Mitochondrial DNA Variations in Russian and Belorussian Populations

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Abstract The sequence of the first hypervariable segment (HVS-I) of mitochondrial DNA (mtDNA) was determined in 251 individuals from three eastern Slavonic populations, two Russian and one Belorussian. Within HVS-I, 78 polymorphic positions were revealed. Within-population diversity of HVS-I varies slightly among three samples; its estimates do not differ strongly from those for European populations. Haplotype diversity for three populations calculated in this study is 0.949; mean pairwise differences estimate is 3.59. To assign mtDNA sequences to major phylogenetic clusters, haplogroup-specific restriction polymorphisms were selectively typed in most samples. The haplogroup distribution in the total Eastern Slavonic sample is similar to that reported for the European sample. However, the separate consideration of three Slavonic samples reveals the complicated structure of the mitochondrial gene pool in the Eastern European area. Data of this study support the proposed model of the origin of modern Eastern Slavs, which implies the admixture of ancient Slavonic tribes with pre-Slavonic populations of Eastern Europe. These data should contribute to general studies of mitochondrial DNA variations in Europe.

European mitochondrial DNA (mtDNA) diversity, despite its comparatively low level, is widely employed in studies of origin and evolution of maternal lineages. Detailed studies were performed to describe mtDNA variations in separate populations as well as to reveal general tendencies in the process of the colonization of Europe, which contributed to the modern European mitochondrial gene pool formation. The identification of phylogenetic mtDNA clades, or haplogroups, and analysis of their distribution were successfully used to reveal the continent-wide mitochondrial variation pattern and to trace prehistoric migrations during the colonization of Europe (Richards et al. 1998; Macaulay et al. 1999; Simoni et al.

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2000; Torroni et al. 2001; Richards et al. 2000). Recently, studies in several populations revealed that particular haplogroups could also be associated with longevity and diseases (Torroni et al. 1997; De Benedictis et al. 1999; Rose et al. 2001). Slavonic and, in particular, Eastern Slavonic populations, which inhabit a large part of the Eurasian territory, were significantly underrepresented in mtDNA diversity studies. Recently, data on coding and control region mtDNA variations and haplogroup distribution in several Russian, one Ukrainian, and one Polish samples were reported (Orekhov et al. 1999; Maliarchuk and Derenko 2000; Malyarchuk et al. 2002) and implicated to the question of origin of the Eastern Slavs (Malyarchuk and Derenko 2001). Here we present data on mtDNA polymorphism in three other native population samples belonging to two Eastern Slavonic peoples, Russians and Belorussians.

Materials and Methods

Populations Studied. Population samples were collected after obtaining informed consent according to the following criteria: all individuals belong to the native population of the regions studied (at least three female generations living in the region), they are maternally unrelated, and they are of Slavonic origin (Russian or Belorussian, depending on the sample). The Belorussian sample (92 individuals) was collected in Bobruisk, located in the central part of the Republic of Belarus. Two Russian samples represent a native rural population of two geographically distant regions of the Russian Plain. The first one (76 individuals) was collected in the settlement of Oshevensk in the Arkhangelsk region of northern Russia. This settlement is situated in the Kargopol district, in the southernmost part of the Arkhangelsk region, which was colonized during the very early period of the formation of the Russian State. Its isolated rural populations are supposed to be little affected by recent migrations and are very interesting with respect to genetic studies. The second sample (83 individuals) was collected in Bashkiria, Arkhangelsky district, but includes only ethnically Russian individuals. The Russian population of the Ural region, to which Bashkiria belongs, was formed mostly by migrants from southern areas of the country, and is supposed to differ genetically from the northern population.

