

Boundaries and Clines in the West Eurasian Y-Chromosome Landscape: Insights From the European Part of Russia

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ABSTRACT Previous studies of Y chromosome variation have revealed that western Europe, the Volga-Ural region, and the Caucasus differ dramatically with respect to Y-SNP haplogroup composition. The European part of Russia is situated in between these three regions; to determine if these differences reflect clines or boundaries in the Y-chromosome landscape, we analyzed 12 Y-SNPs in 545 males from 12 populations from the European part of Russia. The majority of Russian Y chromosomes (from 74% to 94%) belong to three Y chromosomal lineages

[I-M170, R1a1-M17, and N3-TAT] that are also frequent in the rest of east Europe, north Europe, and/or in the Volga-Ural region. We find significant but low correlations between haplogroup frequencies and the geographic location of populations, suggesting gradual change in the Y chromosome gene pool across western Eurasia. However, we also find some significant boundaries between populations, suggesting that both isolation and migration have influenced the Y chromosome landscape. *Am J Phys Anthropol* 137:41–47, 2008. © 2008 Wiley-Liss, Inc.

Previous studies have shown that Y-SNP haplogroups form different landscapes in terms of haplogroup composition and their frequencies in Europe, the Volga-Ural region and the Caucasus (Rosser et al., 2000; Semino et al., 2000; Wells, 2001; Nasidze et al., 2003, 2004). The European part of Russia is situated at a critical juncture between these regions, particularly with respect to the most informative haplogroups that vary across Europe: R1a1-M17, I-M170, and N3-TAT (Rosser et al., 2000). Information on the Y-SNP haplogroup composition of the European part of Russia would aid in distinguishing if transitions in the European Y-chromosome landscape are continuous or abrupt. However, the previous studies of Y-SNP variation in this part of the world did not type all of the relevant markers, nor did they address the issue as to how the Y-chromosome landscape changes across the European part of Russia (Malyarchuk et al., 2004; Balanowsky et al., 2008). Therefore, the question of whether the Y chromosome haplogroup landscape changes gradually between west Europe and the Volga-Ural region, or if instead these changes are abrupt and result in the formation of genetic boundaries situated in the European part of Russia is still open.

In this study, we present analyses of Y-SNP haplogroup and Y-STR haplotype variation in 12 groups from the European part of Russia. These new genetic data are combined with previously-published data on Y-SNP variation in the rest of Europe, the Volga-Ural region, the Caucasus and the Near East (Lahermo et al., 1999; Rosser et al., 2000; Semino et al., 2000; Wells et al., 2001; Passarino et al., 2002; Malyarchuk et al., 2004; Nasidze et al., 2003, 2004; Kharkov et al., 2005) to address the following questions: (1) What are the genetic

relationships of the Russian groups with respect to each other and other European, Uralic, Caucasian, and Near Eastern populations? and (2) How does the west European Y-SNP haplogroup landscape change over the European part of Russia towards the Volga-Ural region?

MATERIALS AND METHODS

Samples and DNA extraction

Blood samples from 545 unrelated Russian males were collected in 12 populations from the European part of Russia (see Fig. 1). The sampling was carried out in the administrative centers of the following regions (oblast) of the Russian Federation: Smolenskaja, Brianskaja, Ivanovskaja, Lipezkaja, Penzenskaja, Ryazanskaja, Orlovskaja, Tverskaja, Vologodskaja, Tambovskaja, Archangelskaja, and Nowgorodskaja. Informed consent and information about the birthplace of the donor and his parents and

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Fig. 1. Distribution of Y-SNP haplogroups in the populations from the European part of Russia. Abbreviations of the group names are as follows: *Smo*—Smolenskaja oblast, *Bri*—Brianskaja oblast, *Iva*—Ivanovskaja oblast, *Lip*—Lipezkaja oblast, *Pen*—Penzenskaja oblast, *Rya*—Ryazanskaja oblast, *Orl*—Orlovskaja oblast, *Tve*—Tverskaja oblast, *Vol*—Vologodskaja oblast, *Tam*—Tambovskaja oblast, *Arc*—Archangel'skaja oblast, *Now*—Nowgorodskaja oblast.

grandparents were obtained. DNA was extracted from whole blood samples using the QIAamp DNA Blood Mini Kit (QIAGEN) following the recommendations of the manufacturer.

