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Samara Rubinstein

Matthew C. Dulik

University of Pennsylvania, dulik@sas.upenn.edu

Omer Gokcumen

University of Pennsylvania


Sergey I. Zhadanov

University of Pennsylvania

Ludmila P. Osipova

See next page for additional authors

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Abstract

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Keywords

slavs, haplotypes, haplogroups, founder effects, siberia

Disciplines

Biological and Physical Anthropology | Genetics and Genomics

Author(s)

Samara Rubinstein, Matthew C. Dulik, Omer Gokcumen, Sergey I. Zhadanov, Ludmila P. Osipova, Maggie Cocca, Nishi Mehta, Marina Gubina, Olga Posukh, and Theodore G. Schurr

Russian Old Believers: Genetic Consequences of Their Persecution and Exile, as Shown by Mitochondrial DNA Evidence

SAMARA RUBINSTEIN,^{1,2} MATTHEW C. DULIK,³ OMER GOKCUMEN,³ SERGEY ZHADANOV,^{3,4} LUDMILA OSIPOVA,⁴ MAGGIE COCCA,³ NISHI MEHTA,³ MARINA GUBINA,⁴ OLGA POSUKH,⁴ AND THEODORE G. SCHURR³

Abstract In 1653, the Patriarch Nikon modified liturgical practices to bring the Russian Orthodox Church in line with those of the Eastern (Greek) Orthodox Church, from which it had split 200 years earlier. The Old Believers (*staroveri*) rejected these changes and continued to worship using the earlier practices. These actions resulted in their persecution by the Russian Orthodox Church, which forced them into exile across Siberia. Given their history, we investigate whether populations of Old Believers have diverged genetically from other Slavic populations as a result of their isolation. We also examine whether the three Old Believer populations analyzed in this study are part of a single gene pool (founder population) or are instead derived from heterogeneous sources. As part of this analysis, we survey the mitochondrial DNAs (mtDNAs) of 189 Russian Old Believer individuals from three populations in Siberia and 201 ethnic Russians from different parts of Siberia for phylogenetically informative mutations in the coding and noncoding regions. Our results indicate that the Old Believers have not significantly diverged genetically from other Slavic populations over the 200–300 years of their isolation in Siberia. However, they do show some unique patterns of mtDNA variation relative to other Slavic groups, such as a high frequency of subhaplogroup U4, a surprisingly low frequency of haplogroup H, and low frequencies of the rare East Eurasian subhaplogroup D5.

Although Christianity in Russia can be traced back to A.D. 988, it was not until about 1440 that the Russian Orthodox Church began to separate itself from the Byzantine Orthodoxy in Constantinople. Once the tsar declared the Russian metropolitanate independent of the Byzantines, a long era of reform began within the Russian church. These reforms were attempts to separate the Russian Orthodox

¹Department of Anthropology, Temple University, Philadelphia, PA.

²Current Address: Center for Genomics and Systems Biology, New York University, NY.

³Department of Anthropology, University of Pennsylvania, 344 University Museum, 3260 South Street, Philadelphia, PA 19104.

⁴Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences, Novosibirsk, Russia.

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KEY WORDS: SLAVS, HAPLOTYPES, HAPLOGROUPS, FOUNDER EFFECTS, SIBERIA.

practices from the Byzantine Orthodox practices, from which the church had originated more than 500 years earlier. Over time, the isolation from Constantinople caused many variations of liturgical books and practices to seep into Russian Orthodoxy. It would be another 200 years after this independence from the Byzantine church that the Russian church would experience another major reformation, this time in an attempt to bring liturgical practice back in line with the Greek Orthodoxy from which it had split. Many Russians had embraced their independence from the Greek church and valued their established Russian Orthodox religious practices. As a consequence, the reformation of rituals threatened the core of the Russian church and those opposing such changes would bring about one of the greatest church schisms in history (Zernov 1954; Dvornik 1956; Pares 1965; Cherniavsky 1966; Heard 1971; Robson 1995; Michels 1999; Ziolkowski 2000; Paert 2003; Riasanovsky 2005).

An ambitious metropolitan of Novgorod, Nikon, became Patriarch of Moscow in 1652 and quickly introduced the changes intended to make Russian practices conform to Greek usage. Among the major church reforms were (1) how many fingers would be used to make the sign of the cross; (2) the spelling of Jesus's name; (3) whether *Alleluia* should be sung two or three times; (4) the retention of certain words and phrases in the Creed; (5) the number of hosts to be used in the liturgy; and (6) whether the priests should walk around the altar with or against the passage of the sun. These changes were met with opposition and protest. The clergy and many in mainstream Russian society thought that strict observance of the minute details of Russian Orthodox ritual practice was necessary for attaining salvation and, at the same time, strongly opposed Nikon's abuse of power when he made such changes without the appropriate council of clergy members (Zernov 1954; Dvornik 1956; Pares 1965; Cherniavsky 1966; Heard 1971; Robson 1995; Michels 1999; Ziolkowski 2000; Paert 2003; Riasanovsky 2005).

A group of priests refusing to abandon their traditional Russian Orthodox practices, led by Archpriest Avvakum Petrovich, became known as the "zealots-of-piety" (Cherniavsky 1966; Robson 1995; Michels 1999; Ziolkowski 2000; Paert 2003). Gravely concerned with the church reforms initiated by the state, these priests led the antireformation movement and became known as the founders of the subsequent church schism, leveraging enormous influence over mainstream Russian society. As a result, Nikon had the founders exiled to the prison camp of Pustozersk on the lower Pechora River in the Arctic circle (Cherniavsky 1966; Robson 1995; Michels 1999; Ziolkowski 2000; Paert 2003), from which they continued to write letters and texts to the Russian people disseminating the old beliefs and opposition to church reform.

Nikon acted mercilessly against all dissenters, now known as Old Believers because of their refusal to abandon the traditional practices of the Russian Orthodox Church. Old practices and texts were declared heretical, and those refusing to conform to the changes faced excommunication and death. The founders eventually had their tongues cut out and were burned at the stake in 1682. Many communities sought refuge in different regions of Russia and Asia and lived in

almost complete isolation for centuries. These persecutions also led some conservative dissenters to believe that the age of the Antichrist had come and that the end of the world was near. Many burned themselves to death so that they might join Christ before Judgment Day (Cherniavsky 1966; Robson 1995; Michels 1999; Ziolkowski 2000; Paert 2003). As a result of centuries of persecution, including mass murders that drastically decreased their population size, and as a result of continued isolation from other ethnic Russian populations, it is possible that Old Believers exiled to Siberia became somewhat genetically differentiated from their Russian counterparts.

Although little research into the genetic variation of Old Believer populations exists, the biological derivation of Slavic peoples has become of considerable interest to many researchers, who have conducted molecular genetic studies of these groups (Malyarchuk and Derenko 2001; Malyarchuk et al. 2001, 2002, 2003, 2004; Kravchenko et al. 2002; Belyaeva et al. 2003; Kasperavičiūtė et al. 2004; Peričić et al. 2005). These studies have attempted to elucidate the origin and differentiation of Slavic ethnic groups and to retrace the major migrations and historical events that led to the genetic patterns observed today. In this regard, the Old Believers are an interesting case study because their persecution and banishment caused them to remain virtually isolated, both geographically and culturally, from their Slavic source populations. The extent to which they have genetically diverged from ethnic Russians and other Slavs in the 200–300 years since their exile is the focus of this study.

An earlier mtDNA study of the Old Believers, based on the RFLP analysis of mutations in the mitochondrial DNA (mtDNA) control region, found no significant differences between Old Believer and Eastern Slavic populations but did note differences between these Slavic groups and both Europeans and Mongolians (Kazakovtseva et al. 1998). Although Mongolians may have contributed genes to the Slavic groups during their westward expansions, this population is composed of mainly East Eurasian mtDNA lineages (Kolman et al. 1996; Merriwether and Ferrell 1996; Gokcumen et al. 2008) that are shared with Siberians (Torroni et al. 1993; Schurr et al. 1999; Starikovskaya et al. 1998; Derbeneva et al. 2002a, 2002b; Derenko et al. 2003) but not commonly found in Slavic or European populations, which consist mainly of West Eurasian mtDNA lineages (Torroni et al. 1994, 1996; Richards et al. 1998; Macaulay et al. 1999; Richards et al. 2000; Torroni et al. 2000; Malyarchuk et al. 2001, 2002, 2003, 2004). Therefore the difference between the Eastern Slavs, including the Old Believers, and Mongolians was not a surprising result of the Kazakovtseva et al. (1998) study. However, contrary to Kazakovtseva and colleagues' findings, one would expect a small difference between the Eastern Slavs and Europeans, because Russians are characterized by the same West Eurasian mtDNA lineages that account for more than 95% of mtDNA variation in Europe (Torroni et al. 1996; Richards et al. 2000; Malyarchuk et al. 2002).

Thus in the present study we expand on the research of Kazakovtseva et al. (1998) by screening Old Believer and Eastern Slavic mtDNAs for informa-

tive single nucleotide polymorphisms (SNPs) in the coding region and by directly sequencing hypervariable region 1 (HVR1) of the control region. Haplogroup frequency analysis and statistical comparisons of the data from Old Believers and Slavic and European Russian populations are used to determine the extent to which evolutionary forces such as mutation, genetic drift, and gene flow have influenced the observed patterns of Old Believer mtDNA diversity. Our results indicate that the Old Believers have not significantly diverged genetically from other Slavic populations over the 200–300 years of their isolation in Siberia, although they do exhibit some unique patterns of mtDNA variation relative to other Slavic groups. We discuss these data in the context of Old Believer history and the origins of Slavic populations in Russia.

Materials and Methods

Samples. To assess genetic diversity within and between Old Believer groups and to determine the genetic relationship between Old Believers and other Slavic groups, we analyzed mtDNA variation in both Old Believer and ethnic Russian populations. These samples included 189 unrelated individuals from 3 Old Believer populations in Siberia [Burnyi in the Baikitsk Raion of the Krasnoyarsk Krai ($N = 24$), and Isetsk ($N = 44$) and Kirsanovo ($N = 121$) in the Tyumen Oblast] and 201 ethnic Russians from different parts of Siberia [Novosibirsk ($N = 23$), Dovolnoe ($N = 35$), Krasnoselkup ($N = 104$), northern Altai region ($N = 23$), and other locales ($N = 16$)]. All these samples were collected during field expeditions conducted between 1994 and 2003. Genomic DNAs were extracted from whole blood using a standard phenol-chloroform method (Maniatis 1982).