Hypervariable Segment I Polymorphism Analysis. DNA was isolated from peripheral blood according to the standard phenol-chloroform extraction protocol. The first hypervariable segment (HVS-I) fragment of the mitochondrial control region was amplified by polymerase chain reaction (PCR) using primers con L2 (5'-CAC CAT TAG CAC CCA AAG CT 3') and con H2-B (5'TGA TTT CAC GGA GGA TGG TG-3') (Richards et al. 1996). Amplicons were sequenced in both directions by use of the Sanger dideoxy-chain-termination method and cycle-sequencing protocol with [γ -³³P]-labeled amplification primers. PCR and cycle sequencing reactions were performed in an MJR ptc-100 thermal cycler (MJ Research, MA, USA). Sequences were determined between positions 16040 and 16365 (Anderson et al. 1981). Positions different from the Cambridge reference sequence (CRS, Anderson et al. 1981) were identified. Simple haplotype diversity, h, estimated by the method of Nei (Nei 1987), and mean pairwise differences were determined using DnaSP version 3.53 software (Rozas et al. 1999). The standard error of mean pairwise differences was estimated from 200 bootstrap replications of the primary data set.

Restriction Fragment Length Polymorphism Analysis and Haplogroup As-In some cases, haplogroup assignment of mtDNA sequences could signment. be performed on the basis of diagnostic HVS-I motifs (Macaulay et al. 1999; Richards et al. 2000). For those lineages that do not have a distinctive HVS-I motif, or in which this motif is ambiguous, additional coding-region restriction fragment length polymorphism (RFLP) markers were typed to confirm or exclude the affiliation with a particular haplogroup. In this study, selective RFLP polymorphisms were analyzed in most individual samples. To determine the RFLP status of mitochondrial sequences, restriction endonuclease analysis was performed on mtDNA fragments amplified as described by Torroni et al. (1996, 1997). The 7025AluI site was tested to reveal haplogroup H sequences (-7025AluI). Those +7025AluI samples lacking the 14766MseI site were identified as belonging to the HV cluster; from them, sequences bearing 16298C substitution on the HV background were identified as pre-V. In +7025AluI, +14766MseI sequences, the 12308HinfI site was tested to identify haplogroup U (+12308HinfI). Within haplogroup U, sequences were assigned to subclusters on the basis of HVS-I diagnostic motifs, as was done within haplogroups J and T. In cases of ambiguous sequence motif, affiliation with haplogroup T was determined by +13366BamHI. 10394DdeI, 10397AluI sites were typed in all 16223T samples. The +10394DdeI, +10397AluI status was used as a marker of haplogroup M; +14465AccI was used as a marker of haplogroup X; and +10028AluI, +16389BamHI was used as a marker of haplogroup I. Haplogroups W, C, and N were identified on the basis of HVS-I sequence (Macaulay et al. 1999). Lineages that could not be assigned using HVS-I sequence motif and the restriction markers mentioned above were named "Other." The comparison of haplogroup distribution among samples was performed using POPGENE software version 1.32 (Yeh et al. 1997).

Results and Discussion

HVS-I Sequence Variability. We performed the sequence analysis of the first hypervariable segment of the mitochondrial D-loop in three different Slavonic samples, two Russian and one Belorussian. Mitochondrial DNA of 251 individuals was analyzed, including 92 Belorussian individuals from Bobruisk, 76 and 83

Russian individuals from Arkhangelsk region (Oshevensk) and Bashkiria, respectively.⁵

The total number of HVS-I polymorphic sites revealed in the three populations is 78 (data on sequence variations and their distribution are presented in the Table 1). Most of them are transitions. Of the total number of substitutions in Russians (Bashkiria), 5 (11.1%) are transversions, versus 2 (4.4%) transversions in Russians (Oshevensk) and 3 (5.4%) transversions in Belorussians.

For HVS-I variations, the simple haplotype diversity was determined as a measure of within-population genetic diversity. It shows relatively high values, with the estimate 0.95 for three samples in total and the highest value for the northern Russian population (Table 2). Mean pairwise difference estimates, relatively low, range between 3.33 and 3.80, also reaching the highest value in Russians (Oshevensk). Thus, all three Slavonic samples show high estimates of haplotype diversity combined with low values of mean pairwise differences, which is typical for European mitochondrial DNA diversity described elsewhere. The Russian (Oshevensk) sample shows slightly higher haplotype diversity and number of mean pairwise differences than the two other samples.