Y chromosome bi-allelic markers

All DNA samples were typed for the X- and Y-linked zinc finger protein genes in order to confirm the gender of the sample (Wilson and Erlandsson, 1998). They were then genotyped for 11 Y chromosomal SNP markers: RPS4Y (M130), M9, TAT, M89, M124, M45, M173, M17, M201, M170, and M172 (Underhill et al., 2000) and references therein); the YAP *Alu* insertion polymorphism (Hammer and Horai, 1995) was also typed. The markers M9, TAT, and RPS4Y were typed by means of PCR-RFLP as described elsewhere (Zerjal et al., 1997; Kayser et al., 2000). The markers M17, M124, M170, M172, M173, M45, and M201 were typed using PIRA-PCR (primer introduced restriction analysis) assays (Yoshimoto et al., 1993) as described elsewhere (Cordaux et al., 2004; Nasidze et al., 2004). M89 was typed as described elsewhere (Ke et al., 2001), while the YAP *Alu* insertion was typed as described by Hammer and Horai (1995). The samples were genotyped according to the hierarchical order of the markers as described by the Y chromosome consortium (YCC) (Y-chromosome-consortium, 2002). The Y-SNP haplogroup nomenclature used here is according to the recommendations of the YCC (2002). The phylogenetic relationships of the analyzed haplogroups are shown in Figure 2.

Published Y-SNP data from European, Near Eastern, Caucasian, and Uralic populations were compiled and used for comparative analysis (Lahermo et al., 1999; Helgason et al., 2000; Rosser et al., 2000; Semino et al., 2000; Raitio et al., 2001; Zerjal et al., 2001; Kasperavičiute et al., 2003; Malyarchuk et al., 2004; Nasidze et al., 2003, 2004; Rootsi et al., 2004).

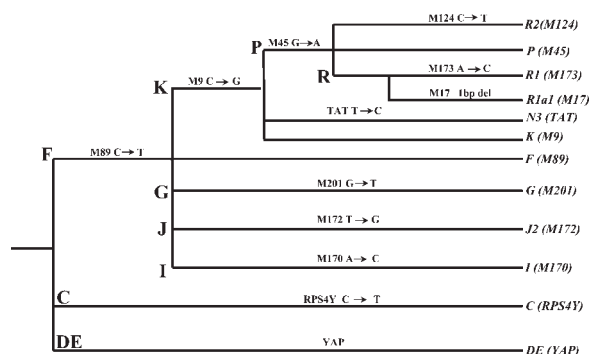


Fig. 2. Hierarchical relationship of the analysed Y chromosomal haplogroups (Del—Deletion, Ins—Insertion).

Statistical analysis

Basic parameters of molecular diversity and population genetic structure, including analyses of molecular variance (AMOVA), as well as Mantel test were carried out using the software package Arlequin 2.000 (Schneider et al., 2000). Grouping of populations according to linguistic classification for AMOVA analysis was carried out based on subdivision of major linguistic families (Ethnologue, 2000). Populations were also grouped broadly on the basis of geography into Western, Northern and Eastern European, Volga-Ural, and Caucasian subgroups. The statistical significance of F_{st} values was estimated by permutation analysis, using 10,000 permutations. The statistical significance of the correlation between genetic and geographic distance matrices was evaluated by the Mantel test with 10,000 permutations. The STATISTICA7 package (StatSoft Inc.) was used for principal component (PC) analysis. The R package Wombsoft (Crida and Manel, 2007) was used to detect potentially significant genetic boundaries between popu-

lations. This method is similar to the approach suggested by Barbujani et al. (1989) and also based on the Wombling algorithm (Womble, 1951).

