

# From East to West: Patterns of Genetic Diversity of Populations Living in Four Eurasian Regions

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## Key Words

Polymorphisms · Alu insertion · Population genetics

## Abstract

We have analyzed the distribution and patterns of the genetic diversity of eight Alu loci (ACE, ApoA1, PV92, TPA25, NBC27, NBC102, NBC148, and NBC182) in 1,049 individuals representing 16 populations of the Volga-Ural region (Bashkirs, Tatars, Komis, Maris, Mordvins, and Udmurts), Central Asia (Kazakhs, Uzbeks, and Uighurs), the North Caucasus (Karachays, Kumyks, Kuban Nogays, and Karanogays), and Central South Siberia (Yakuts, Kalmyks and Evenks). Geographic divide between Europe and Asia, e.g. the Ural Mountains and the Caspian Sea, can also be considered as a genetic boundary. The data indicates that the populations of the two boundary regions between Europe and Asia, the Volga-Ural region of Russia, and populations of the North Caucasus are more similar to European than to Asian populations. Finally, Siberian and Central Asian populations are genetically closely related to each other.

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## Introduction

The evolution and genetic relationships of modern human populations continues to be a matter of controversy, in spite of numerous studies utilizing a variety of polymorphic loci, e.g. mtDNA, Y-chromosome, and autosomal markers [1–6].

Most populations inhabiting countries of the former Soviet Union are poorly studied in terms of their genetic relationships. The Eurasian steppe belt has witnessed demographic movements of great influence on the current genetic composition of the human population in Europe, Near East, Southern, and Eastern Asia.

Here we report our results on the genetic diversity and relationships of populations from the Volga-Ural region, the North Caucasus, Central Asia, and Central South Siberia.

These geographically and ethnically diverse regions were chosen for their complex population history within this continent. The Volga-Ural region is located at the border between Europe and Asia and has been the arena of permanent genetic exchanges among Siberian, European, Central Asian and other populations. Consequently, the indigenous populations of the Volga-Ural region

are anthropologically, ethnically, historically and culturally heterogeneous. The North Caucasus, situated on the border between Europe, West Asia, and the Near East is characterized by an extremely high linguistic and ethnic diversity. The Caucasus Mountains, a major geographic barrier, separate the Northern and Southern sub-regions of the Caucasus. The Caucasus is therefore an interesting region to examine the relative influence of linguistic diversity and geographic barriers on the genetic structure of its inhabitants. The ethnic and anthropological structure of modern populations of Central Asia (Uzbeks, Kazakhs, Uighurs) is heterogeneous. Turkic and Iranian ethnic components participated to different extents to the ethnic history of Central Asian populations. One of the most Northern populations of Siberia are the Yakuts. Presumably, the main contributors to the ethnogenesis of the Yakuts were Tungusian tribes and Paleoasiatic inhabitants of Yakutia.

Recent work revealed specific genetic patterns of inhabitants of different regions of the world [1, 7–12]. Despite of huge datasets for different populations of the world, little is known for inhabitants of large regions of Russia.

## Materials and Methods

A total of 1,049 individuals from the Volga-Ural region of Russia, Central Asia, the North Caucasus, and Central South Siberia were analyzed. Those unrelated to any other subject enrolled in this study by at least three generations were eligible to participate. The Volga-Ural region samples comprised Turkic-speaking Bashkirs (34), Tatars (76), and Uralic-speaking Komis (70), Maris (49), Mordvins (37), and Udmurts (70). The Central Asia dataset comprised Turkic-speaking Kazakhs (83), Uzbeks (72), and Uighurs (63). Populations of the North Caucasus were Altaic-speaking Karachays (81), Kumyks (60), and two ethnogeographic groups of Nogays – Kuban Nogays (63), and Karanogays (75). Yakuts (85) and Evenks (41) inhabit Central South Siberia.

Although Kalmyks (90) live in the Kalmyk Republic situated at the North of the North Caucasian Dagestan Republic of Russia, we also included Kalmyks into the Siberia dataset. They migrated from Mongolia approximately three centuries ago and preserved cultural and anthropological features of their ancestors [13–14].