The percentage of unique HVS-I haplotypes has the lowest value (68.3%) in Russians (Oshevensk) and the highest (84.6%) in Russians (Bashkiria). These estimates show that the female population of Oshevensk represents a more restricted pool than those of the two other Slavonic samples. The percentage of unique haplotypes estimated for the three populations in total (77.3%) is close to the estimate of approximately 77% for the European population (Richards et al. 1996). This finding suggests that treating Russians as one total population, as has been done in earlier studies, could mask significant heterogeneity and differences among local groups.

HVS-I and RFLP Combined Data. In addition to the sequence analysis, major haplogroup-defining RFLP markers were typed selectively in those samples that could not be assigned to any cluster on the basis of a diagnostic HVS-I motif. The HVS-I and RFLP typing revealed 139 different lineages (Table 1).

A relatively high number of lineages in Russians from Bashkiria ("Other," 15.7%; Table 3) was not assigned to any group. HVS-I and determined RFLP markers (+7025*Alu*I, +14766*Mse*I, -13366*Bam*HI, -12308*Hinf*I, and also -10397*Alu*I, -10394*Dde*I for 16223T-sequences) imply that most probably these lineages belong to pre-*HV* or other clusters encompassed by *R* (Macaulay et al. 1999), excluding *HV*, *U*, and *JT*. At the least, the status of the 00073 position should be determined in assigning these sequences, but 00073 typing was not performed in this study.

The most abundant HVS-I type in all populations was CRS. Additional RFLP typing performed on these sequences revealed the heterogeneity of this

⁵Sequence variants corresponding to HVSI haplotypes determined in this study were deposited in the Gen-BankTM under accession numbers AY005336-AY005390 (Belorussian sample), AY005827-AY005866 (Russians, Oshevensk) and AF292943-AF292943 (Russians, Bashkiria).

group. Interestingly, a relatively high proportion of CRS sequences belongs to haplogroup U (+12308HinfI). In Belorussian and Russian (Bashkiria) populations it constitutes 33.3% and 36.8% of CRS lineages, correspondingly. Data from earlier studies reported that within Europe CRS lineages were assigned predominantly to haplogroup H (Richards et al. 2000). Haplogroup H constitutes the majority of all three samples analyzed in this study, a finding similar to those for other European and Middle Eastern groups (Richards et al. 1998, 2000), as well as to those for previously reported Slavonic samples (Orekhov et al. 1999; Malyarchuk and Derenko 2001; Malyarchuk et al. 2002). Two 16223T substitutions were observed among haplogroup H sequences, one in each Russian sample. Sequences bearing 16223T substitutions on the haplogroup H background were described also in another Slavonic sample, Ukrainians (Malyarchuk and Derenko 2001). As mentioned by the authors of this study, this substitution is rare among European sequences not belonging to I, W, or X groups. In addition, five more 16223T sequences observed in Russians (Bashkria) were assigned to "Other" and do not belong to M, I, W, or X clusters. A high representation of 16240C sequences could be mentioned as another peculiarity of haplogroup H in the northern Russian population. This rare substitution, also reported by Helgason et al. (2001) in a Scottish sequence, was observed in seven maternally unrelated individuals, five of them bearing the single 16240C transversion, and in two sequences representing probable derivatives.

The distribution of haplogroup pre-*V* in our samples could be of some interest, because in studies of Torroni et al. (1998, 2001) a postglacial recolonization of Europe and population expansion from southwestern to northeastern Europe was inferred from the haplogroup *V* distribution. Pre-*V* lineages have equally significant frequencies (5.4% and 5.3%) in Belorussians and Russians (Oshevensk), while in Russians (Bashkiria) this cluster is represented by a single individual sequence. This observation is consistent with the higher frequency of *V* in northern European populations.

