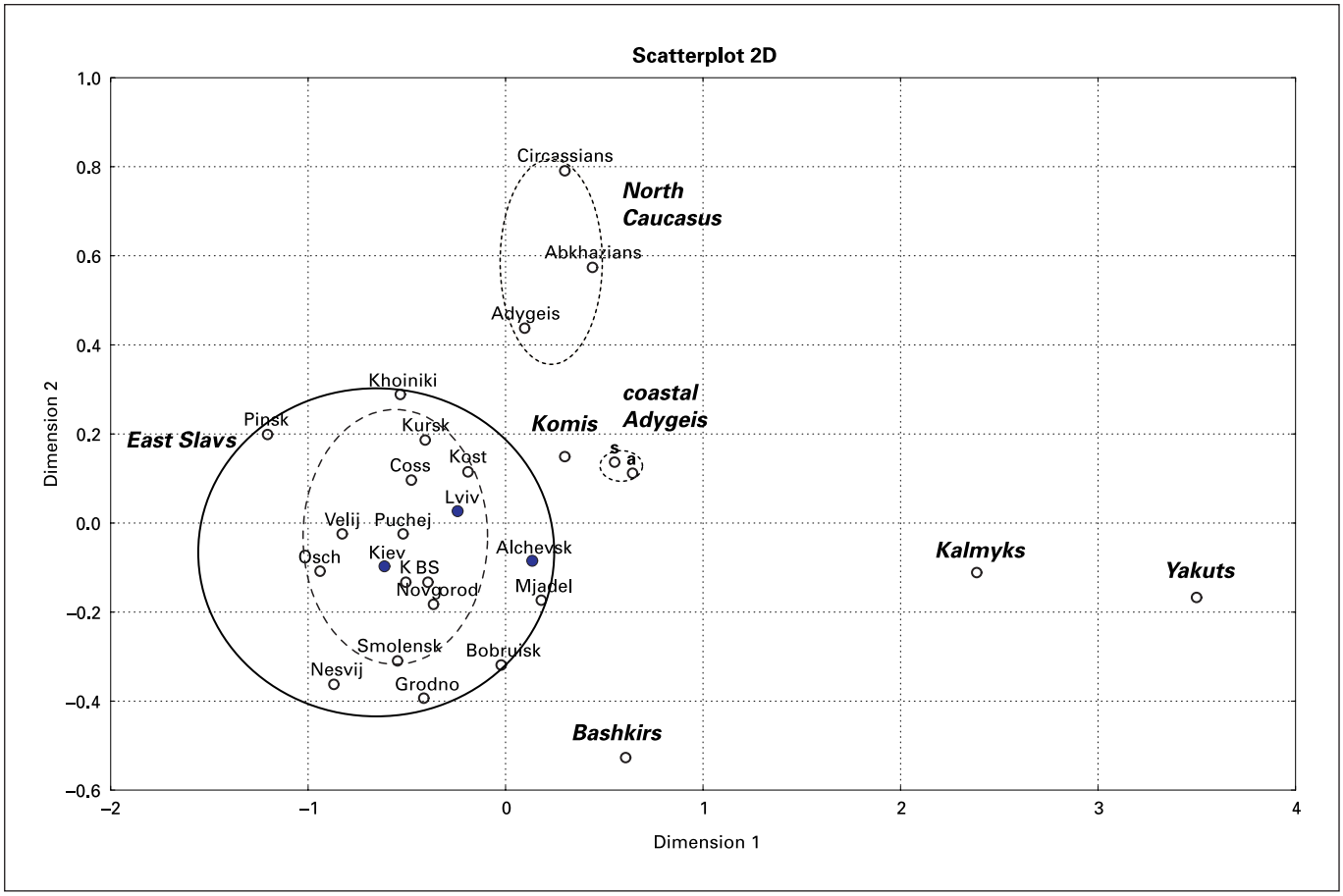

Fig. 2. The multidimensional scaling plot (two dimensions) of Nei's genetic distances between 28 East European populations based on 3′ApoB VNTR variability. Abbreviations are: s, Shapsugs; a, western Adygeis; Adygeis, eastern Adygeis; Coss, Kuban Cossacks; Kost, Kostroma; Osch, Oschevensk; K, Kholmogory; BS, Belaia Sluda. Ethnic communities of the northern Caucasus, East Slavonic and coastal Adygei are circled to make comparisons easier. Bold circle designate East Slavonic populations: Byelorussian populations are arranged closest to the circle; dark points are Ukrainians, and others (inside ellipse with long dashes) are Russian populations. Additional data were analyzed for Ukrainians (populations from Kiev, L'vov, and Alchevsk) [26], for Russians (populations from Kursk, Novgorod, Kostroma, Smolensk, and Oschevensk), for Byelorussians (the Mjadels, and the Bobruisks), the Kalmyks and the Yakuts [8], and for Kuban Cossacks, Abkhazians, Circassians, Shapsugs, eastern Adygeis (highlanders) and western (coastal) Adygeis [25].

relationships. The resulting plot required two dimensions for statistical robustness (fig. 2). One can see the differentiation between the populations of different ethnic groups, whereas there was some uniformity within any given ethnic group. Most of the populations in the left part of the plot belong to Indo-European and Northern Caucasian speaking peoples, and this supercluster may be further subdivided. For the ethnic groups represented here by several populations, Eastern Slavonic populations are close together, whereas a group of coastal Adygeis (the Shapsugs and western Adygeis) is remote from other Northern Caucasian speaking populations (Adygei highlanders, Circassians and Abkhazians), which form their own subcluster. The Komi population is the closest neighbor of East Slavs, followed by the coastal Adygeis. The Bashkir population is located as far from the East Slavs as is the Northern Caucasian cluster. The Yakut and Kalmyk populations, of Asian origin, are placed far from the others on the plot and are positioned closest to the Bashkir.