DNA samples were isolated from peripheral blood lymphocytes using phenol-chloroform extraction [15].

PCR amplification of each Alu insertion polymorphism was performed in a 20- $\mu$ l reaction volume containing up to 100 ng of target DNA, 50 pM of each oligonucleotide primer, 200  $\mu$ M dNTPs in 50 mM KCl, 2.0 mM MgCl<sub>2</sub>, 10 mM Tris-HCl (pH 8.4), and 1 unit Taq DNA polymerase. Each sample was subjected to the following amplification cycle, an initial denaturation for 4 min at 94°C, 1 min denaturation at 94°C, 1 min at the annealing temperature, 2 min extension at 72°C, repeated for 30–34 cycles, followed by a final extension at 72°C for 10 min. Twenty microliters of each sam-

ple were separated by electrophoresis on a 7% polyacrilamide gel followed by ethidium bromide staining. PCR products were visualized using UV fluorescence. The sequences of the oligonucleotide primers, the sizes of the respective PCR products and their chromosomal location have been reported previously [8, 16–19].

### Data Analysis

Allele frequencies were calculated by direct counting. The unbiased estimator of heterozygosity was used to calculate the heterozygosity according to Nei's (1987) equation [20]. A principal component analysis and the Kruskal-Wallis test was implemented into the Statistica 6.0 package [21].

The Hardy-Weinberg equilibrium was evaluated by an exact test [22].

A spatial autocorrelation analysis was performed using the Passage software version 1.1 [23].

## Results

### Within Population Differentiation

1,049 individuals from 16 Eurasian populations were typed for each of 8 Alu insertion polymorphisms. Frequencies of the 8 Alu insertion polymorphisms found in the sixteen populations are shown in table 1. All loci are biallelic, thus only the frequency of the presence of the Alu insertion is shown. All loci were polymorphic in all populations. A total of 128 tests for Hardy-Weinberg equilibrium were performed. Thirteen results indicated significant deviations from the equilibrium ( $p < 0.05$ ); the loci concerned are ACE in the Karanogay population, Tatars, Uzbeks and Mordvins, ApoA1 in Bashkirs populations and Yakuts, PV92 in Uighur and Mari populations, TPA25 in Bashkirs and Kalmyks, NBC27 in Komis, as well as NBC148 in Uighurs and Evenks. Since these deviations do not cluster in specific loci or populations, they most likely represent the random statistical fluctuation.

The heterozygosity for each population (table 2) averaged across the 8 Alu loci was substantial ranging from 0.364 in Mordvins to 0.475 in Uighurs (table 1). The lowest average value was observed in the Volga-Ural region (0.399), the highest in Central Asia (0.452). The latter value is the highest observed for any other region of the world (table 3).

The heterozygosity for each marker averaged across all populations examined varied from 0.229 for ApoA1 to 0.483 for NBC102. The lowest average heterozygosity was observed in the Volga-Ural region (0.399), the highest in Central Asian populations (0.452). The level of differences within populations does not differ significantly between these four regions when analyzed by the Kruskal-Wallis test ( $H = 5.994822$ ,  $p = 0.1119$ ).