Significant differences were noted in the representation of the *HV* monophyletic cluster. While more than half of individual lineages in Belorussians and Russians (Oshevensk) belong to this cluster, the population of Russians (Bashkiria) demonstrates the decreased level of 32.5%.

Haplogroup U sequences are widely distributed in the Eastern Slavonic samples described here. Their frequency in both Russian samples is higher than in the Russian sample reported by Malyarchuk and Derenko (2001) (28.6% and 26.3%, against 14.0%), though closer to the frequency in the Russian sample from the Malyarchuk et al. (2002) study (20%). In Russians (Bashkiria) haplogroup U has higher diversity than in two other samples, with a greater number of different subclusters. As mentioned above, one unusual feature of haplogroup U in the two Eastern Slavonic populations consists of a high content of CRS lineages. Also unlike findings for earlier reported Slavonic samples, haplogroup K has a significant frequency (7.9%) in the northern Russian population, but is rare in Belorussians and Russians (Bashkiria). U5, the most ancient European

	Nun	Number of Individuals	iduals						RF	RFLP Status	SI			
	Belo-	Russians	Russians	HVS-I	Hanloom	IulA 2007	Msel	Hinfl 12200	BamHI	Alul	Ddel	BamHI 16290	Alul Accl	Accl
	russians	russians Osnevensk	Bashkirta	Haptotype	Haplogroup	CZU/	14/00	12308	00551	16501	10394	68601	10028	C0++1
-	13	10	11	CRS	Н	I								
0	1			069-093-172-189	Н	I								
б		1		080-183i-189i	Н	I								
4		1		080-189	Н	I	I	I						
5		1		092	Н	I								
9	1			092-140	Н	I								
٢	1		1	093	Н	I								
8	1			093-129-316	Н	I								
6		1		093-192-223-240C	Н	I	I			I	I		I	
10	-			126-183d-189	Н	I			I					
11	1			129-181-183d-189-318	Н	I								
12	1			140-293-311	Н	I								
13			1	151	Н	I								
14		4	1	162	Н	I								
15	-			162-163	Н	I								
16			1	162-183i-189	Н	I								
17	1			162-259	Н	I								
18		1		162-274	Н	I								
19		2		162-311	Н	I								
20		7		167	Н	I								
21			1	172	Н	I								
22	-			176	Н	I								
23			1	183C-189	Н	I								
24	1			189	Н	I								
25	-			189-192	Н	I								
26		1		189-291-345	Н	I								

Table 1. MtDNA Variants in Byelorussian and Russian Samples

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192-304-311 193 209-229 209-304 223	235-261-291 240C-242-304 240C 261-304 261	263-278 263 278 278-293-311 278-293-311-347 278-293-311-347	304 311 362 298 126-298 CRS	144-172-189-311 269 CRS 126-270 129-1834-189 1834-189-304-311 189 189-291G-311 271A
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-	5	n 6	- m - m	
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27 28 30 31	32 35 36 36	37 38 39 41 41	. 44 45 49 49 49 49	50 51 53 55 55 57 58

Т

	Nun	Number of Individuals	iduals						RF	RFLP Status	SI			
	Belo- russians	Russians Oshevensk	Russians Bashkiria	HVS-I Haplotype ^a	Haplogroup	Alul 7025	Msel 14766	Hinfl 12308	BamHI Alul 13366 10397	Alul 10397	Ddel 10394	BamHI 16389	Alul 10028	AccI 14465
59			3	223	Other	+	+	T		I	T			
60			1	223-291	Other	+	+	Ι	I	I	Ι		I	
61			1	223-291-319	Other	+	+	I		I	I			
62	7	1	7	CRS	U^*	+	+	+						
63			1	093-223	U^*	+	+	+	I	I	+		I	
64			1	093-223-256-311	U^*	+	+	+	I	I	+		I	
65	1			126-298	U^*	+	+	+						
99	1			183d-189i	U^*	+	+	+						
67			1	186-192	U^*	+	+	+	I					
68	4	7	1	189	U^*	+	+	+						
69	1			189-294	U^*	+	+	+	I					
70			1	223	U^*	+	+	+	I	I	I	I	I	
71			1	223-256-327	U^*	+	+	+		I	I		I	
72	1			240G-286A	U^*	+	+	+						
73		1		256	U^*	+	+	+						
74	1			278-294	U^*	+	+	+	I					
75			1	311	U^*	+	+	+		I	I			
76			1	129C-189-256	U2			+						
LL			1	311-356	U4			+						
78		4		356	U4			+						
<i>6L</i>	1			192-270	U5a									
80	1			145-189-192-256-270	U5aI									
81	1			168-192-256-261-270-304	U5al									
82			1	189-192-234-256-270-311	U5aI									
83	1			189-192-256-270-294	U5aI									
84			1	192-256-270-291	U5aI									