RESULTS

Y-SNP haplogroups

Overall, eleven Y-SNP haplogroups were found in the twelve Russian groups (Table 1, Fig. 1). The haplogroup R1a1 (M17) was found at the highest frequency in the west Russian groups, followed by haplogroups I-M170 and N3-TAT; together these three haplogroups account for from 73.8% to 93.9% of Russian Y chromosomes. The remaining haplogroups occur in considerably lower frequencies; the haplogroup P-M45 was absent in all groups. The frequency of haplogroup N3-TAT varies significantly among the groups ($\chi^2 = 21.091$; $P = 0.033$), mainly due to the higher frequencies of this haplogroup in the Archangelskaja and Nowgorodskaja groups. When these two groups are removed from the analysis, the remaining groups do not exhibit significant differences in the frequency of the N3-TAT haplogroup. There were no significant frequency differences among the Russian groups for any of the other Y-haplogroups.

Comparisons of the distribution of haplogroup R1a1-M17 across western Eurasia (see Figure 3) reveals that the highest frequencies of this haplogroup are in eastern Europe and the Volga-Ural region. A regression analysis indicates a significant correlation between the frequency of haplogroup R1a1-M17 and latitude ($R = 0.473$; $P < 0.001$) but not longitude ($R = 0.167$; $P = 0.206$). The same pattern holds when only the Russian groups are analyzed, with generally higher frequencies of this haplogroup in the southern part of western Russia (Table 1, Fig. 1). There is a highly significant boundary between western and eastern Europe in the frequency of this haplogroup (see Fig. 3).

The haplogroup N3-TAT is largely confined in this part of Eurasia to eastern and northern Europe and the Volga-Ural region. A regression analysis showed a significant correlation between the frequency of haplogroup N3-TAT and latitude ($R = 0.630$; $P < 0.001$) but not longitude ($R = 0.269$; $P = 0.071$). However, there is a significant boundary separating the Volga-Ural groups from eastern Europe (see Fig. 4).

Haplogroup I-M170 is found in almost every group in western Eurasia, with the highest frequencies in the Balkans (see Fig. 5). The haplogroup frequency is significantly correlated with both latitude ($R = 0.336$; $P = 0.005$) and longitude ($R = 0.272$; $P = 0.023$). Significant genetic boundaries separate: groups from the Volga-Ural region from eastern European groups; the Balkans from eastern Europe; the Iberian peninsula from western Europe; and one Caucasian group (Darginians) from other Caucasian groups (see Fig. 5).

Comparison of the Russian groups with their geographic neighbors

All pairwise F_{st} comparisons between Russian groups showed quite low genetic distances between each other (Table 2). None of the corresponding P -values were statistically-significant after Bonferroni correction. A PC analysis based on the Y-SNP haplogroups shows closest affinities of Russian groups with groups from northern Europe and the Volga-Ural region, in accordance with their geographic location (see Fig. 6).

TABLE 1. Y-SNP haplogroup frequencies and haplogroup diversity (HD) in different groups from the European part of Russia