**Table 1.** Alu insertion frequencies in investigated populations

Population	2N	ACE	ApoA1	PV92	TPA25	NBC27	NBC102	NBC148	NBC182
Volga-Ural region									
Bashkirs	68	0.515	0.794	0.294	0.426	0.294	0.647	0.235	0.529
Tatars	152	0.395	0.914	0.204	0.507	0.204	0.414	0.263	0.651
Komis	140	0.607	0.914	0.193	0.429	0.407	0.571	0.264	0.736
Maris	98	0.306	0.857	0.235	0.184	0.163	0.367	0.286	0.449
Mordvins	74	0.703	0.892	0.189	0.351	0.230	0.351	0.135	0.649
Udmurts	140	0.536	0.843	0.264	0.486	0.443	0.557	0.279	0.807
Average		0.510	0.869	0.230	0.397	0.290	0.485	0.244	0.637
Central Asia									
Kazakhs	166	0.554	0.801	0.488	0.464	0.307	0.560	0.283	0.500
Uighurs	126	0.579	0.706	0.516	0.492	0.206	0.556	0.389	0.579
Uzbeks	144	0.542	0.903	0.514	0.465	0.257	0.604	0.229	0.472
Average		0.558	0.803	0.506	0.474	0.257	0.573	0.300	0.517
Central South Siberia									
Kalmyks	90	0.606	0.839	0.656	0.550	0.150	0.667	0.372	0.483
Yakuts	85	0.565	0.847	0.724	0.453	0.171	0.571	0.318	0.494
Evenks	41	0.695	0.890	0.537	0.476	0.232	0.646	0.366	0.415
Average		0.622	0.859	0.639	0.493	0.184	0.628	0.352	0.464
North Caucasus									
Karachays	162	0.525	0.963	0.259	0.370	0.420	0.556	0.204	0.506
Kumyks	120	0.383	0.908	0.242	0.325	0.217	0.442	0.242	0.550
Kuban Nogays	126	0.444	0.921	0.349	0.508	0.389	0.389	0.278	0.603
Karanogays	150	0.467	0.893	0.527	0.480	0.260	0.473	0.293	0.493
Average		0.455	0.921	0.344	0.421	0.321	0.465	0.254	0.538
Average		0.526	0.868	0.387	0.435	0.272	0.523	0.277	0.557

N = Number of individuals.

### *Among Population Differentiation*

A test of homogeneity of allele frequencies across populations indicated substantial heterogeneity among populations studied ( $\chi^2 = \text{infinity}$ , d.f. = 20,  $p < 0.0001$ ). Next we calculated the  $G_{ST}$  value for each locus (table 2). The  $G_{ST}$  value expresses the fraction of the total variance due to differences among populations. The  $G_{ST}$  values were substantial and ranged from 0.011 for the NBC148 locus to 0.116 for PV92. The average  $G_{ST}$  value of the whole dataset was 0.043.

To assess the relationships among our populations we compared our data with published information of European and Asian populations [11] on the variation of the same eight Alu loci (ACE, ApoA1, PV92, TPA25, NBC27, NBC102, NBC148, and NBC182) included in this study.

The genetic differentiation in various regions of the world was fairly substantial (table 3). Based on informa-

tion of the 8 Alu loci, the  $G_{ST}$  value for the world dataset was 0.089. The highest level of genetic differentiation was observed in East and Southeast Asia with 0.083 very close to the overall world value. The lowest  $G_{ST}$  value was found in Central South Siberia (0.001).

The low  $G_{ST}$  value for Siberia is evidence of close genetic relationships of Kalmyks, Evenks and Yakuts. Historical records, ethnographical observations, and our unpublished data on mtDNA and the Y chromosome confirm this close relationship of the Siberian populations.

Interestingly, the level of population differentiation in the Caucasus (0.014) reported here is much lower than that published by Nasidze et al. [9]. Formally it is incorrect to directly compare various datasets of different Alu loci. Moreover, the present study includes only North Caucasus populations while Nasidze et al. [9] investigated North and South Caucasus populations.