Previously published HVR1 sequence data from various Slavic, Baltic, and native Siberian populations were used for comparison. These data included European Russian populations from Pskov in the northwest, Tula, Kaluga, Yaroslav'l, and Vladimir in central Russia, Saratov in the southeast, and Stavropol in the southwest (Malyarchuk et al. 2002, 2004); Ukrainians from Magadan in northeastern Siberia (Malyarchuk and Derenko 2001); Belarussians from Bobruisk (Belyaeva et al. 2003); Bosnians and Slovenians (Malyarchuk et al. 2003); Lithuanians (Kasperavičiūte et al. 2004); and indigenous Siberian populations of southern Altaians, Khakassians, and Tuvinians (Derenko et al. 2000, 2003). Haplotype data from these populations, along with data from the present study, were statistically assessed to determine genetic distances and demographic events influencing genetic affinities.

mtDNA Sequence Analysis. All Old Believer and ethnic Russian mtDNAs were surveyed for coding region SNPs using a PCR-RFLP approach. This analysis involved screening the samples for the diagnostic mutations of West Eurasian haplogroups (H, I, J, K, N, R, T, U, V, W, X) (Torroni et al. 1994, 1996, 1998; Macaulay et al. 1999) and East Eurasian haplogroups (A, B, C, D, F, G, M, Y, Z) (Torroni et al. 1993, 1994; Schurr et al. 1999) to understand their phylogeographic

Table 1. Primers and Reaction Conditions Used in PCR-RFLP Analysis of mtDNAs

Primer Coordinates (Forward, Reverse) ^a	Size (bp)	Polymorphic Site(s) ^b	Restriction Enzyme	Haplogroup
4500-4519, 4678-4659	178	-4529	<i>Hae</i> II	I
4500-4519, 4678-4659	178	-4577	<i>Nla</i> III	V
4318-4325, 4668-4649	200	+4831	<i>Hha</i> I	G
5151-5170, 5481-5464	298	-5176	<i>Alu</i> I	D
6890-6909, 7131-7115	241	-7025	<i>Alu</i> I	H
8925-8953, 9100-9081	156	-9052	<i>Hae</i> II	K
		-9053	<i>Hha</i> I	K
8925-8953, 9100-9081	156	-8994	<i>Hae</i> III	W
10235-10254, 10569-10550	290	+10394	<i>Dde</i> I	M
		+10397	<i>Alu</i> I	M
10718-10736, 10930-10910	212	+10871	<i>Mn</i> I	N
12104-12124, 12338-12309	234	+12308	<i>Hin</i> fI	U
12385-12405, 12576-12557	352	-12406	<i>Hinc</i> II	F
12599-12620, 12804-12784	205	+12705	<i>Mbo</i> II	R
13001-13020, 13403-13384	402	-13259	<i>Hinc</i> II	C
		+13262	<i>Alu</i> I	C
13537-13556, 13851-13832	314	-13704	<i>Bst</i> NI	J
14407-14424, 14810-14791	403	-14766	<i>Mse</i> I	HV
14407-14424, 14810-14791	403	+14465	<i>Acc</i> I	X
15409-15428, 15728-15709	319	+15606	<i>Alu</i> I	T
15838-15857, 16159-16142	321	-15925	<i>Hpa</i> II	T

a. Primers used to flank polymorphic sites in the coding region, which characterize known mtDNA haplogroups. Primers appear in numerical order of position around the mtDNA genome.

b. Polymorphic sites preceded by a plus sign refer to site gains, and those with a minus sign refer to site losses relative to the Revised Cambridge Reference Sequence.

relationships and to determine the extent of genetic affinities that these ethnic groups have with populations from Europe, West and Central Asia, and Siberia (Table 1).

Old Believer and ethnic Russian samples were assigned to haplogroups using a hierarchical approach. Initial designations were made through the detection of diagnostic SNP markers in the mitochondrial coding region to discriminate between macrohaplogroups M and N. Those that tested positive for haplogroup N, as indicated by an *Mn*I 10871 site gain relative to the Revised Cambridge Reference Sequence, were then tested for SNPs diagnostic for West Eurasian haplogroups branching from the R root, as indicated by an *Mbo*II 12705 site gain relative to the Revised Cambridge Reference Sequence (Anderson et al. 1981; Andrews et al. 1999). These included haplogroups J, T, UK, HV, H, and V from R, and haplogroups A, I, W, and X from N. The other samples that tested positive for the haplogroup M marker combination, *Dde*I 10394 and *Alu*I 10397 site gains, were further tested for the markers defining East Eurasian lineages C, D, G, and Z.

Haplogroup designations made by PCR-RFLP analyses were confirmed by direct sequencing of the HVR1, which also provided information about haplotype variation in these individuals. The HVR1 was sequenced using published methods (Schurr et al. 1999; Gokcumen et al. 2008). DNA sequences were read on ABI 3100 Gene Analyzers at the University of Pennsylvania Core Sequencing facility. All sequences were aligned and edited using Sequencher 4.0 (Gene Codes).

For some samples, hypervariable region 2 (HVR2) was sequenced to confirm the presence of markers that are diagnostic for known haplogroups. For instance, samples assigned to East Eurasian haplogroups C and Z based on PCR-RFLP and HVR1 sequence data were further screened for a deletion at nucleotide position (np) 249, which is a diagnostic HVR2 mutation for these lineages (Yao et al. 2002; Tanaka et al. 2004; Metspalu et al. 2005). Samples assigned to haplogroups HV0 and V were screened for a transition at np 72 that is diagnostic for these lineages (Torroni et al. 2001, 2006; Malyarchuk et al. 2002; Achilli et al. 2004; Palanichamy et al. 2004). Samples assigned to haplotype H5 had a transition at np 456, and those assigned to haplotype H6, based on the PCR-RFLP analysis of the *Nla*III 4727 site, were confirmed by the presence of additional HVR2 mutations at np 239 and np 482 (Achilli et al. 2004; Loogvali et al. 2004).

Phylogenetic Analysis. Phylogenetic relationships between haplotypes observed in the Old Believers and ethnic Russians from Siberia were determined through the generation of a median-joining network constructed with the program Network 4.111 (Bandelt et al. 1999). Following the guidelines recommended by Bandelt et al. (2002), SNPs in the coding region were given more weight than those found in the control region. Within HVR1, nucleotide positions between 16051 and 16365 at which transitions were estimated to occur at a rate at least as high as the average transitional rate (“speedy transitions”) were given a lower weight than other “weighty transitions,” which were estimated to occur less frequently (Bandelt et al. 2002). Most coding region SNPs were given a weight of 10, with the exceptions of 10398, 13704, 7025, and 12308, which were given a weight of 9, and most HVR1 transitions were given a weight of 8 or less. Transversions were also weighted more than transitions, with transversions being weighted at 10.

Statistical Analysis

Intrapopulation Statistics. In addition to the newly generated data from Old Believers and ethnic Russians from Siberia, previously published HVR1 sequence data from European Russian, Slavic, and ethnic Siberian populations were statistically assessed with intra- and interpopulation diversity indexes using methods available in Arlequin 3.11 (Excoffier et al. 2005a, 2005b). Intrapopulation diversity statistics included measures of genetic diversity, population pairwise differences, and Tajima’s *D* test of neutrality. The gene diversity index indicates whether a population has undergone drift or founder effects by estimating the probability that two randomly chosen haplotypes are different in the sample (Nei and Saitou

1987). In a population experiencing decreased genetic diversity, as predicted for founder populations, the probability of choosing two different haplotypes would be low. The mean number of pairwise differences between all pairs of haplotypes in each population is used to determine the total genetic variance within the population by estimating the number of mutations that have occurred since the divergence of haplotypes found in the sample (Reynolds et al. 1983).

Tajima's (1983) test of selective neutrality compares the population parameter based on the number of segregating sites in the sample with the parameter based on the mean pairwise difference between haplotypes. If both parameters are the same, the population has not been changing in size and is in neutral equilibrium. However, differences between the parameters can arise under selection, population change, or nonrandom mutation rates among sites. In general, negative values of Tajima's D indicate population expansion, whereas positive values indicate population reduction.

To statistically determine the genetic affinities between Old Believer and Slavic populations, we calculated genetic distances using the population pairwise F statistic (F_{ST}) in Arlequin 3.11. The pairwise F_{ST} measures genetic variances, taking into account not only haplotype frequency differences between populations but also the distances between mitochondrial HVR1 sequences. The resulting values reflect short-term genetic distances between populations, an appropriate measure for the comparative data set because speculated divergence times are relatively recent. P values were calculated to test the null hypothesis of no difference between populations.

Interpopulation Statistics. Intersubpopulation diversity statistics were calculated by direct counting of shared haplotypes between populations and by using the population pairwise F statistic (F_{ST}), used to measure relatively short-term genetic distances between populations (Reynolds et al. 1983; Hudson et al. 1992). The obtained F_{ST} values were used in the analyses of molecular variance (AMOVAs) to determine the genetic structure of groups of Slavic populations. P values were calculated to test the null hypothesis of no significant difference between populations. They were also plotted on a multidimensional scale to visualize genetic distances between all populations in two-dimensional form, using the program SPSS 11.0.3.