Population (oblast)	N	Haplogroups												HD
		DE (YAP)	C (RPS4Y)	F (M89)	K (M9)	P (M45)	R2 (M124)	R1 (M173)	R1a1 (M17)	N3 (TAT)	G (M201)	I (M170)	J2 (M172)	
Smolenskaja	43	0.023	0.023	0.023	0.023	0	0	0.023	0.558	0.163	0	0.093	0.070	0.66
Brianskaja	43	0	0	0.023	0	0	0	0.070	0.465	0.163	0	0.256	0.023	0.70
Ivanovskaja	40	0.050	0	0	0	0	0	0.025	0.450	0.225	0.050	0.200	0	0.72
Lipezkaja	47	0.064	0	0.021	0.021	0	0	0.043	0.511	0.106	0.021	0.213	0	0.69
Penzenskaja	81	0.025	0	0.012	0.025	0	0.012	0.049	0.519	0.099	0	0.210	0.049	0.68
Ryazanskaja	36	0.028	0.028	0	0.028	0	0	0.111	0.472	0.083	0	0.222	0.028	0.73
Orlovskaja	42	0.024	0	0	0.024	0	0	0.095	0.452	0.119	0.095	0.167	0.024	0.75
Tverskaja	43	0.047	0	0.023	0	0	0	0.070	0.558	0.093	0	0.209	0	0.64
Vologodskaja	40	0.075	0	0	0	0	0	0.050	0.375	0.150	0	0.275	0.075	0.77
Tambovskaja	48	0.021	0	0.021	0	0	0	0	0.563	0.063	0.021	0.313	0	0.59
Archangelskaja	42	0	0	0	0.024	0	0	0.048	0.310	0.286	0	0.310	0.024	0.74
Novgorodskaja	40	0	0	0	0.050	0	0	0.050	0.375	0.275	0.050	0.150	0.050	0.77

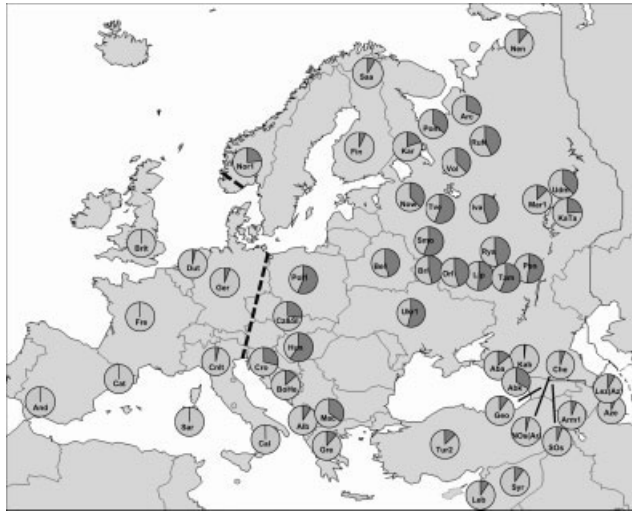


Fig. 3. Distribution of the haplogroup R1a1-M17 in western Eurasia. Dash lines indicate significant boundaries as found by analysis with Wombsoft. Abbreviations of the group names are as follows: Aba–Abazinian, Abk–Abkhazian, Alb–Albanian, And–Andalusian, Arc–Archangelskaja oblast, Arm–Armenian, Aze–Azerbaijani, Bel–Belarussian, BoHe–Bosnia-Herzegovina, Bri–Brianskaja oblast, Brit–British, Cal–Calabrian, Cat–Catalan, Che–Chechenian, CnIt–Central-Northern Italian, Cro–Croatian, Cz&Sl–Czech & Slovakian, Dut–Dutch, Fin–Finnish, Fre–French, Geo–Georgian, Ger–German, Gre–Greek, Hun–Hungarian, Iva–Ivanovskaja oblast, Kab–Kabardinian, Kar–Karelian, KaTa–Kazan Tatars, Leb–Lebanese, Lez(Az)–Lezgi (Azerbaijan), Lip–Lipenskaja oblast, Mac–Macedonian, Mar–Mari, Nen–Nenets, Nor–Norwegian, NOs(Ar)–North-Ossetian (Ardon), Now–Nowgorodskaja oblast, Orl–Orlovskaja oblast, Pen–Penzenskaja oblast, Pol–Polish, Pom–Pomor, RuN–North Russian, Rya–Ryazanskaja oblast, Saa–Saami, Sar–Sardinian, Smo–Smolenskaja oblast, Sos–South Ossetian, Syr–Syrian, Tam–Tambovskaja oblast, Tur–Turks, Tve–Tverskaja oblast, Udm–Udmurt, Ukr–Ukrainian, Vol–Vologodskaja oblast; Data from the present study and (Semino et al., 2000; Raitio et al., 2001; Wells et al., 2001; Passarino et al., 2002; Nasidze et al., 2003, 2004; Kharkov et al., 2005; Lappalainen et al., 2006). For clarity not all groups are depicted in the figure, although data from all groups were included in the boundary analysis.