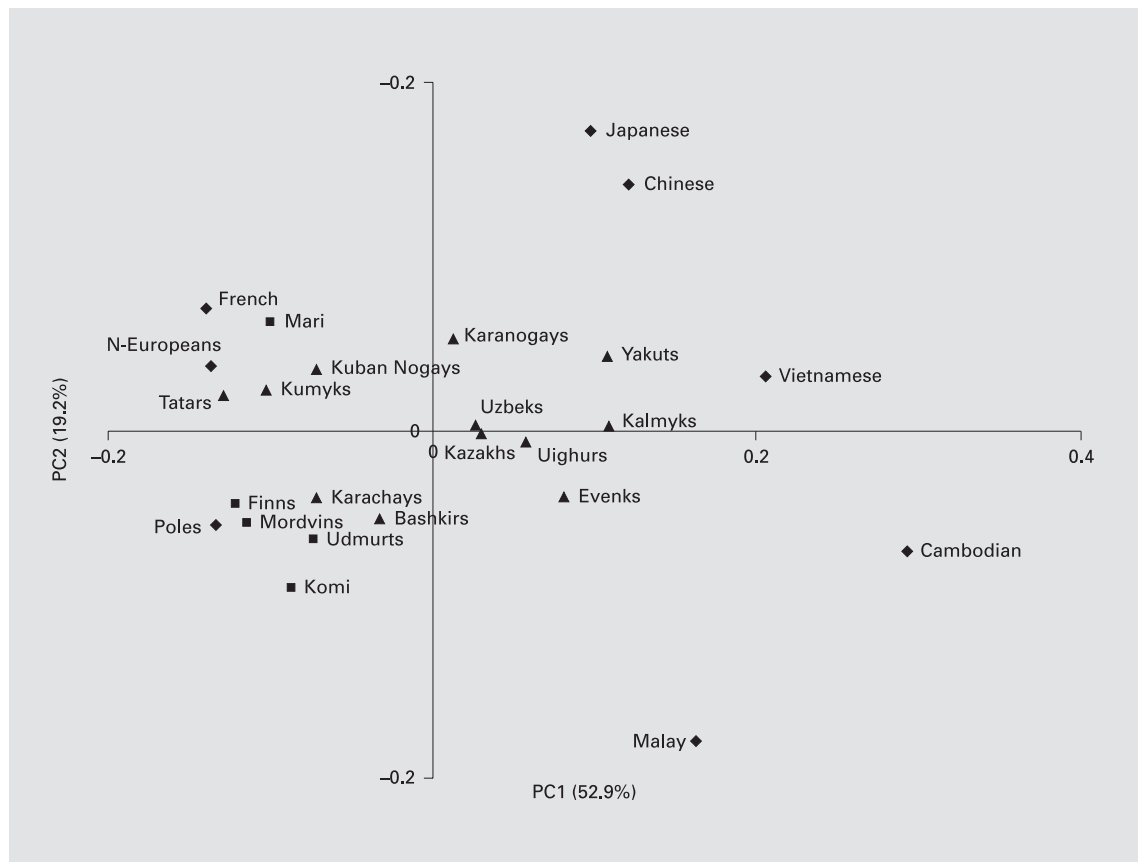
**Table 2.** Heterozygosity and  $G_{ST}$  values in investigated populations

Population	ACE	ApoA1	PV92	TPA25	NBC27	NBC102	NBC148	NBC182	Average
Volga-Ural region									
Bashkirs	0.507	0.332	0.421	0.496	0.421	0.464	0.365	0.506	0.439
Tatars	0.481	0.157	0.327	0.503	0.327	0.489	0.390	0.457	0.391
Komis	0.480	0.158	0.314	0.493	0.486	0.493	0.392	0.392	0.401
Maris	0.429	0.247	0.363	0.303	0.276	0.470	0.412	0.500	0.375
Mordvins	0.424	0.195	0.311	0.462	0.359	0.462	0.237	0.462	0.364
Udmurts	0.501	0.267	0.392	0.503	0.497	0.497	0.405	0.314	0.422
Average	0.470	0.226	0.355	0.460	0.394	0.479	0.367	0.438	0.399
Central Asia									
Kazakhs	0.497	0.320	0.503	0.500	0.428	0.496	0.408	0.503	0.457
Uighurs	0.491	0.418	0.503	0.504	0.330	0.498	0.479	0.491	0.464
Uzbeks	0.500	0.177	0.503	0.501	0.385	0.482	0.356	0.502	0.426
Average	0.496	0.305	0.503	0.502	0.381	0.492	0.414	0.499	0.452
Central South Siberia									
Kalmyks	0.480	0.272	0.454	0.498	0.256	0.447	0.470	0.502	0.422
Yakuts	0.495	0.261	0.402	0.499	0.285	0.493	0.436	0.503	0.422
Evenks	0.429	0.198	0.503	0.505	0.360	0.463	0.470	0.491	0.427
Average	0.468	0.243	0.453	0.500	0.301	0.468	0.459	0.499	0.424
North Caucasus									
Karachays	0.502	0.072	0.386	0.469	0.490	0.497	0.326	0.503	0.406
Kumyks	0.477	0.168	0.370	0.442	0.342	0.497	0.370	0.499	0.396
Kuban Nogays	0.498	0.147	0.458	0.504	0.479	0.479	0.404	0.483	0.432
Karanogays	0.501	0.192	0.502	0.503	0.387	0.502	0.417	0.503	0.438
Average	0.494	0.145	0.429	0.480	0.425	0.494	0.379	0.497	0.418
Hs	0.481	0.224	0.420	0.480	0.382	0.483	0.396	0.476	0.418
Ht	0.499	0.229	0.474	0.492	0.396	0.499	0.401	0.493	0.435
$G_{ST}$	0.036	0.024	0.116	0.023	0.035	0.032	0.011	0.036	0.041