Results

Haplogroup Distribution. Results from the PCR-RFLP analysis and control region sequencing indicate that West Eurasian haplogroups are the predominant mtDNA lineages present in Old Believers, comprising approximately 95% of those sampled (Table 2). Of the West Eurasian haplogroups present in the Old Believer sample as a whole, haplogroup U comprises 30%, haplogroup H comprises 29%, haplogroup T comprises 12%, haplogroup K comprises 6%, and haplogroup J comprises 5% of the mtDNAs. Other West Eurasian lineages found in Old Believers include those assigned to the nodal haplogroup HV, which has a frequency of

Table 2. Old Believer and Ethnic Russian Haplotypes Found in the Present Study

Haplotype Number	Haplogroup	Coding Region SNP(s)	HVRI (16024-16569)	Old Believers			Russians			Grand Total	
				Burnyi	Isetsk	Kirsanovo	Krasnoselkup	Dovolnoe	Novosibirsk		Altai
1	C	10398, 10400, 13263	093-129-223-298-327-517	1	0	0	0	0	0	0	1
2	C	10398, 10400, 13263	093-223-298-327	0	0	1	0	0	0	0	1
3	C	10398, 10400, 13263	223-287-298-327	0	1	0	1	0	0	0	1
4	C	10398, 10400, 13263	223-298-327	0	1	1	2	1	0	0	2
5	C4a	10398, 10400, 13263	171-223-298-327-344-357	0	0	0	0	0	0	1	1
6	C4a	10398, 10400, 13263	171-223-278-298-327-344-357	0	0	0	0	0	0	1	1
7	D	5178A, 10398, 10400	223-362	0	0	0	0	0	0	1	1
8	D4	5178A, 10398, 10400	093-223-232-290-362-471	0	0	0	0	1	0	0	1
9	D5	5178A, 10397, 10398, 10400	126-136-189-223-360-362	1	1	3	5	0	0	0	5
10	G	4833, 10398, 10400	093-223-278-362	0	0	0	0	0	0	1	1
11	G2	4833, 10398, 10400	223-227-278-362	0	0	1	1	0	0	0	1
12	Z	10398, 10400	129-185-223-224-260-298	0	1	0	1	0	0	0	1
13	R	10873, 12705	311	0	0	0	0	1	0	0	1
14	R	10873, 12705	092-192-256-292-399	1	0	0	1	0	0	0	1
15	R2	10873, 12705, 14305	071-093-172	0	0	0	0	1	0	0	1
16	R2	10873, 12705, 14305	042-071-172	0	0	0	0	0	0	1	1
17	R2	10873, 12705, 14305	037-071-172	0	0	0	0	0	0	1	1
18	H	7028, 10873, 12705, 14766	114	0	0	0	0	1	0	0	1
19	H	7028, 10873, 12705, 14766	129	0	0	0	0	2	0	0	1
20	H	7028, 10873, 12705, 14766	168	0	1	0	1	0	0	0	1
21	H	7028, 10873, 12705, 14766	184	0	0	1	1	1	0	0	1
22	H	7028, 10873, 12705, 14766	192	0	0	1	1	0	0	0	1
23	H	7028, 10873, 12705, 14766	224	0	0	0	0	1	0	0	1
24	H	7028, 10873, 12705, 14766	249	0	0	0	0	0	0	0	1
25	H	7028, 10873, 12705, 14766	256	0	1	0	1	0	0	0	1
26	H	7028, 10873, 12705, 14766	261	0	0	0	0	1	0	0	1
27	H	7028, 10873, 12705, 14766	265	1	0	0	1	0	0	0	1
28	H	7028, 10873, 12705, 14766	293	0	0	1	1	0	0	0	1
29	H	7028, 10873, 12705, 14766	298	0	0	0	0	1	0	0	1
30	H	7028, 10873, 12705, 14766	299	0	0	0	0	0	1	0	1
31	H	7028, 10873, 12705, 14766	304	0	0	1	1	0	0	0	1

Table 2. *Continued*

Haplotype Number	Haplogroup	Coding Region SNP(s)	HVRI (16024-16569)	Old Believers			Russians			Grand Total				
				Burnyi	Isetsk	Kirsanovo	Total	Krasnoyelkup	Dovolnoe		Novosibirsk	Altai	Other	
67	H2	4769, 7028, 10873, 12705, 14766	CRS	0	1	1	2	0	1	0	1	0	2	4
68	H2a	4769, 7028, 10873, 12705, 14766	354	0	0	0	0	2	0	2	0	0	4	4
69	H2a	4769, 7028, 10873, 12705, 14766	193-224-354	0	0	0	0	1	0	0	0	0	1	1
70	H2a	4769, 7028, 10873, 12705, 14766	193-354	0	0	1	1	0	1	0	0	0	1	2
71	H2a1	4769, 7028, 10873, 12705, 14766	249-354	0	0	0	0	1	0	0	2	0	3	3
72	H2c	4769, 7028, 10873, 12705, 14766	274-304	0	0	0	0	0	0	1	0	0	1	1
73	H5	456, 7028, 10873, 12705, 14766	270	0	0	1	1	0	0	0	0	0	0	1
74	H5	456, 7028, 10873, 12705, 14766	304	0	0	1	1	3	0	2	0	1	6	7
75	H5	456, 7028, 10873, 12705, 14766	145-304	0	0	0	0	1	0	0	0	0	1	1
76	H5	456, 7028, 10873, 12705, 14766	183-189	0	0	0	0	1	0	0	0	0	1	1
77	H5	456, 7028, 10873, 12705, 14766	294-304	0	0	2	2	0	0	0	0	0	0	2
78	H5	456, 7028, 10873, 12705, 14766	CRS	0	0	1	1	0	0	0	0	0	0	1
79	H6	4727, 7028, 10873, 12705, 14766	295	0	1	0	1	0	0	0	0	0	0	1
80	H6	4727, 7028, 10873, 12705, 14766	362	0	1	0	1	0	2	0	0	0	2	3
81	H6	4727, 7028, 10873, 12705, 14766	362, 482	0	0	1	1	1	0	0	0	1	2	3
82	H11	7028, 10873, 12705, 14766	124-278-293-311	0	0	0	0	1	0	0	0	0	1	1
83	H11	7028, 10873, 12705, 14766	187-278-293-311	0	0	1	1	0	0	0	0	0	0	1

84	H11	7028, 10873, 12705, 14766	278-293-311	1	1	2	4	0	0	0	0	2	0	0	0	2	6
85	HV	10873, 12705, 14766	114	0	0	0	0	1	0	0	0	0	0	0	0	1	1
86	HV	10873, 12705, 14766	184	0	1	0	0	0	0	0	0	0	0	0	0	0	1
87	HV	10873, 12705, 14766	189	0	0	0	0	0	0	0	0	0	0	0	0	0	1
88	HV	10873, 12705, 14766	304	0	1	0	1	0	0	0	0	0	0	0	0	0	1
89	HV	10873, 12705, 14766	311	0	0	0	1	1	0	0	0	0	0	0	0	0	1
90	HV	10873, 12705, 14766	249-311	0	0	0	0	0	0	0	0	0	0	0	0	0	1
91	HV	10873, 12705, 14766	CRS	0	3	0	3	0	0	0	0	0	1	0	0	1	4
92	HV	10873, 12705, 14766	249-261-311	0	0	1	1	1	2	0	0	0	0	0	0	3	4
93	HV	10873, 12705, 14766	189-311	0	0	1	1	0	0	0	0	0	0	0	0	0	1
94	HV	10873, 12705, 14766	162-189	0	0	0	0	0	0	0	0	0	1	0	0	1	1
95	HV	10873, 12705, 14766	N/A	0	1	0	1	0	0	0	0	0	0	0	0	0	1
96	HV0	10873, 12705, 14766	126	0	0	1	1	0	0	0	0	0	0	0	0	0	1
97	HV0	10873, 12705, 14766	298	0	0	1	1	0	0	0	0	0	0	0	0	0	1
98	HV0	10873, 12705, 14766	126-298	0	0	3	3	1	0	0	0	0	0	0	0	0	4
99	V	4580, 10873, 12705, 14766	298	0	0	0	0	0	0	0	0	1	0	0	0	1	1
100	V	4580, 10873, 12705, 14766	153-298	0	0	0	0	0	1	0	0	0	0	0	0	2	2
101	V	4580, 10873, 12705, 14766	153-298-319	0	0	0	0	0	0	0	0	0	0	0	1	1	1
102	J	10398, 10873, 12705, 13708	063-069-126	0	0	0	0	0	0	0	0	0	0	0	0	2	2
103	J	10398, 10873, 12705, 13708	069-126	1	1	2	4	3	0	0	0	0	1	1	5	9	9
104	J	10398, 10873, 12705, 13708	069-126-147-242	0	0	1	1	0	0	0	0	0	0	0	0	0	1
105	J	10398, 10873, 12705, 13708	069-126-172-189	0	0	0	0	0	1	0	0	0	0	0	0	1	1
106	J	10398, 10873, 12705, 13708	126-189-291A	0	1	0	1	0	0	0	0	0	0	0	0	0	1
107	J1	10398, 10873, 12705, 13708	069-124-126-261	1	0	0	1	0	0	0	0	0	0	0	0	0	1
108	J1	10398, 10873, 12705, 13708	069-126-145-172-222-249-261-293	0	0	0	0	0	0	0	0	0	0	0	1	1	1
109	J1	10398, 10873, 12705, 13708	069-126-145-172-222-261	1	0	0	1	0	0	0	0	0	1	0	0	1	2
110	J1	10398, 10873, 12705, 13708	126-145-261-278	0	1	0	1	0	0	0	0	0	0	0	0	0	1
111	J1	10398, 10873, 12705, 13708	069-126-261	0	0	0	0	0	0	0	0	0	0	0	0	0	1
112	J2	10398, 10873, 12705, 13708	069-126-145-179-231-261	0	0	0	0	0	0	0	0	0	0	0	0	1	1
113	J2	10398, 10873, 12705, 13708	069-126-145-189-231-261	0	0	0	0	0	0	0	0	0	0	0	0	1	1
114	J2	10398, 10873, 12705, 13708	069-126-145-231-261	0	0	0	0	0	0	0	0	0	0	0	0	1	1
115	T	10873, 12705, 15607, 15928	126-294-304	1	0	1	2	1	0	0	0	0	1	0	0	2	4
116	T	10873, 12705, 15607, 15928	126-294	0	0	0	0	0	2	0	0	0	0	0	0	2	2
117	T1	10873, 12705, 15607, 15928	126-189-266-294-304	0	0	0	0	0	0	0	0	0	1	0	0	1	1
118	T1a	10873, 12705, 15607, 15928	093-126-163-186-189-294-296	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Table 2. Continued