Effects of geography and linguistics on genetic structure

The influence of geographic and linguistic variation on the genetic structure of western Eurasian populations, as assessed by Y chromosome variation, was investigated by the AMOVA procedure. Populations were grouped into the following six geographic localities: northern, eastern, and western Europe; the Volga-Ural region; the Near East; and the Caucasus. Populations were also grouped according to linguistic classification (Indo-European, Uralic, Turkic, North Caucasian, South Caucasian, and Afro-Asiatic) (Ethnologue, 2000). The geographic classification gave a better fit to the genetic data than the linguistic classification (Table 3), in that the among-groups variance (11.98%) was larger than the among-populations-within-groups variance (6.37%). Moreover, the correlation between the genetic and geographic distances between groups from the European part of Russia was significantly positive (Mantel test; $Z = 0.498$; $P < 0.001$).

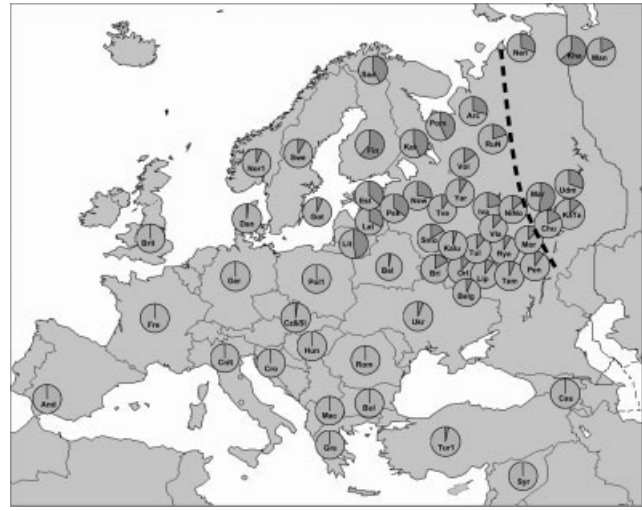


Fig. 4. Distribution of haplogroup N3-TAT in western Eurasia. Dash lines indicate significant boundaries as found by analysis with Wombsoft. Abbreviations of the group names are as in Figure 3, with the following additional groups: Belg–Belgorod oblast, Bul–Bulgarian, Cau–Caucasian, Chu–Chuvash, Dan–Danes, Est–Estonian, Got–Gotlander, Kalu–Kaluga oblast, Kha–Khanty (Ob-Ugrians), Lat–Latvian, Lit–Lithuanian, Man–Mansi (Ob-Ugrians), Mor–Mordvins, NiNo–Nizhniy Novgorod oblast, Psk–Pskov oblast, Rom–Romanian, Swe–Swedes, Tul–Tula oblast, Vla–Vladimir oblast, Yar–Yaroslavl oblast. As for the Figure 3 and (Lahermo et al., 1996; Rosser et al., 2000; Malyarchuk et al., 2004). For clarity not all groups are depicted in the figure, although data from all groups were included in the boundary analysis.