Table 1. Continued

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+ + + +	+ +		
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	+ +		+ + +
U5al U5ala U5b U5b U5b U5bl	ダメメメメメ] *] *] /] *] /] /] /]] /]] /]] /]] /]] / *	*1
192-256-270 256-270 093-189-270 093-189-270-278-356 147-172-189-223-270 189-270 144-189-270	079-224 093-224-261-311 176-224-299-311 224 224-245-311 224-261-311 224-311	069-126 069-126-189 069-126-291-319 069-126-291-319 069-126-145-172-186-222-261 069-126-145-172-261 069-126-145-172-261 069-126-145-221 069-126-145-231 126-294-296	126-186-189 126-294-296-299-304 294-296-304-356 126-162-186-189-258-292-294-311 126-163-186-189-213-239-294 126-163-186-189-294 126-163-186-189-294 163-186-188-294
	-		
- v	2		
	1 1	1 1 2 1	
85 86 88 88 89 90 91	$92 \\ 94 \\ 95 \\ 96 \\ 97 \\ 97 \\ 97 \\ 97 \\ 97 \\ 97 \\ 97$	99 100 101 102 103 104 105 107 107	109 111 111 112 1112 1113 1114 1115

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	Nur	Number of Individuals	iduals						RF	RFLP Status	SI			
	Belo- russians	Russians Oshevensk	Russians Bashkiria	HVS-I Haplotypea	Haplogroup	Alul 7025	Alul Msel 7025 14766	Hinfl 12308	BamHI Alul 13366 10397	Alul 10397	Ddel 10394	BamHI 16389	Alul 10028	AccI 14465
117		1		163-186-189-294	TI				+					
118	1			126-163-189-243-294	TI				+					
119		1		126-294-296-304	T2									
120		7		126-292-294	T3									
121	1			126-294-324	T4									
122	1			126-153-207-294	T5									
123			2	129-172-223-311	Ι					I				
124	7			129-223	Ι					I				
125			1	172-223	Ι					I	+	+	+	
126			1	223	Ι	+	+		I	I	+	+	+	
127	-			192-223-292	М									
128		1		223-234-292	М									
129	1			069-189-192-223-278-292	X									
130			1	189-223-278	X									
131		1		129-185-223-224-260-298	Z					+	+			
132			1	182-189-223-298	Μ					+	+		I	
133	-			129-153-214G-223-271	Μ					+	+		I	
134			1	223-245	Μ					+	+		I	
135			1	223-270-327	Μ					+	+		I	
136	1		1	223	Μ	+	+			+	+		I	
137			1	223-298-327	С									
138			1	172-223-248-256-320-355	NIa					I	+			
139	1			145-176G-209-223	NIb	+	+	I		I	I			
a. <i>H</i> al.	<i>VS-I</i> haplo 1981). 18	type column 33i and 189i r	shows nucleo mean single ''	a. <i>HVS-I</i> haplotype column shows nucleotide positions between 16069 and 16362 (-16000) that are different from the CRS (Cambridge reference sequence, Anderson et al. 1981). 183i and 189i mean single "C" insertions in polycystosine motif, 183d—single nucleotide deletion.	16362 (–16000) i if, 183d—single	that are of incleding	different de deleti	from the on.	CRS (C	umbridge	referenc	se sequen	ce, Ande	rson et