Despite their wide geographical distribution, the Eastern Slavonic populations (Russians, Ukrainians, Byelo-

Table 3. 3′ApoB VNTR molecular diversity within groups studied

Linguistic family:	Indo-European			Northern Caucasian			Altaic		
Fst	0.0069			0.0044			0.0231		
Probability value (R × C testing)	0.021			0			0		
Linguistic group:	Eastern Slavonic			Abkhaz-Adygei			Turkic		Mongolic
Ethic group:	Russians	Byelorussians	Ukrainians	Adygeis	Circassians	Abkhazians	Yakuts	Bashkirs	Kalmyks
	10 populations	6 populations	3 populations	3 populations					
Fst	0.0041	0.0083	0.0040	0.0030					
Probability value (R × C testing)	0.298	0.029	0.916	0.021					

russians) have a common historical lineage [10–13, 21] and are also closely associated according to their 3′ApoB polymorphisms. For example, although Kuban Cossacks (an ethnic community of Russians from the Krasnodar region) inhabit part of the northern Caucasus, they are closer to the Eastern Slavonic populations than to other populations of their locality [12]. The closest relationships among the latter groups are between the Russian and Ukrainian populations. The greatest diversity is shown by the Byelorussian populations, which are located around other Eastern Slavonic populations on the plot. This diversity was possibly caused by long-term gene flow during numerous migrations through Belarus region. The proximity of the Komi to East Slavs in this analysis may be caused by a recent admixture of Komi-Permyats with Russians [10–12, 29].

Statistical testing of genetic heterogeneity of AFDs was performed using R × C software [33]. Pairwise comparisons between populations revealed remarkable differences between the Yakut, Bashkir and Kalmyk ethnic groups, which show extreme heterogeneity when compared with any other population ($p < 0.00001$). Pairwise comparisons among other populations studied revealed homogeneity among Eastern Slavonic populations. AFDs for the Northern Caucasian speaking population demonstrate homogeneity both among themselves and with Ukrainians, and the heterogeneity with others. The Komi population also shows heterogeneity with others ($p < 0.05$), but statistical homogeneity was found with the Kholmogory, Oschevensk and Alchevsk groups.

Genetic diversity was estimated using the F-statistic [35, 36]. The total F_{st} value was 0.0177. This was lowest for the Northern Caucasian linguistic family (table 3; 0.0044), while approximately half as great again for the Indo-European linguistic family (0.0069). The greatest genetic diversity (0.0231) was noted in the Altaic linguistic family. Thus, 3′ApoB variability varies considerably across linguistic families. Genetic heterogeneity testing of the Eastern Slavonic AFD contingency tables revealed maximum diversity among the Byelorussians ($p = 0.029$), followed by Russians ($p = 0.298$), and Ukrainians ($p = 0.915$). The Russian and Ukrainian populations fall within the range of variability seen for Byelorussians, and it is likely that Byelorussians are much more heterogeneous than other Eastern Slavonic groups: being grouped with Russians and Ukrainians also makes the Eastern Slavonic pool appear more heterogeneous. Such heterogeneity among these people has also been shown by mitochondrial DNA studies [14–16]. An analysis of 3′ApoB minisatellite AFDs among the pool of Eastern Slavonic populations showed little heterogeneity ($p = 0.021$), whereas significant heterogeneity was found for the populations from the north Caucasus region ($p < 0.00001$). The pooled group of Adygei populations (Eastern, Western Adygeis and Shapsugs) was also found to be slightly heterogeneous, but the probability level (0.021) in this case was lower than for any Eastern Slavonic ethnic groups.

Polymorphism distributions for this locus display similar characteristics both among related Eastern Slavonic populations, and in the Northern Caucasian speaking populations, which are less related to each other. We found similar locus diversity among Eastern Slavonic, northern Caucasus, Komi and Bashkir ethnic groups. However, there were significant differences for the Kalmyk and Yakut populations of Asian origin. Thus, these differences between populations revealed with

3′ApoB minisatellite locus polymorphisms are similar to those based on some other DNA polymorphisms [14–20, 22–24, 27, 28], and are in good agreement with ethnohistorical [12], and anthropological data [10, 11, 13, 21]. These observations thus underscore the significance of the 3′ApoB minisatellite locus for population genetic research.

The 3′ApoB locus has revealed genetic homogeneity among 19 broadly distributed Eastern Slavonic populations, in contrast to significant genetic heterogeneity among Northern Caucasian speaking populations and among Altaic speaking populations. This homogeneity may reflect the integrity of the Eastern Slavonic gene pool and suggests negligible influences from neighboring ethnic groups during the process of origin and differentiation of Eastern Slavs.

Most of the DNA marker studies available to date tend to support the hybridization theory of the origin of East Slavs, but reflects the complicated structure of the gene pool in Eastern Europe. Despite the homogeneity of the Eastern Slavonic gene pool according to the 3′ApoB variability, there is still certain segregation between individual populations of the this group. This suggests that there was less hybridization into Slavonic peoples than among neighboring ethnic groups. We believe that, when used in combination with other such specific loci, this 3′ApoB VNTR marker is suitable for the accurate tracing of population lineages.

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