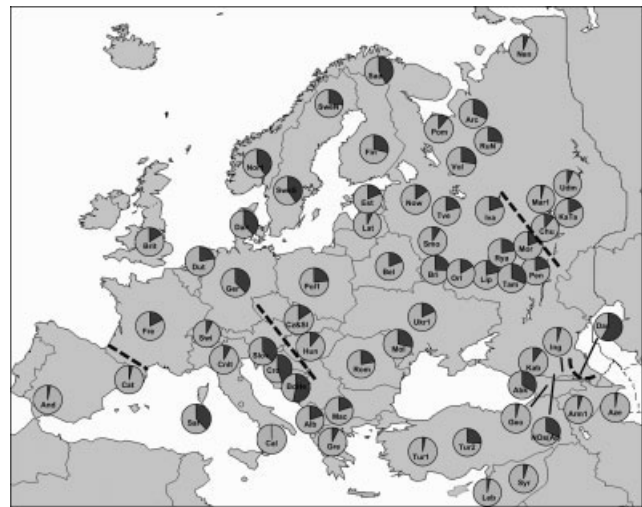


Fig. 5. Distribution of haplogroup I-M170 in western Eurasia. Dash lines indicate significant boundaries as found by analysis with Wombsoft. For abbreviations of the group names see Figures 3 and 4; additional groups are: Dar–Darginian, Ing–Ingushian, Mol–Moldavians, SweN/SweS–Swedes North/South, Swi–Swiss. Data from the present study and (Semino et al., 2000; Wells et al., 2001; Passarino et al., 2002; Nasidze et al., 2003, 2004; Rootsi et al., 2004; Marjanovic et al., 2005; Lappalainen et al., 2006). For clarity not all groups are depicted in the figure, although data from all groups were included in the boundary analysis.

TABLE 2. Pairwise F_{st} values between Russian groups based on Y-SNP data

Population (oblast)	Smo	Bri	Iva	Lip	Pen	Rya	Orl	Tve	Vol	Tam	Arc
Smolenskaja											
Brianskaja	0.007										
Ivanovskaja	0.003	0									
Lipezkaja	0	0	0								
Penzenskaja	0	0	0.001	0							
Ryazanskaja	0.004	0	0	0	0						
Orlovskaja	0.002	0	0	0	0	0					
Tverskaja	0	0	0.001	0	0	0	0				
Vologodskaja	0.026	0	0	0	0.004	0	0	0.010			
Tambovskaja	0.029	0	0.019	0	0	0.001	0.017	0	0.019		
Archangelskaja	0.064	0.007	0.004	0.037	0.044	0.028	0.029	0.055	0	0.063	
Nowgorodskaja	0.014	0.002	0	0.017	0.023	0.014	0	0.032	0.003	0.059	0