Haplotype Number	Haplogroup	Coding Region SNP(s)	HVRI (16024-16569)	Old Believers			Russians			Grand Total		
				Burnyi	Kirsanovo	Total	Krasnoelkup	Dovolnoe	Novosibirsk		Altai	Other
119	T1a	10873, 12705, 15607, 15928	126-163-186-188-189-294	0	0	1	1	0	0	0	0	1
120	T1a	10873, 12705, 15607, 15928	126-163-186-189-261-294	0	0	0	0	1	0	0	0	1
121	T1a	10873, 12705, 15607, 15928	126-163-186-189-294	2	3	3	8	0	2	0	1	3
122	T2	10873, 12705, 15607, 15928	126-294-296	0	0	1	1	0	0	0	0	0
123	T2	10873, 12705, 15607, 15928	126-294-296-324	0	0	2	2	0	0	0	0	2
124	T2	10873, 12705, 15607, 15928	126-294-296-324-399	0	0	0	0	1	0	0	0	1
125	T2	10873, 12705, 15607, 15928	126-264-286-294-296-362	0	0	0	0	0	0	0	1	1
126	T2	10873, 12705, 15607, 15928	126-231-258-294-296-324	0	0	0	0	1	0	0	0	1
127	T2	10873, 12705, 15607, 15928	126-209-294-296	0	0	0	0	1	0	0	0	1
128	T2b	10873, 12705, 15607, 15928	126-129-294-296-304	0	0	1	1	0	0	0	0	1
129	T2b	10873, 12705, 15607, 15928	126-169-294-296-304	0	0	1	1	0	0	0	0	1
130	T2b	10873, 12705, 15607, 15928	126-255-294-296-304-310	1	0	0	1	0	0	0	0	1
131	T2b	10873, 12705, 15607, 15928	126-261-294-296-304	0	0	1	1	0	0	0	0	1
132	T2b	10873, 12705, 15607, 15928	126-294-296-304	1	0	3	4	6	0	0	1	7
133	T2b	10873, 12705, 15607, 15928	126-294-296-304-399	0	0	2	2	0	0	0	0	2
134	T2b	10873, 12705, 15607, 15928	126-189-294-296-304	0	0	0	0	0	0	1	0	1
135	T2b	10873, 12705, 15607, 15928	126-189-292-294-296-304	0	0	0	0	0	0	1	0	1
136	U	10873, 12308, 12705	126	0	0	0	0	1	0	0	0	1
137	U2e	10873, 12308, 12705, 15907	051-129C-189-362	0	0	1	1	0	0	1	0	2
138	U2e	10873, 12308, 12705, 15907	051-092-129C-189-194C-362	0	0	0	0	0	0	0	1	1
139	U3	10873, 12308, 12705	343	0	0	0	0	0	1	0	0	1
140	U3a	10873, 12308, 12705	343-356-390	0	0	2	2	0	0	0	0	2
141	U4	4646, 10873, 12308, 12705	184-343	0	0	1	1	0	0	0	0	1
142	U4	4646, 10873, 12308, 12705	263	0	0	1	1	0	0	0	0	1
143	U4	4646, 10873, 12308, 12705	356	2	2	5	9	1	0	0	0	10
144	U4	4646, 10873, 12308, 12705	093-134-186-187-356	1	0	0	1	0	0	0	0	1
145	U4	4646, 10873, 12308, 12705	134-356	0	0	0	0	1	0	0	0	1
146	U4	4646, 10873, 12308, 12705	154-356	1	0	0	1	0	0	0	0	1
147	U4	4646, 10873, 12308, 12705	223-356	0	1	1	2	0	0	0	0	2
148	U4	4646, 10873, 12308, 12705	263-519	0	0	0	0	1	0	0	0	1
149	U4	4646, 10873, 12308, 12705	263-523A	0	0	1	1	0	0	0	0	1

Table 2. Continued

Haplotype Number	Haplogroup	Coding Region SNP(s)	HVRI (16024-16569)	Old Believers			Russians			Grand Total				
				Burnyi	Izetsk	Kirsanovo	Krasnoselkup	Dovolnoe	Novosibirsk	Altai	Other	Total		
186	U5b1	10873, 12308, 12705, 13617	144-189-270-278	0	0	0	1	0	0	0	0	1	1	
187	K	9055, 10398, 10873, 12308, 12705	093-172-224-311	0	1	0	1	0	0	0	0	0	0	1
188	K	9055, 10398, 10873, 12308, 12705	093-224-261-311	0	0	0	0	0	2	0	0	0	2	2
189	K	9055, 10398, 10873, 12308, 12705	093-224-311	0	0	2	2	0	0	0	0	0	0	2
190	K	9055, 10398, 10873, 12308, 12705	192-224-311	0	0	0	0	0	1	0	0	0	1	1
191	K	9055, 10398, 10873, 12308, 12705	224-311	1	0	7	8	3	1	0	1	0	5	13
192	N1	1719, 10873	261-325	0	0	0	0	1	0	0	0	0	1	1
193	N1	1719, 10873	201-223-265-324	0	0	0	0	1	0	0	0	0	1	1
194	N1b	1719, 10873	145-157-176G-223-234-286-390	0	1	0	1	0	0	0	0	0	0	1
195	N1b	1719, 10873	145-176G-223-390	0	0	0	0	0	0	0	0	0	1	1
196	I	1719, 4529, 10398, 10873	129-145-223-391	0	0	1	1	0	0	0	0	0	0	1
197	I	1719, 4529, 10398, 10873	129-172-223-311-319-391	0	0	0	0	1	1	0	0	0	2	2
198	I	1719, 4529, 10398, 10873	129-223-325-391	0	0	4	4	0	0	0	0	0	0	4
199	I	1719, 4529, 10398, 10873	129-223-391	0	0	0	0	1	0	0	0	0	1	1
200	I	1719, 4529, 10398, 10873	129-172-223-311-391	0	1	0	1	0	0	1	0	0	1	2
201	X	1719, 10873, 14470	126-189A-223-278	0	0	0	0	1	0	0	0	0	1	1
202	X	1719, 10873, 14470	189-278	0	0	0	0	0	1	0	0	0	1	1
203	X	1719, 10873, 14470	189-223-234-248-278	0	0	0	0	1	0	0	0	0	1	1
204	X	1719, 10873, 14470	189-223-278	0	0	0	0	1	0	0	0	0	1	1
205	X	1719, 10873, 14470	108-189-223-278	1	0	0	1	0	0	0	0	0	0	1
206	X	1719, 10873, 14470	189-223-255-278	0	0	1	1	0	0	0	0	0	0	1
207	W	8994, 10873	189-223-292	0	0	1	1	0	0	0	0	0	0	1
208	W	8994, 10873	111-223-292-294-295	0	0	0	0	1	0	0	0	0	1	1
209	W	8994, 10873	223-292-311	0	0	0	0	1	0	0	0	0	1	1
210	A	10873	223-227-230-290-311-319	24	44	121	189	104	35	23	23	16	201	390

5% in the sample, and those designated HV0, which comprises 2.6% of the overall sample, although it appears only in the Kirsanovo population.

Although the high frequency of West Eurasian lineages among the Old Believers is not a surprising result, given the predominance of these maternal lineages in Slavic groups, the frequencies of individual haplogroups, such as HV0 in Kirsanovo, varies considerably among the Old Believer populations. For instance, despite having the smallest sample size ($N = 24$), the Burnyi sample shows the highest frequencies of haplogroups T (21.0%), J (12.5%), and X (4.2%) and the lowest frequency of haplogroup H (16.7%) of the three populations. In addition, East Eurasian lineages have the highest frequency in the Burnyi population (8.0%). These differences in haplogroup frequencies between the Burnyi sample from the Krasnoyarsk Krai in central Siberia and the Isetsk and Kirsanovo samples from the Tyumen Oblast in the west could reflect founder effects, lineal (familial) effects, or some other stochastic influences, if, in fact, the populations were restricted in size and geographically isolated from other Old Believer communities.

Interestingly, each Old Believer population sampled exhibits moderate frequencies of mtDNAs belonging to East Eurasian macrohaplogroup M, which appears at a frequency of 6% in the Old Believer sample as a whole. By contrast, the frequency with which East Eurasian lineages appear in the ethnic Russians from Siberia is 3.5% (see Table 2). There are also differences in the frequencies of West Eurasian haplogroups between the Old Believers and ethnic Russians from Siberia. The ethnic Russians have a considerably higher frequency of haplogroup H (46%), and moderately higher frequencies of haplogroups J (6.0%), V (2.0%), and X (2.0%) than the Old Believers. In addition, they exhibit a considerably lower frequency of haplogroup U (15.3%) and moderately lower frequencies of haplogroups T (1.0%) and K (4.0%).

Phylogenetic Analysis. We examined the patterns of mtDNA variation in the Old Believer and ethnic Russian populations from Siberia using network analysis. Figure 1 shows the phylogenetic relationships between known mtDNA lineages and their subbranches in the Old Believers and Russians, based on the mutational data given in Table 2. Figure 2 presents a median-joining network that indicates the frequencies of each haplotype in the Old Believers and Russians. The most frequent and diverse mtDNA lineages found in the sample are those derived from macrohaplogroup R, which is delineated by a 12705 SNP relative to the Revised Cambridge Reference Sequence. These lineages include HV, JT, and UK. Haplogroups H and U are the most diverse clusters in the sample set and exhibit starlike patterns reflecting the considerable haplotype variation within them. In fact, more than 44 branches originate from the founder node of haplogroup H, and more than 35 branches stem from the founder node of haplogroup U.

The considerably higher frequency of haplogroup U in the Old Believers (30%) compared to the ethnic Russians from Siberia (15%) is due primarily to the high frequency of subhaplogroup U4 in the Old Believers (13.4%). Subhaplogroup U5 also appears more frequently in the Old Believers (13.4%) than in the Russians

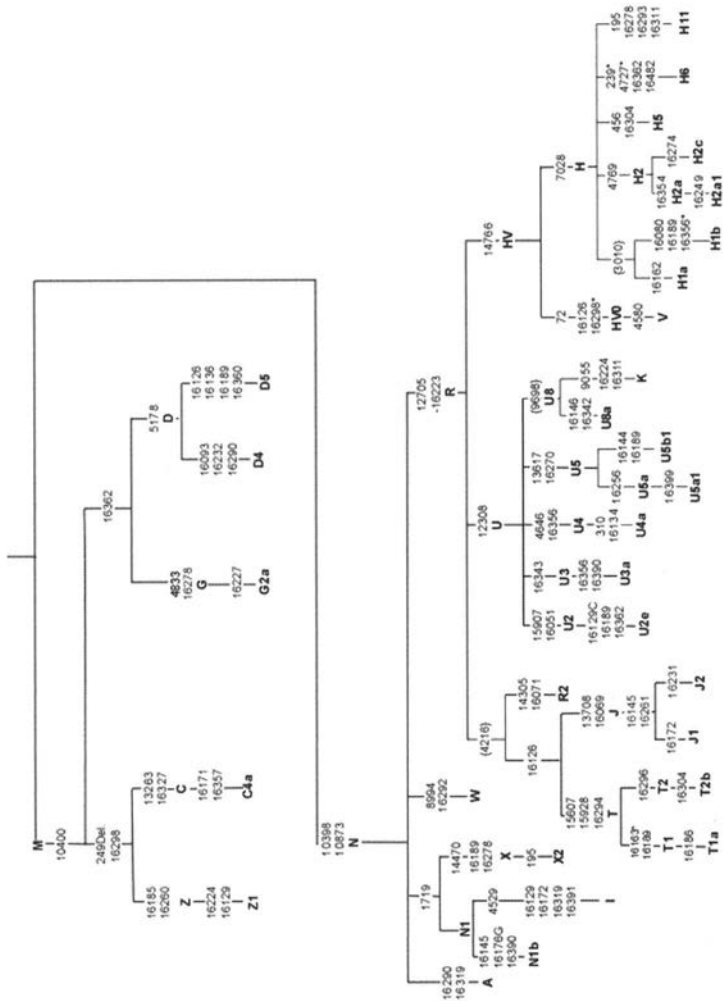


Figure 1. Phylogenetic relationships between mtDNA haplotypes observed in Old Believers and Russians. Samples were assigned to haplogroups based on diagnostic SNP markers detected by PCR-RFLP and HVRI sequencing. An asterisk refers to recurrent mutations.