**Table 3.** Genetic differentiation of investigated populations

Region	Populations	N	$H_S$	$H_T$	$G_{ST}$	$D_{ST}$
Volga-Ural region	6	336	0.399	0.413	0.034	0.014
North Caucasus	4	279	0.418	0.424	0.014	0.006
Western, Central and Northern Europe <sup>1</sup>	4	236	0.373	0.379	0.016	0.006
All Europe	14	851	0.397	0.411	0.034	0.014
Central Asia	3	218	0.449	0.450	0.002	0.001
Central South Siberia	3	216	0.424	0.424	0.001	0.001
East and Southeast Asia <sup>1</sup>	5	122	0.389	0.424	0.083	0.035
South Asia (India) <sup>1</sup>	12	730	0.430	0.442	0.028	0.012
All Asia	23	1,286	0.423	0.448	0.056	0.025
Africa <sup>1</sup>	10	310	0.372	0.388	0.041	0.016
World	44	2,447	0.404	0.444	0.089	0.039

<sup>1</sup> Data of Watkins et al., 2003 [11].



**Fig. 1.** Principal component analysis of investigated populations. Altaic speakers are shown as triangles; Uralic speakers are shown as squares.

Within Europe the highest level of among population differentiation is observed in the Volga-Ural region of Russia. This region is inhabited by Turkic-speaking Bashkirs, Chuvashis, Tatars, and Uralic-speaking Komis, Maris, Mordvins, and Udmurts. These populations are very diverse in culture, language, and tradition including religion [24]. Previous genetic analyses based on nuclear markers and mtDNA also revealed higher genetic diversity among populations of the Volga-Ural region when compared to Western and Central European populations [3, 25, 26].

#### *Principal Component Analysis*

To assess the population relationships further, we carried out a principal component analysis (fig. 1). The first two principal components account for 72.1% of the observed variance.