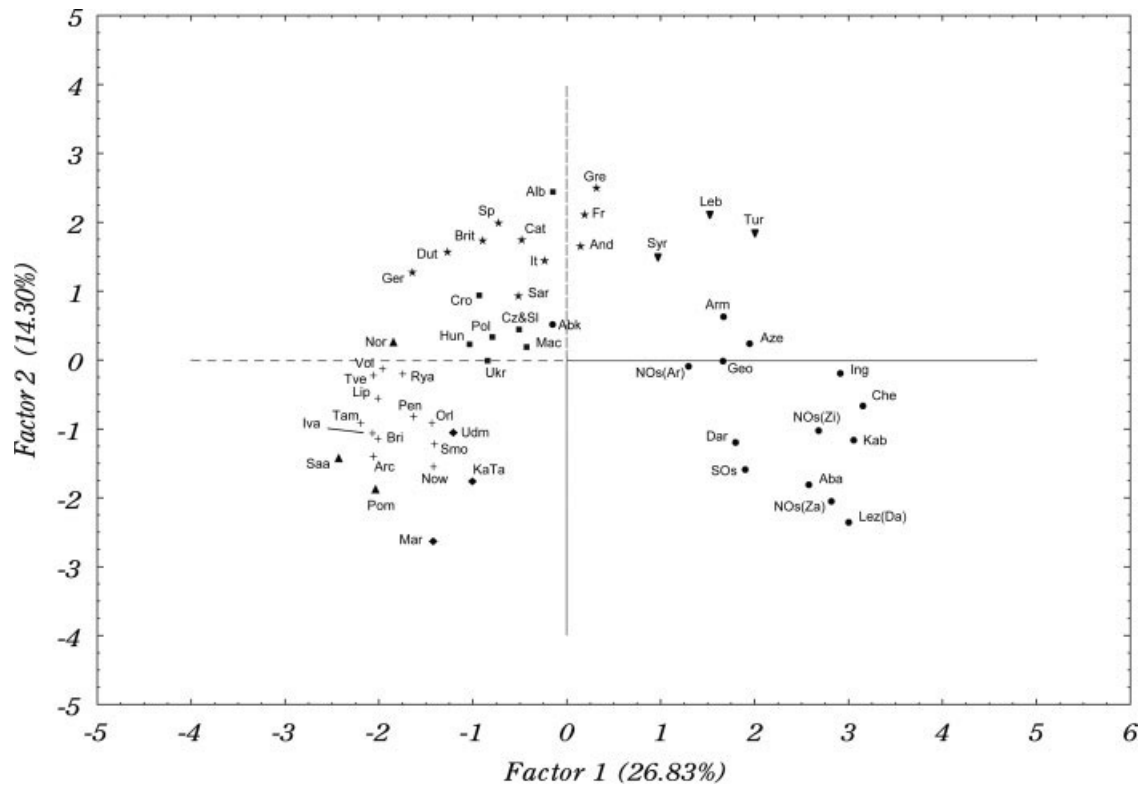


Fig. 6. PC analysis plot for western Eurasian groups, based on Y-haplogroups. Sign assignment is as follows: crosses—Russia, squares—east Europe, circles—Caucasus, stars—west Europe, triangles—north Europe, flipped triangles—Near East, diamonds—Volga-Ural. For abbreviations of the group names see Figures 3–5 with additional groups: **Lez(Da)**—Lezgi (Dagestan), **NOs(Za)**—North-Ossetian (Zamankul), **NOs(Zi)**—North-Ossetian (Zil’ga).

TABLE 3. AMOVA results according to different classifications

Classification	Among groups	Among populations within groups	Within populations
Geography	11.98	6.37	81.65
Linguistics	4.63	13.24	82.13

Geography—western, northern and eastern Europe, Volga-Ural, Caucasus, Near East. Linguistics—Indo-European, Uralic, Turkic, North and South Caucasian, Afro-Asiatic.

DISCUSSION

Previous analyses of Y chromosome variation in Europe revealed striking geographic differences in the

distribution of Y-SNP haplogroups. Namely, the western European Y chromosome gene pool is mainly marked by the haplogroup R1-M173, along with haplogroup I-M170, whereas the haplogroup R1a1-M17 is predominantly found in eastern Europe. A high frequency of haplogroup N3-TAT is common in the Volga-Ural region. Northern Europe is split into two parts: the western part shows the western European pattern, while the eastern part shows the haplogroup distribution typical for eastern Europe and the Volga-Ural region (Semino et al., 2000). For the Caucasus, in contrast, a different Y-SNP haplogroup pattern is found, in which haplogroups G-M201 and F-M89 are predominant (Semino et al., 2000; Nasidze et al., 2004).

The present study shows that the Russian Y chromosome gene pool conforms to the above pattern, with the

exception of generally low frequencies for haplogroup R1-M173 (Table 1). In particular, 74–94% of Russian Y chromosomes belong to haplogroups R1a1-M17, N3-TAT, or I-M170. Overall, the Russian Y-chromosome variation is most similar to that of groups from eastern Europe and the Volga-Ural region, as evidenced in the frequency diagrams (Figures 3–5) and the PC analysis (see Fig. 6).