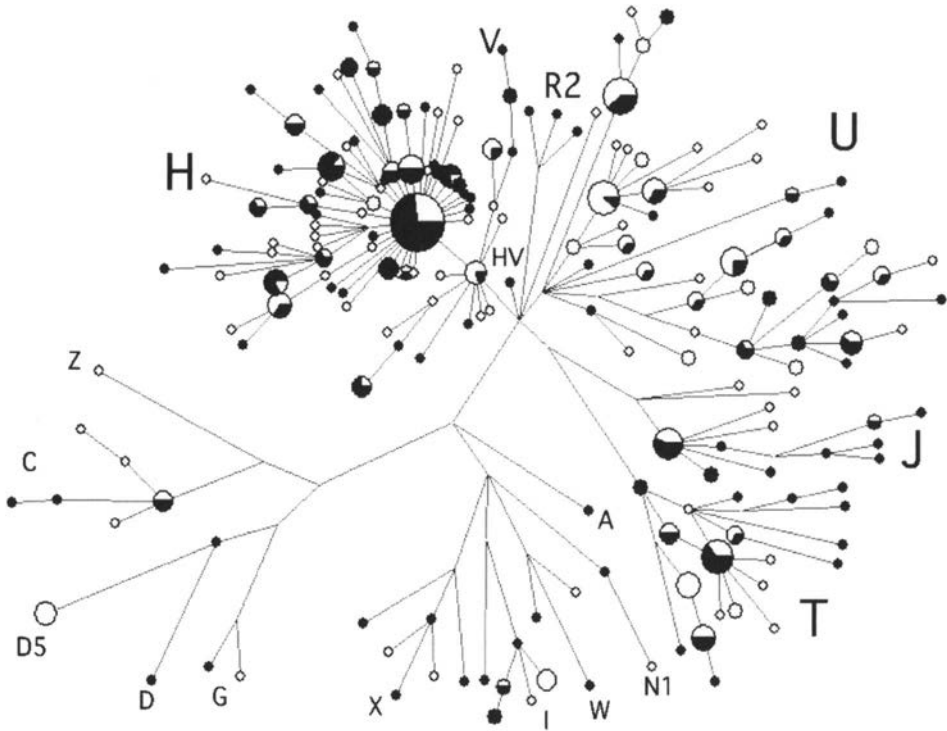


Figure 2. A median-joining network of Old Believer and ethnic Russian haplotypes. The frequency of each haplotype in each population is indicated in white (Old Believer) and black (Russian).

from Siberia (10.4%). The only subhaplogroup more frequent in the ethnic Russian sample is U5a, which occurs at a frequency of 7.4%, compared to 6.7% in the Old Believers (see Table 2).

The great diversity of haplogroup H in the sample set is not a surprising result, given that it is the most common mtDNA lineage found in Europe (Richards et al. 2000; Achilli et al. 2004; Loogvali et al. 2004). However, the relatively low frequency of haplogroup H and the high frequency of haplogroup U in the Old Believers were not expected, particularly in light of data from the Russians from Siberia and other Slavic populations.

East Eurasian haplotypes deriving from macrohaplogroup M are observed in the Old Believers. They represent haplogroups C, D, G, and Z. Interestingly, these haplogroups, which are found at high frequency among indigenous Siberian populations (Schurr et al. 1999; Derbeneva et al. 2002b; Derenko et al. 2003), appear more frequently in the Old Believers than in the Russians from Siberia. Specifically, subhaplogroup D5, which rarely occurs in Slavs (e.g., Malyarchuk et al. 2001, 2002), Saami (Lahermo et al. 1996; Delghandi et al. 1998), and native

Siberians (e.g., Derbeneva et al. 2002b; Derenko et al. 2003; Dulik et al. 2006, 2007; Zhadanov et al. 2006), appears in five Old Believer individuals but in none of the ethnic Russians from Siberia analyzed in this study (see Table 2). The presence of this and other East Eurasian lineages in the Old Believers might be the result of intermarriage with local native Siberian populations, although this would be inconsistent with their presumed endogamous marriages practices and cultural isolation.

Population Statistics

Within-Population Diversity. The genetic diversity index of the Old Believers as a whole is 0.979 and that of the ethnic Russians from Siberia is 0.980, values that are not significantly different from one another. When these groups are divided into populations, they show comparable levels of genetic diversity to each other and to ethnic Russians from Siberia (Table 3). This is a surprising result considering the small sample size and relative geographic isolation of Burnyi, located in central Siberia, compared to the other Old Believer populations of Isetsk and Kirsanovo from the Tyumen Oblast in western Siberia. Because each of the Old Believer communities has theoretically existed in relative isolation for more than 300 years, we expected to find evidence of decreased diversity in these smaller, more geographically isolated groups.

To further investigate whether populations were expanding or contracting in size, we also calculated Tajima's test of selective neutrality (see Table 3). The resulting data indicate that population expansions had occurred, with the pairwise mismatch analysis (data not shown) indicating that one major expansion led to mtDNA diversity observed within both the Old Believer and other Russian populations. These results suggest that Old Believers retained similarly high levels of mtDNA diversity as the larger Russian populations from which they split.

Interpopulation Diversity. Intergroup diversity in these populations was also measured using the HVR1 sequence data obtained in the present study and those available in the published literature. Direct counting of shared haplotypes between populations was performed to initially assess the affinities between populations (see Table 2). The results from haplotype sharing show that Old Believer samples from Isetsk and Kirsanovo (Tyumen Oblast) share 11 haplotypes, Burnyi and Kirsanovo share 8, and Burnyi and Isetsk share 6. Haplotypes 9 (D5; HVR1 motif 16126-16136-16189-16223-16360-16362), 84 (H11; HVR1 motif 16278-16293-16311), 103 (J; HVR1 motif 16069-16126), 121 (T1a; HVR1 motif 16126-16163-16186-16189-16294), and 143 (U4; HVR1 motif 16356) are shared by all three Old Believer populations.

Furthermore, the haplotype sharing shows that the fewest mtDNA types are shared between the Old Believers and indigenous Siberian populations. This is not a surprising result considering the nature of these endogamous religious groups and their respective genetic roots. However, the Old Believers had been living

Table 3. Intrapopulation Statistics

	Old Believers ^a			Russians from Siberia ^a					Comparative Russians					Comparative Slavs			Native Siberians					
	KIR	IS	BUR	KIR	DOV	NOV	ALT	TUL ^b	KAL ^b	VLD ^b	YAR ^b	PSK ^b	SAR ^c	STAV ^c	UKR ^d	BEL ^e	LITH ^f	SLOV ^g	BOS ^h	SALT ^h	KHK ^h	TUV ^h
N	121	44	24	104	35	23	23	70	71	71	42	68	63	62	18	91	180	104	153	110	53	90
Number of haplotypes	72	34	22	70	24	17	19	51	51	48	35	54	42	43	16	55	98	65	81	53	30	42
Genetic diversity	0.98	0.97	0.99	0.99	0.97	0.95	0.97	0.97	0.99	0.98	0.99	0.99	0.97	0.96	0.99	0.93	0.97	0.97	0.97	0.98	0.97	0.96
Pairwise differences	5.0	6.0	6.1	4.8	5.0	5.3	5.1	6.2	8.1	10.5	5.4	7.7	5.1	4.9	6.3	4.6	5.8	5.7	4.2	11.3	10.1	7.4
Tajima's D	-1.7	-1.7	-1.8	-2.0	-1.5	-1.3	-1.9	-1.9	-1.1	-0.8	-1.8	-1.2	-1.7	-1.7	-0.7	-1.8	-1.8	-1.7	-2.0	-0.8	-0.2	-1.4

KIR, Kirsanovo; IS, Isetsk; BUR, Burnyi; DOV, Dovolnoe; NOV, Novosibirsk; ALT, Altai; TUL, Tula; KAL, Kaluga; VLD, Vladimir; YAR, Yaroslav'; PSK, Pskov; SAR, Saratov; STAV, Stavropol; UKR, Ukrainians; BEL, Belarussians; LITH, Lithuanians; SLOV, Slovenians; BOS, Bosnians; SALT, southern Altaians; KHK, Khakassians; TUV, Tuvinians.
 a. Present study.
 b. Malyarchuk et al. (2002).
 c. Malyarchuk et al. (2004).
 d. Malyarchuk and Derenko (2001).
 e. Belyaeva et al. (2003).
 f. Kasperavičiute et al. (2004).
 g. Malyarchuk et al. (2003).
 h. Derenko et al. (2003).

Table 4. AMOVA of F_{ST} Estimates for Old Believer and Slavic Populations^a

	<i>Old Believers vs. Slavic Populations</i>	<i>European Slavic Populations vs. Siberian Slavic Populations</i>	<i>Siberian Slavs vs. Ethnic Siberians</i>
Between groups	0.18% ($P > 0.05$)	0.07% ($P > 0.05$)	25.36% ($P < 0.05$)
Between populations, within groups	0.51% ($P < 0.05$)	0.70% ($P < 0.05$)	6.92% ($P < 0.05$)
Within populations	99.32% ($P < 0.05$)	99.23% ($P < 0.05$)	67.72% ($P < 0.5$)

a. Based on 10,000 permutations. P values greater than 0.05 are not significantly different from 0. P values less than 0.05 are significantly different from 0.

for 300 years in relative proximity to indigenous Siberians and possessed East Eurasian lineages at moderate frequencies. Thus the presence of these haplotypes may be explained by recent admixture with indigenous Siberians. Alternatively, if these East Eurasian lineages were carried by the Old Believers from Russia, where they appear at low frequency, then their frequency may have increased within the populations once they settled into isolated populations in Siberia through genetic drift.