	Sample Size	Number of Haplotypes	Unique Haplotypes (%)	Haplotype Diversity, Standard Deviation	Mean Pairwise Differences, Standard Deviation
Belorussians	92	56	47 (83.9)	0.937 ± 0.021	3.65 ± 0.54
Russians (Oshevensk)	76	41	28 (68.3)	0.961 ± 0.012	3.80 ± 0.58
Russians (Bashkiria)	83	52	44 (84.6)	0.940 ± 0.020	3.33 ± 0.55
Total	251	128	99 (77.3)	0.949 ± 0.011	3.59 ± 0.54

Table 2. HVS-I Diversity in Eastern Slavonic Populations

subcluster of *U*, is well represented in all three samples with frequencies close to the European average (Richards et al. 2000). The presence of the *U5b1* subcluster in the northern Russian population should also be noted. *U5b1* sequences in Russians were also reported by Malyarchuk et al. (2002). This subcluster was described as specific for the Saami population (Lahermo et al. 1996). Its presence in the Russian (Oshevensk) sample seems to reflect an admixture of a Finno-Ugric component, but it is unclear how old this admixture could be. All individuals included in our sample were characterized as ethnically Russian, and inhabited the area where the sample was collected for at least three maternal generations. Currently, due to geographical and sociological peculiarities, the Russian population of the Oshevensk settlement can be considered an isolate. The southern part of the Arkhangelsk region, where the Oshevensk settlement is situated, does not have immediate contact with Saami populations. So, a recent admixture seems to be less probable than an earlier admixture during the peopling of northern areas by Slavonic groups.

Haplogroup J shows a significant diversity in our Slavonic samples and includes five different subclusters, in contrast to Russian samples reported earlier, where J sequences were represented mostly by 16069T-16126C types. Haplogroup T is also diversified and occurs at a significant level in Belorussians and Russians (Oshevensk), but is less frequent in Russians (Bashkiria).

European-specific haplogroups I, W, and X are rare, with the exception of Russians (Bashkiria), where I contains four individual sequences.

In comparison to frequencies of cluster M in Belorussians and the northern Russian population, the frequency of cluster M in Russians (Bashkiria) is notably but not dramatically increased (five sequences). Although we collected samples from individuals who are ethnically Russian for at least three generations, we cannot exclude the possibility of some admixture with neighboring Asian populations characterized by high frequencies of the cluster M. In the meantime, those undetermined "Other" sequences, which contain the 16223T motif (six individuals), were tested for 10397AluI and 10394DdeI status. Because they lack restriction sites at these positions, however, this portion of the "Others" group could not contribute to the cluster M in Russians (Bashkiria). Thus, this population differs