There is some influence of geography on the patterning of the Y chromosome landscape in west Europe (Rosser et al., 2000). This is also evidenced in the AMOVA analyses on the larger geographic scale, which show a greater influence of geography rather than language family on Y-chromosome variation (Table 3), the significant correlation between genetic distance and geographic distance in the Mantel test, and by the significant correlations between the frequency of the three predominant Y-SNP haplogroups [R1a1-M17, N3-TAT, and I-M170] and the geographic location of the west Eurasian groups analyzed. Interestingly, the correlation is significant for latitude with all three Y-haplogroups, but is only significant for longitude with one haplogroup, I-M170, and even for this haplogroup the correlation is stronger with latitude than with longitude. The significant correlations with latitude would suggest that north-south movements, rather than east-west movements, have played the more important role in producing the present Y-chromosome landscape in western Eurasia. This is unexpected, given that east-west migrations have been assumed to be of central importance in Eurasia (such as the spread of farmers and farming from the Near East), and indeed have been presumed to be responsible for the ascendancy of west Eurasian culture (Jared Diamond, *Guns, Germs and Steel*). Of course, there is no inherent temporal information in any of the analyses in this study regarding the timing of the population movement(s) that contributed to the present-day west Eurasian Y chromosome landscape, so we do not know when these migration(s) may have occurred.

However, despite the overall strong correlations between geography and the Y-chromosome landscape in west Eurasia, there are also some significant boundaries in the distribution of particular Y-SNP haplogroups, suggesting barriers to migration. One of these occurs in the Caucasus, which is not surprising given that it is already known that there are significant fluctuations in the mtDNA and Y-chromosome composition of groups inhabiting this mountainous region (Nasidze et al., 2003, 2004). Another significant boundary was identified between western and eastern Europe for R1a1-M17; this boundary was previously analyzed in detail (Kayser et al., 2005), and it was shown that genetic differentiation was mainly, but not exclusively, due to the frequency distribution of two Y-SNP haplogroups and their associated Y-STR haplotypes: R1a1-M17, most frequent in Poland, and R1-M173, most frequent in Germany. This pattern was explained by the recent historical events in Europe, namely the forced human resettlement of many millions of Germans and Poles during and, especially, shortly after World War II (Kayser et al., 2005). Moreover, it was shown recently that the Polish population was homogeneous also before World War II (Wozniak et al., 2007).

The distribution of haplogroup N3-TAT probably reflects more ancient demographic events. The N3-TAT haplogroup probably arose in the area of present day China and expanded via a series of bottlenecks into Siberia, with secondary expansion into east Europe (Rootsi et al., 2007). We identified a significant boundary separating eastern

Europe from the Volga-Ural region, in keeping with the hypothesis that there was a primary expansion of this haplogroup into Siberia, followed by a secondary expansion into eastern Europe (Rootsi et al., 2007).

Haplogroup I-M170 is the only major clade of the Y chromosome phylogeny which is widespread over Europe and almost absent elsewhere (Rootsi et al., 2004). The frequency of haplogroup I-M170 is highest in groups from Scandinavia and northwest of the Balkans, and accounts for more than one-third of the Y chromosomes in these regions. We find several boundaries in the distribution of haplogroup I-M170 (see Fig. 5), more than for the other haplogroups analyzed. One of these, between eastern Europe and the Volga-Ural region, overlaps with a significant boundary in the distribution of haplogroup N3-TAT, further confirming the distinction of the Volga-Ural region from the rest of Europe.

In conclusion, this analysis of Y-haplogroups from the European part of Russia adds considerably to our knowledge of the Y-chromosome landscape across western Eurasia. Overall, all of the major haplogroups show significant correlations between latitude and/or longitude and haplogroup frequency, emphasizing a major role for migrations and isolation by distance. However, at the same time there are significant boundaries in the distribution of all of the major haplogroups (in particular, between eastern Europe and the Volga-Ural region), indicating that isolation has also played an important role in determining the Y-chromosome landscape of western Eurasia. It should of course be kept in mind that the Y chromosome is a single locus and therefore it has certain limitations in detecting evolutionary forces shaping the demographic history of human populations. Analyses using multilocus genetic markers are needed to determine if the patterns observed in this study are a general phenomenon of the European genetic landscape, or instead reflect peculiarities in the history of the Y chromosome in Europe.

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