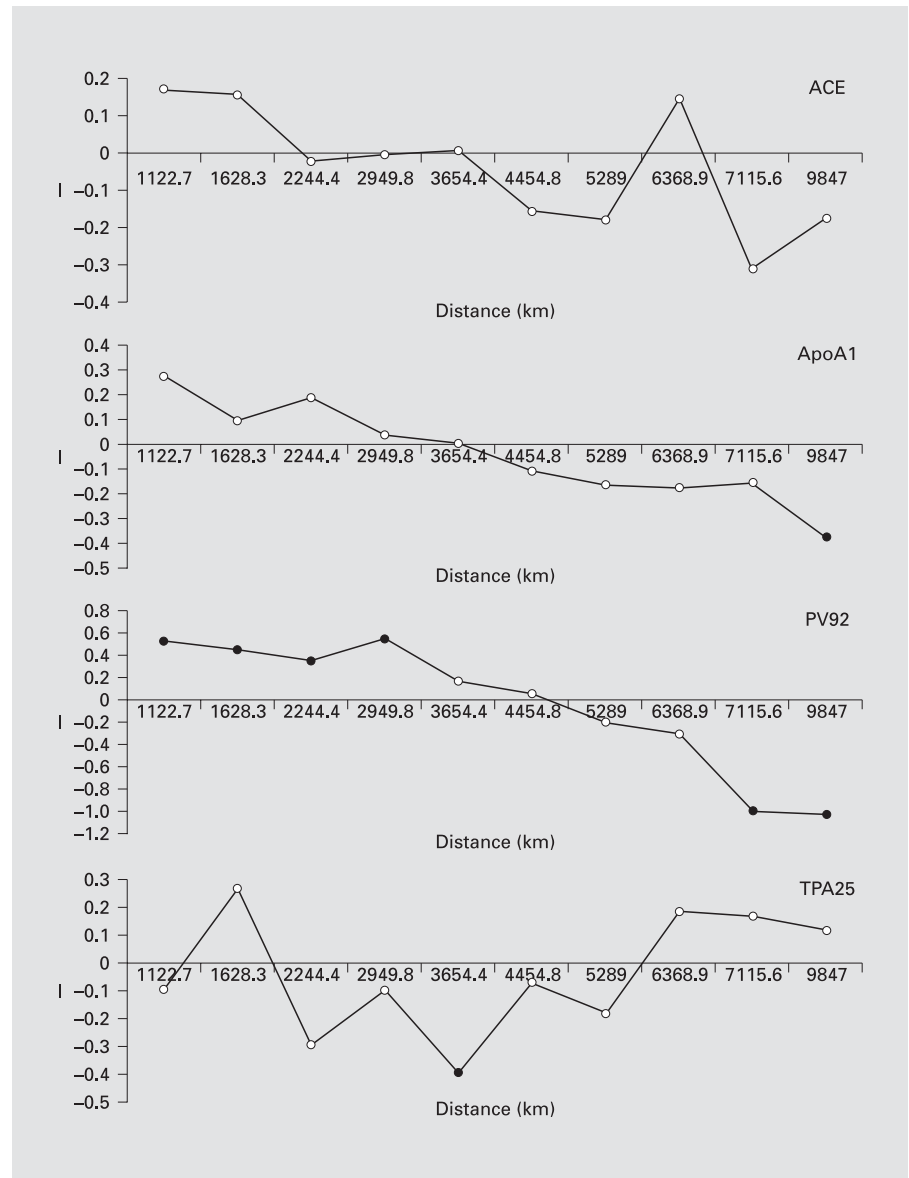
The first principal component accounts for 52.9% of the allele frequency variation and separates Asian and

European populations. European populations do not form distinct clusters according to their geographic or linguistic affiliation. Likewise, populations of our study belonging to the same linguistic family and group like Kumyks, Karachays, Tatars, Nogays, Bashkirs, Uzbeks, Kazakhs, Uighurs, Evenks, and Yakuts belonging to Altaic family or Mari, Udmurts, Komi, Finns, and Mordvins, belonging to Uralic family and Finno-Ugric group are scattered among each other on the PC plot.

All of the Volga-Ural populations are plotted close to the European populations. Populations of Central Asia and Central South Siberia form a distinct cluster together with Karanogays separate from populations of East and Southeast Asia.

#### *Spatial Autocorrelation Analysis*

We analyzed the geographic variation patterns of the 8 allele frequencies by a spatial autocorrelation method. Spatial autocorrelation is the dependence of the values of