The Baltic population of Lithuanians and the Slavic population of Bosnians share the most haplotypes with the Old Believers (22%). However, it is possible that the high frequency of U4 haplotypes in both populations has inflated the observed similarity. This interpretation is supported by the population pairwise F_{ST} values, which show the Bosnian sample to be significantly different from two of the three Old Believer populations. Of the European Russian populations, Kaluga shares quite a few haplotypes with the Old Believers, with these shared haplotypes representing 18% of the total mtDNAs present in the group. A comparison of the Old Believers to other ethnic Russians living in Siberia shows that they also share 24% of their haplotypes with individuals from Krasnoselkup in north-central Siberia.

Although the number of shared haplotypes is useful for a preliminary assessment of mtDNA diversity between populations, this method of interpopulation diversity can be biased by the sharing of one specific type between populations, which may be present at inflated frequencies for several reasons. Therefore we also used the AMOVA to determine whether the Old Believers as a group have significantly diverged from other Slavic populations. The AMOVA results show that the between-group variation is not significantly different from 0 ($p > 0.05$), meaning that there is no significant difference between them (Table 4). However, there is a significant difference for the within-group estimates ($p < 0.05$), although the AMOVA does not determine between which populations this significant variation lies.

Consequently, we reviewed the p values for each set of populations in the F_{ST} distance matrix to determine which populations within each group are, in fact,

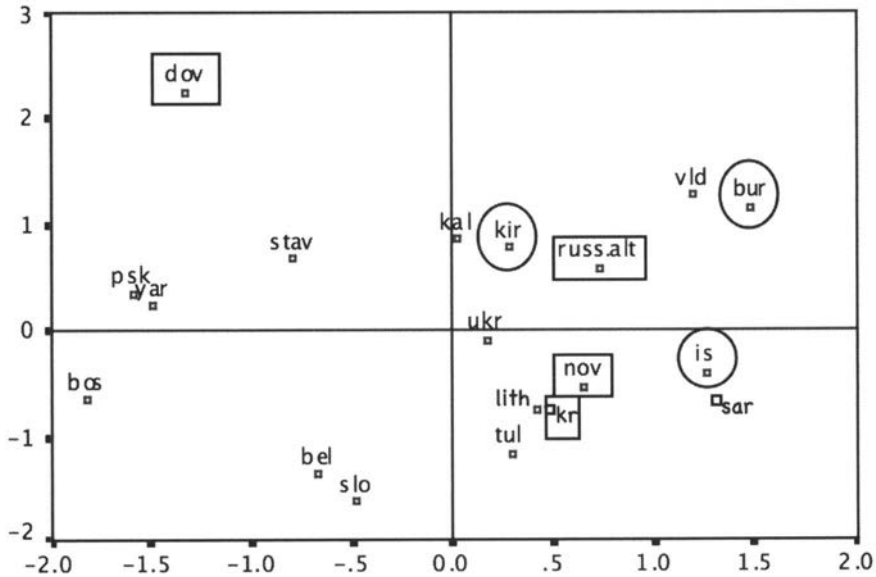


Figure 3. A multidimensional scaling plot of F_{ST} values for Old Believers (circles), ethnic Russians from Siberia (open squares), and comparative Slavic populations (filled squares). The stress value for this plot is 0.231.

significantly different from one another (Appendix 1). Not unexpectedly, these estimates indicate that all Old Believer and Slavic populations are significantly different from the three ethnic Siberian populations used for comparison. In addition, within the Old Believer group, none of the three populations significantly differ from one another. However, the European Russian population of Vladimir and the Slavic populations of Belarussians and Bosnians significantly differ from most other Slavic populations and are probably the cause of the significant variation between populations within a group as determined by AMOVA.

Overall, none of the three Old Believer populations significantly differ from one another. However, when F_{ST} values are plotted on a multidimensional scaling plot (Figure 3), we note that the three Old Believer populations each show different patterns of genetic affinities with Slavic populations and do not cluster as tightly together as each does with one or another Slavic group.

Discussion

The mtDNA data generated in this study have been used to address three major questions about the population history of the Old Believers. First, have the Old Believers living in isolation in Siberia for 200–300 years significantly diverged

from other Slavic populations? Second, if they have not significantly diverged, are there any signs of mtDNA differentiation between the Old Believers and other Slavic populations? Finally, do the three Old Believer populations analyzed in this study represent a single mtDNA gene pool? The answers to these questions are important because of the implications for the history of this population and for Slavic populations more broadly.

Unlike the Ashkenazi Jews and Amish examples of founder effects, both resulting in restricted mtDNA diversity and the wider prevalence of severe genetic diseases (Tishkoff and Verrelli 2003; van der Walt et al. 2005; Behar et al. 2004, 2006), the genetic diversity in the three Old Believer populations shows that, maternally speaking, they are as diverse as any other Slavic population used for comparison. In other words, there is no significant reduction of mtDNA diversity within these groups in terms of haplogroup frequencies or genetic diversity estimates and levels of selective neutrality compared to other Slavic populations.

It is important to note here that these intrapopulation genetic diversity indexes reflect levels of only maternal genetic variation. If Y-chromosome markers had been used for these diversity estimates, a different pattern might have emerged. For instance, in patriarchal societies, one might expect to find a restricted set of paternally inherited haplotypes as a consequence of closely related men forming the core of the social structure, with unrelated women brought in from different natal groups (e.g., Seielstad et al. 1998). Such a patriarchal system could, in fact, contain high levels of mtDNA diversity, such as those seen in the Old Believers.

Although we would expect to observe higher levels of mtDNA diversity than Y-chromosome diversity in patriarchal societies, we would still expect to find a reduction in mtDNA diversity after a founder event leading to the isolation of small endogamous populations for 300 years, especially compared to the larger parental populations from which they split. Because this is not the case, as seen in the AMOVA results (see Table 4), it appears that the Old Believers did not experience any significant founder events during their dispersal into Siberia.

Although the Old Believers have not significantly diverged from other Slavic populations, some unique patterns of mtDNA frequency distributions distinguish them (Table 5). Most Slavic populations typically have about 45% haplogroup H mtDNAs and about 14% haplogroup U mtDNAs. By contrast, the Old Believers have the lowest haplogroup H frequency (29%) and the highest frequency of haplogroup U (30%) seen in such groups, with an unusual frequency and distribution of subhaplogroup U4. Furthermore, the Old Believers show increased frequencies of East Eurasian haplogroups compared to other Russian populations, specifically the occurrence of the rare subhaplogroup D5 in five individuals, a possible sign of native Siberian contribution to the Old Believer mtDNA gene pool. Each of these specific haplogroups is discussed in some detail in what follows.

Subhaplogroup U4. Haplogroup U is an ancient maternal lineage estimated to be 50,000 years old (Richards et al. 1996, 1998; Torroni et al. 1996; Finnilä et al. 2000). Over time, this predominantly West Eurasian lineage has diversified

Table 5. Haplogroup Frequencies (%) in Old Believers and Slavic Populations

Haplogroup	Old Believers (N = 189) ^a	Trans-Ural Bashkirs (N = 59) ^b	Russians from Siberia (N = 201) ^a	Russians from Eastern Europe (N = 201) ^c	Bosnians (N = 144) ^c	Slovenians (N = 104) ^c	Poles (N = 436) ^d
D5	2.6	?	0	0.5	0	0	0
H	29.0	29.0	44.6	42.3	47.9	47.1	45.2
I	3.2	0	2.0	2.5	2.8	1.9	1.8
J	4.8	2.0	7.0	8.0	6.9	9.6	7.8
K	5.8	2.0	4.0	3.0	4.2	3.8	3.4
M	6.0	19.0	3.5	1.5	1.4	0	1.8
T	12.7	3.0	11.4	10.9	4.9	5.8	11.5
U2	0.5	2.0	1.0	1.5	0	1.0	0.9
U4	13.4	12.0	2.5	3.5	5.6	5.8	5.0
U5	11.6	2.0	10.4	10.4	11.8	10.6	8.7
W	0.5	2.0	1.0	2.0	1.4	4.8	3.7
X	1.0	3.0	2.0	3.5	1.4	1.0	1.8

Boldface frequencies distinguish the Old Believers from other Russian and Slavic populations;

D5 mtDNAs are included in the M frequencies.

Russians from Eastern Europe include the specific Russian populations used for statistical analyses.

a. Present study.

b. Bermisheva et al. (2001).

c. Malyarchuk et al. (2003).

d. Malyarchuk et al. (2002).

into many subhaplogroups, including U4, with this lineage having an estimated age of more than 25,000 years (Richards et al. 2000). Although haplogroup U has been said to be almost entirely confined to Europe (Richards et al. 1996, 1998; Torroni et al. 1996; Finnilä et al. 2000), recent genetic studies have shown that the frequency of subhaplogroup U4, as well as its percentage of the U gene pool, increases eastward, reaching its maximum in northwestern Siberian populations (Derbeneva et al. 2002a; Derenko et al. 2003; Malyarchuk et al. 2004).

In the Old Believer communities living in Siberia, subhaplogroup U4 occurs at a frequency of 13.4% and represents 44% of the haplogroup U mtDNAs present in these groups. Such numbers are in stark contrast to the frequency with which subhaplogroup U4 appears in ethnic Russians from Siberia (2.5%), in which it constitutes 16% of the haplogroup U mtDNAs present in that population. In addition, the frequency of subhaplogroup U4 in Old Believers is considerably higher than the frequencies found in Russians from Eastern Europe (16.7% of haplogroup U mtDNAs in the sample), in the Baltic region (22.9% of haplogroup U mtDNAs in the sample), and in the Volga-Ural region (34.2% of haplogroup U mtDNAs in the sample) (Malyarchuk 2004). In fact, the Old Believer subhaplogroup U4 frequency is one of the highest reported for any European population (Macaulay et al. 1999; Richards et al. 2000; Tambets et al. 2004; Torroni et al. 2000; Finnilä et al. 2001; Malyarchuk et al. 2002; Malyarchuk 2004; Achilli et al. 2004).