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	Belorussians	Russians (Oshevensk)	Russians (Bashkiria)	Total Eastern Slavonic sample
Haplogroup	N^a (frequency)	N (frequency)	N (frequency)	N (frequency)
HV	46 (0.500)	42 (0.053)	27 (0.325)	115 (0.458)
HV^*	4 (0.043)	1 (0.013)		5 (0.020)
Н	37 (0.402)	37 (0.487)	26 (0.313)	100 (0.398)
pre-V	5 (0.054)	4 (0.053)	1 (0.012)	10 (0.040)
U	26 (0.283)	20 (0.263)	25 (0.301)	71 (0.283)
U^*	16 (0.174)	4 (0.053)	14 (0.169)	34 (0.135)
Κ	2 (0.022)	6 (0.079)	1 (0.012)	9 (0.036)
U2	-	-	1 (0.012)	1 (0.004)
U4	-	4 (0.053)	1 (0.012)	5 (0.020)
U5:	8 (0.087)	6 (0.079)	8 (0.096)	22 (0.088)
U5a	1 (0.011)	-	-	1 (0.004)
U5a1	3 (0.033)	-	3 (0.033)	6 (0.024)
U5a1a	-	1 (0.013)	2 (0.024)	3 (0.012)
U5b	4 (0.043)	-	2 (0.024)	6 (0.024)
U5b1	-	5 (0.066)	1 (0.012)	6 (0.024)
JT	12 (0.130)	11 (0.145)	7 (0.084)	30 (0.120)
J	4 (0.043)	4 (0.053)	4 (0.048)	12 (0.048)
J^*	1 (0.011)	3 (0.039)	2 (0.024)	6 (0.024)
J1*	2 (0.022)	_	_	2 (0.008)
Jla	-	-	1 (0.012)	1 (0.004)
J1b	_	1 (0.013)	-	1 (0.004)
J1b1	1 (0.011)	-	1 (0.012)	2 (0.008)
Т	8 (0.087)	7 (0.092)	3 (0.036)	18 (0.072)
T^*	2 (0.022)	_	2 (0.024)	4 (0.016)
T1	4 (0.044)	4 (0.053)	1 (0.012)	9 (0.036)
T2	_	1 (0.013)	_	1 (0.004)
<i>T3</i>	-	2 (0.260)	_	2 (0.008)
T4	1 (0.011)	-	_	1 (0.004)
<i>T5</i>	1 (0.011)	-	_	1 (0.004)
Ι	2 (0.022)	_	4 (0.048)	6 (0.024)
W	1 (0.011)	1 (0.013)	-	2 (0.008)
Χ	1 (0.011)	-	1 (0.012)	2 (0.008)
М	2 (0.022)	1 (0.013)	4 (0.048)	7 (0.028)
Ζ	_	1 (0.013)	-	1 (0.004)
С	-	-	1 (0.012)	1 (0.004)
Ν	1 (0.011)	-	1 (0.012)	2 (0.008)
Nla	-	-	1 (0.012)	1 (0.004)
N1b	1 (0.011)	-	-	1 (0.004)
Other	1 (0.011)	1 (0.013)	13 (0.157)	15 (0.060)
Total	92	76	83	251

Table 3. Haplogroup Distribution in Three Eastern Slavonic Populations

a. N = number of individual lineages.

remarkably in the distribution of haplogroups within cluster R (Macaulay et al. 1999). Therefore, only the recent admixture, to which Russians (Bashkiria) are more exposed geographically, cannot easily explain the differences between this population and two others.

Conclusions. As follows from the above discussion, three eastern Slav samples considered in total demonstrate mtDNA variations that are very close to variations found in the European population as a whole. MtDNA haplotypes are similar to those found in Western and Central European populations. Nevertheless, the comparison of Slavonic samples of different ethnic and geographic origins reveals the complicated structure of the mitochondrial gene pool in this area. This structure could reflect traces of female admixture between Slavonic and pre-Slavonic groups-in particular, Finno-Ugric tribes-during a colonization of northern Eastern Europe by Slavs. In this sense our data are in agreement with those from previous studies of Slavonic mtDNA (Malyarchuk and Derenko 2001) and a hybridization theory of the origin of Eastern Slavs (Alekseeva 1973), which imply their central European origin and subsequent admixture and assimilation of pre-Slavonic populations of Eastern Europe. This study also revealed no or low Mongoloid admixture in the mitochondrial gene pool of Eastern Slavs. However, the analysis of maternally inherited mtDNA could not effectively reveal the influence of Mongoloid migrations, since they included mostly male individuals. Haplogroup distribution in Belorussians and northern Russians has more similarity to that in northern European populations than in eastern Russian populations. The Russian (Bashkiria) population differs from the two other samples in the representation of several clusters, namely, HV, V, K, T. Besides the local admixture and assimilation of pre-Slavonic groups, this difference could support an existing opinion that Russian migrants of different geographic origin were involved in the processes of colonizing the northern and eastern parts of the Russian Plain. More detailed studies of Eastern European mtDNA variations, complemented by analysis of Y-chromosome loci, will allow revelation of some tendencies, which could reflect the main aspects of European gene pool formation.

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