More specifically, in the easternmost Old Believer community, Burnyi, located in the Baikitsk Raion of the Krasnoyarsk Krai in central Siberia, subhaplogroup U4 represents 25% of the total sample and 86% of the haplogroup U mtDNAs present there. These values are even more considerable compared to the frequency with which subhaplogroup U4 appears in the other two Old Believer communities, both located in the Tyumen Oblast, just west of Krasnoyarsk Krai. Here, subhaplogroup U4 makes up 54% of the haplogroup U mtDNAs in Isetsk and 33% of the haplogroup U mtDNAs in Kiransovo.

Clearly, the distribution of subhaplogroup U4 in the Old Believers is not consistent with the patterns observed in other ethnic Russian populations from Eastern Europe or Siberia. However, it is consistent with the geographic distribution of subhaplogroup U4 among the indigenous populations of northwest Siberia, including the Mansi, Nganasans, and Kets, where it appears at a frequency of 16–29% (Derbeneva et al. 2002a, 2002b; Malyarchuk 2004). Even so, the subhaplogroup U4 HVR1 haplotypes most typical of these native Siberian populations (16189-16356 and 16311-16356) are not present in the Old Believers, who instead commonly exhibit U4 HVR1 haplotypes 16134-16356 or 16356 alone, with the U4 designation confirmed by PCR-RFLP detection of the diagnostic marker *RsaI* 4646.

The U4 haplotypes found in the Old Believers belong to the subclade U4a, which is characterized by HVR mutations at np 16134 and np 16356 (back mutation) and HVR2 mutations at np 152 and np 310 (Malyarchuk et al. 2002; Achilli et al. 2005). These and other U4 haplotypes are also found at moderate frequency in Russians and Poles and in some non-Slavic populations (Bermisheva et al. 2001;

Pliss et al. 2006). For instance, U4a haplotypes 156, 157, and 158 (see Table 2) are found in Russian individuals from different parts of European Russia. More specifically, haplotype 158 (16134-16356) is found in individuals from two eastern European Russian populations (Tula and Vladimir), whereas the U4 haplotype marked by the 16356 mutation (haplotype 143) appears in Tula and the Russian population of Kaluga (Malyarchuk et al. 2002, 2004). Five Bosnian individuals assigned to subhaplogroup U4 also have the HVR1 haplotype 16356, and another one has the U4a HVR1 haplotype 16134-16356 (Malyarchuk et al. 2003). However, the frequency at which subhaplogroup U4 appears in Bosnians is only 5.6%, considerably lower than in the Old Believers (13.4%). An additional U4 haplotype found in the Old Believers, marked by mutations at 16223 and 16356 (haplotype 147), is also present in Russians, Poles, and Finns (Malyarchuk et al. 2002). In addition, populations from the Volga-Ural region share some U4 haplotypes with Old Believers. For instance, the U4 haplotype 16093-16134-16186-16187-16356 (haplotype 144) has been found in Komi and Tatar populations, and the U4 haplotype 16134-16311-16356 (haplotype 157) has been detected in the Bashkirs (Bermisheva et al. 2001).

The distribution of these U4 haplotypes leads to the questions of how the Old Believers acquired them and why they appear so frequently in this population living in Siberia. A potential source of the Old Believer U4 haplotypes might be European Russian populations, although one must also consider the possibility that the source could be the indigenous populations of the Volga-Ural region, specifically the Trans-Ural Bashkir population from Beloretskii. This Bashkir population is reported to have 12% U4 mtDNAs defined by the 16356 mutation, previously one of the highest observed frequencies reported for European populations (Bermisheva et al. 2001).

Another subhaplogroup, U5, appears at a frequency of 13.4% in Old Believers, the same frequency at which U4 appears. However, subhaplogroup U5 is more common in Russian populations and therefore does not place the Old Believers outside the range of variation of Slavic mtDNA diversity. Subhaplogroup U5 is widely distributed in European populations (Simoni et al. 2000; Bermisheva et al. 2001) and predominates among the Saami (Orekhov et al. 1999; Bermisheva et al. 2001; Tambets et al. 2004; Achilli et al. 2004). The rare occurrence of subhaplogroup U2, another subbranch, in Old Believers is also consistent with data from other European and Slavic populations, in which subhaplogroup U2 is often absent or appears at extremely low frequency.

Haplogroup H. The low frequency at which haplogroup H appears in the Old Believers (29%) is also unusual relative to other European and Slavic populations. Haplogroup H is the most common mtDNA lineage in Europe. Among European Russian populations, haplogroup H appears at a frequency of 42.3% (Malyarchuk et al. 2003) and at a frequency of 44.6% among the ethnic Russians from Siberia analyzed in the present study. Among other Slavic groups, such as Bosnians, Slovenians, and Poles, haplogroup H appears at a frequency between

45% and 48% (Malyarchuk et al. 2002, 2003). On the other hand, the relatively low frequency of haplogroup H has also been seen in indigenous populations from the Volga-Ural region, in which haplogroup H appears at a frequency of about 32% (Bermisheva et al. 2001). Most notably, haplogroup H appears in the Trans-Ural Bashkir population from the Volga-Ural region at a frequency of 29% (Bermisheva et al. 2001), the same frequency at which it appears in the Old Believers (see Table 5).

Subhaplogroup D5. It is possible that other mtDNA haplogroups present in the Old Believers but rarely seen in other Russian populations may have come from the Volga-Ural region as well. For instance, each Old Believer population sampled exhibits moderate frequencies of East Eurasian macrohaplogroup M mtDNAs, which appear at a frequency of 6% in the Old Believer sample as a whole. This is an interesting result because East Eurasian mtDNA haplogroups present in the Old Believers and frequently appearing in ethnic Siberians, such as haplogroups C, D5, and G2a, are not usually found in ethnic Russians. They appear at a frequency of only 3.5% in the ethnic Russians from Siberia sampled in the present study and are found at even lower frequencies in Russians from Eastern Europe (1.5%), Bosnians (1.4%), Slovenians (0%), and Poles (1.8%) (Malyarchuk et al. 2002, 2003) (see Table 5).

These results lead to two different hypotheses about the higher frequencies of East Eurasian mtDNAs in Old Believers compared to ethnic Russians or other Slavic populations. The first hypothesis suggests that these East Eurasian mtDNAs were introduced at low frequencies into ethnic Russian and Slavic groups during the Mongol invasion of Europe approximately 800 years ago and that they have been maintained at low levels in Russians and Slavs since that time. There is also evidence that East Eurasian mtDNAs entered the Slavic gene pool when the Slavs invaded the Volga-Ural region in the mid-16th century and mixed with the resident indigenous populations, who themselves had accumulated East Eurasian lineages from the ancestors of Finno-Ugric and Turkic groups who invaded this region before the 4th century (Bermisheva et al. 2001).

Following this model, when the Russian church schism of the 1650s and subsequent persecution of the Old Believers forced them to split off from the larger Russian population, they may have carried a disproportionate frequency of these East Eurasian haplotypes with them to Siberia, where they increased in frequency in isolated Old Believer communities as a result of genetic drift. This idea is supported by the lower frequencies but not the absence of East Eurasian mtDNAs in the ethnic Russian populations analyzed in this and other studies (Malyarchuk et al. 2001, 2003, 2004).

Interestingly, five of the East Eurasian mtDNAs observed in the Old Believers belong to haplogroup D. In fact, all of them belong to subhaplogroup D5, which lacks the M-specific RFLPs *DdeI* 10394 (np 10398) and *AluI* 10397 (np 10400) because of a mutation at np 10397 that abolished them (Derbeneva et al. 2002b; Yao et al. 2002; Derenko et al. 2003; Tanaka et al. 2004) and shares the same

HVR1 sequence (16126-16136-16189-16223-16360-16362). If the Old Believers had experienced genetic drift causing this East Eurasian haplotype to increase in frequency, as the second hypothesis posits, then this D5 motif should appear, to some extent, in the Slavic or Russian parental population, because 300 years of Old Believer isolation is not long enough to accumulate all these novel mutations. However, only one such D5 sequence was detected in comparative Russian or Slavic populations (Malyarchuk et al. 2002, 2003; Malyarchuk 2004).

It is possible, therefore, that the East Eurasian M haplotypes present in the Old Believers were introduced into Slavic populations from the Volga-Ural region after they entered this territory in the mid-16th century. In this scenario the indigenous populations of the region accumulated East Eurasian haplotypes through successive expansions by the ancestors of modern Finno-Ugric and Turkic peoples (Bermisheva et al. 2001). The high frequency (17%) of M haplotypes in a Russian population from Bashkortostan would therefore reflect intermixing between Slavic and indigenous populations of the region.

In addition, haplogroups D and Z and other East Eurasian M haplotypes have been found in Russians from Velikii Novgorod (3.7%) and Volot (6.3%), which are located close to the border with Pskov (Lunkina et al. 2004). The Volot population contains the same frequency of East Eurasian types as the Old Believers. Subhaplogroup D5 is also found at a frequency of 8.7% in Finnish Saami (Tambets et al. 2004). Therefore the presence of subhaplogroup D5 in Russians from Novgorod could be explained by contribution of Finnish populations to Russians from the northwestern part of Russia (Lunkina et al. 2004). These explanations for the presence of East Eurasian haplogroups in Russian populations support the idea that the Old Believers carried to Siberia low frequencies of the East Eurasian mtDNAs originally introduced to their Slavic ancestors through invasions and admixture, where they subsequently increased in frequency as a result of genetic drift in isolated populations.

Alternatively, the presence of East Eurasian mtDNA lineages in the Old Believers could have resulted from admixture with local Siberians during their exile in remote Russia. Although it is not known how frequently admixture took place, this practice might reflect the conversion and assimilation of members of local native Siberian populations into Old Believer groups and/or individual deviations from the typical practice of religious endogamy. As a whole, mtDNA haplogroup D is the most abundant lineage found in Central and East Asia (Schurr et al. 1999; Derbeneva et al. 2002a, 2002b; Yao et al. 2002; Derenko et al. 2003; Tanaka et al. 2004). In southern Siberia, the highest frequency of haplogroup D is found among the Buryats (33%) and Sojots (46.7%) from the Baikal region (Derenko et al. 2003).

Subhaplogroup D5 is prevalent in southern Siberia as well. For instance, Derenko et al. (2003) reported one case of subhaplogroup D5 (named D5b) with the HVR1 motif 16126-16136-16189-16223-16360 in the Turkic-speaking Altaians from the Altai Republic, and the same sequence was found in the Saami from northern Norway at a frequency of 4.7% (Delghandi et al. 1998). However,

Gokcumen et al. (2008), Zhadanov et al. (2006), and Dulik et al. (2006) also detected D5c haplotypes in Altaian ethnic groups. In addition, one Mansi individual from northwest Siberia has the same D5 HVR1 motif, 16126-16136-16189-16223-16360-16362 (Derbeneva et al. 2002b), that appears in five Old Believer individuals: 1 from Burnyi, 1 from Isetsk, and 3 from Kirsanovo.

Although the genetic diversity and AMOVA results show that the Old Believers have not significantly diverged from ethnic Russians or other Slavic populations, the atypical frequencies of haplogroups D5, H, and U4 distinguish them from their source populations, although this differentiation is not statistically significant. Although this small-scale divergence is not of the same magnitude observed in other schismatic populations and although neutrality tests confirm that no selective force has significantly reduced the genetic diversity in Old Believer populations, these anomalous patterns may be a sign that the maternal gene pool of Old Believers from Siberia is somewhat differentiated from that of other Slavic populations.

The Old Believer mtDNA Gene Pool. The next logical question is whether the three Old Believer populations analyzed in this study for mtDNA variation represent a single maternal gene pool. AMOVA results show that the overwhelming majority of variation that exists among the Old Believers resides within rather than between the populations. This lack of interpopulation genetic structure implies that the Old Believer group cannot be divided into separate gene pools (represented by settlements). The Old Believer populations also share a moderate number of haplotypes between at least two of them, with five types shared across all three populations sampled (D5, H11, J, T1a, and U4).

The inference that the Old Believers represent a single maternal gene pool is further supported by F_{ST} values, which indicate no significant differences between any of the Old Believer populations ($p > 0.05$). Considering that the F_{ST} values for the interpopulation comparisons of the Old Believer populations are not significantly different from 0, it is logical to conclude that there is no structure within the Old Believer group as a whole.

Despite this conclusion, however, the genetic distances between each Old Believer population and the other Slavic populations are different. As shown in the multidimensional scaling plot (Figure 3), the three Old Believer populations each show a different pattern of genetic affinity with other Slavic groups and do not cluster tightly together as each does with certain Slavic populations. In addition, the significant difference between Pskov and the Old Believer populations of Isetsk and Kirsanovo seemingly contradicts the claim that Old Believers moved to the Tyumen Oblast from the Pskov region 300 years ago (Makovetskii and Maslova 1975). Based on the population pairwise F_{ST} estimates, Burnyi emerges as the Old Believer population most genetically similar to the other Slavic populations, whereas Kirsanovo emerges as the least genetically similar to the other Slavic populations.

These differing patterns of genetic affinities to Slavic populations may reflect the fact that Old Believers do not compose one “ethnic” group. From the beginning of the schism, practitioners of the Old Belief were divided into the priest and priestless sects, and divisions within each, based on the acceptance or rejection of specific rituals, have continued to the present day. Some Old Believer groups split off after the schism because they agreed to be a part of the Russian Orthodox Church while still retaining the old rites. Others split off because they rejected marriage, a divisive practice still observed by many groups of Old Believers today, but which also led to the extinction of many others. These differences have led many Old Believer groups not to acknowledge one another and to view the other’s offspring as illegitimate. Therefore endogamy may not necessarily have been practiced within the Old Believer populations as a whole, especially because many groups have been intolerant of each other since the schism (Armstrong 1965; Robson 1995; Paert 2003).

It is difficult to say with certainty why each of the Old Believer populations sampled in this study shows a different pattern of genetic affinity relative to other Slavic populations while still apparently representing one mtDNA gene pool. One conclusion is that their shared religion has not been the primary factor influencing the observed mtDNA diversity. This view is also supported by the fact that the modern Slavic candidates for their potential source populations, with whom they still genetically cluster, presumably did not practice the Old Beliefs (or else they too would have been exiled). Therefore geographic origin appears to be a greater influence on the patterns of genetic diversity in the Old Believer populations than shared religion and subsequent centuries of isolation from their source populations.

Conclusions

This study makes an important contribution to our understanding of mtDNA diversity in Slavic populations, which, to date, has not included analyses of Russian Old Believers. This population represents a biocultural split from a larger source population, resulting in 300 years of isolation. However, the Old Believers have retained the same level of genetic diversity as the larger Slavic source population(s) from which they separated. This result leads to the conclusion that the geographic origins of the Old Believers are still reflected in their mtDNA composition and are greater influences on their modern genetic diversity than the religious practices that define them.

The fact that the Old Believers do not show signs of founder effects after 200–300 years of isolation from their source also leads to the conclusion that the founder groups consisted of many individuals. Although it is not known exactly how many individuals made up the initial Old Believer founder populations, it is documented that, by the 1820s, their numbers had reached 800,000 (Mel’nikov 1897). These numbers imply that the Old Believer founder populations were too

large in number to experience significant founder effects. Therefore, although the demographic history of this schismatic population is undoubtedly compelling and worthy of future study, there is limited evidence that it fluctuated in size and structure enough to significantly affect patterns of genetic variation.

Future research will focus on the Y-chromosome diversity of the Old Believers. Because the merchants and invaders of Russia were predominantly men, they likely introduced Y chromosomes rather than mtDNA haplotypes to the Russian gene pool. Therefore we might expect the Y-chromosome variation of the Russian source population from which the Old Believers split to be diverse and the Old Believers to retain much of this diversity. However, one must consider the patriarchal family structure of the Old Believers, which would potentially have decreased Y-chromosome diversity within their populations compared to mtDNA variants introduced by women from other families. In addition, previous NRY analyses of Old Believers in Poland revealed significant differences between the Old Believers and the autochthonous Poles and suggested a certain degree of genetic isolation of this religious minority (Pepinski et al. 2004, 2005). Thus Y-chromosome marker data from Russian Old Believers may provide a more detailed perspective on the population history of these groups than the mtDNA results.

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Appendix 1. Population Pairwise F_{ST} Values for Old Believers, Russians, and Other Slavic Populations^a

	TUL	KAL	VLD	YAR	PSK	SAR	STV	BEL	SLO	BOS	BUR	ISK	KIR	UKR	KR	DOV	NOV	ALT	LITH	SALT	KHK	TUV
TUL	0.002	0.017	-0.002	0.008	0.000	0.005	0.005	0.007	-0.003	0.003	0.001	0.004	0.007	-0.012	0.000	0.017	-0.008	-0.003	0.000	0.132	0.801	0.823
KAL	-	0.009	-0.003	0.005	0.006	0.004	0.011	0.002	0.010	-0.007	0.008	0.008	0.004	-0.013	0.006	0.003	-0.010	-0.004	0.007	0.122	0.780	0.806
VLD	+		0.016	0.021	0.017	0.020	0.024	0.024	0.032	0.002	0.017	0.024	-0.002	0.020	0.017	0.010	0.010	0.001	0.022	0.127	0.756	0.786
YAR	-	+		0.007	0.014	-0.004	0.010	0.000	0.000	0.011	0.009	0.009	-0.007	0.007	0.003	-0.005	0.009	0.003	0.019	0.798	0.825	0.825
PSK	+	-	+		0.005	0.005	0.011	0.004	0.015	0.002	0.013	0.011	-0.005	0.008	0.004	0.000	0.001	0.011	0.134	0.785	0.810	0.810
SAR	-	+	+	+		0.007	0.009	0.005	0.012	-0.008	0.010	0.003	-0.010	-0.004	0.017	-0.001	-0.008	0.001	0.141	0.811	0.832	0.832
STV	-	+	+	-	+		0.004	0.008	0.023	0.010	0.005	0.000	-0.007	0.004	0.006	-0.008	0.002	0.025	0.125	0.812	0.833	0.833
BEL	+	+	+	+	+	+		0.012	0.010	0.010	0.006	0.008	0.006	0.004	0.012	0.009	-0.006	0.000	0.149	0.828	0.842	0.842
BOS	-	+	+	+	+	+	+		0.005	0.010	0.017	0.008	0.007	-0.002	0.004	0.017	-0.002	0.006	0.146	0.816	0.832	0.832
BUR	-	+	+	+	+	+	+	+		0.017	0.008	0.008	0.003	0.007	0.010	0.003	0.011	0.003	0.167	0.847	0.856	0.856
ISK	-	+	+	+	+	+	+	+	+		0.000	0.000	-0.020	-0.002	0.013	0.004	-0.016	0.000	0.116	0.781	0.817	0.817
KIR	-	+	+	+	+	+	+	+	+	+		0.003	-0.009	0.009	0.013	0.000	-0.005	0.000	0.112	0.793	0.821	0.821
UKR	-	+	+	+	+	+	+	+	+	+	+		-0.010	0.000	0.006	0.000	-0.003	0.002	0.151	0.829	0.841	0.841
KR	-	+	+	+	+	+	+	+	+	+	+	+		-0.006	0.000	-0.017	-0.008	-0.006	0.101	0.775	0.815	0.815
DOV	-	+	+	+	+	+	+	+	+	+	+	+	+		0.015	0.003	-0.009	0.001	0.151	0.829	0.842	0.842
NOV	-	+	+	+	+	+	+	+	+	+	+	+	+	+		0.016	0.011	0.009	0.131	0.797	0.826	0.826
ALT	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+		0.001	0.001	0.104	0.785	0.820	0.820
LITH	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		-	-0.007	0.110	0.785	0.821
SALT	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		0.155	0.823	0.834
KHK	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		0.733	0.759
TUV	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		0.022

TUL, Tula; KAL, Kaluga; VLD, Vladimir; YAR, Yaroslavl; PSK, Pskov; SAR, Saratov; STV, Stavropol; BEL, Belarusians; SLO, Slovenians; BOS, Bosnians; BUR, Burmyi; IS, Iseitsk; KIR, Kirsanovo; UKR, Ukrainians; KR, Krasnoselkup; DOV, Dovolnoe; NOV, Novosibirsk; ALT, Altai; LITH, Lithuanians; SALT, southern Altaians; KHK, Khakassians; TUV, Tuvinians.

a. Population pairs marked with a plus sign are significantly different from each other, whereas those marked with a minus sign are not.