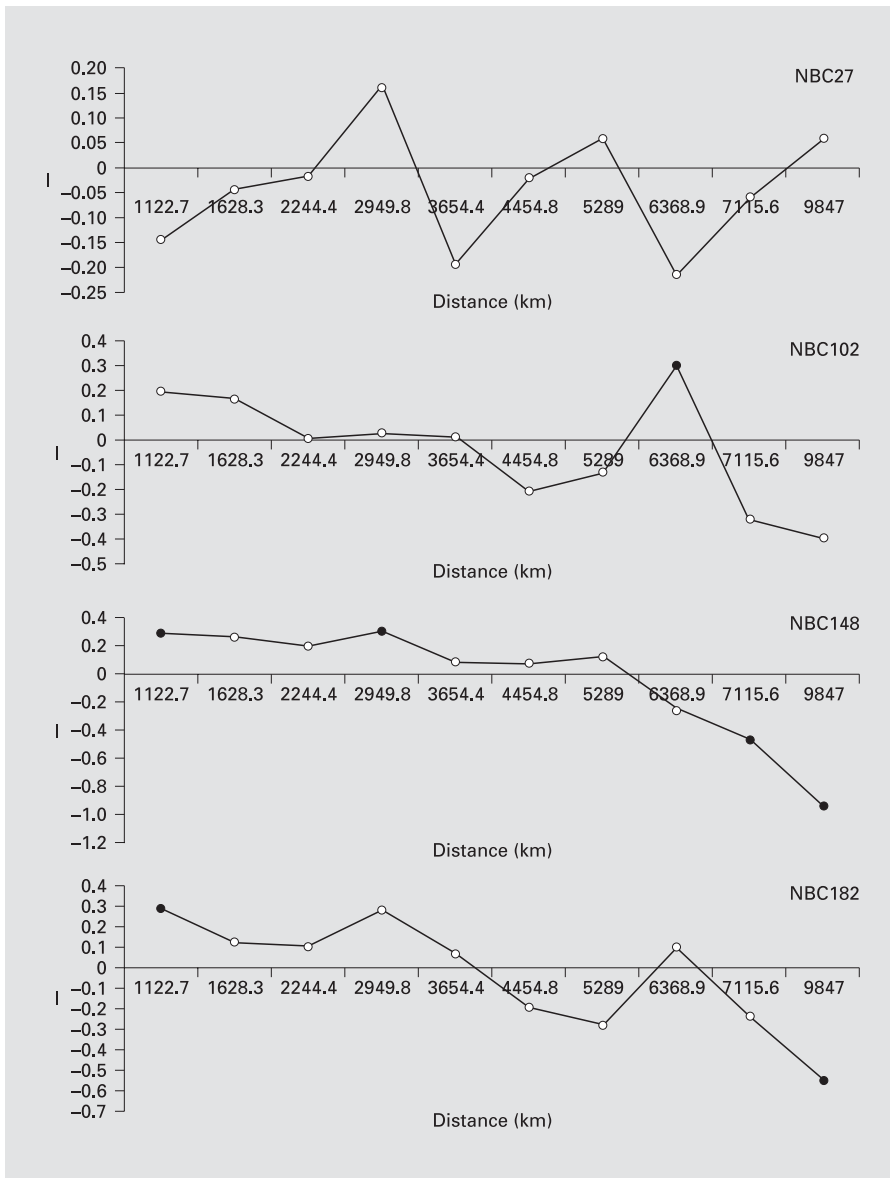
**Fig. 2.** Geographic patterns of genetic variation, described by spatial correlograms. x axis: distance between localities (kilometres); y axis: Morans' I. Filled circles indicate significant I values.

a variable on values of the same variable at specified physical distances. Figure 2 demonstrates the results of this analysis for each of the 8 Alu loci. Three of 8 correlograms were significant (PV92, NBC148, NBC182) at  $p < 0.05$ .

Frequency of PV92 decreases from East to West. It is highest in Cambodians (1.000) (0.851 overall in East Asia), and lowest in Poles (0.111) (0.232 overall in Europe) [11]. NBC148 demonstrates the same genetic pattern. Its frequency is changed from 0.611 in Vietnamese (0.426 overall in East Asia) to 0.150 in French (0.199 overall in Europe) [11]. The frequency of NBC182 is changed in the opposite direction decreasing eastwards

from 0.725 in Finns (0.650 overall in Europe) to 0.375 in Japanese (0.466 overall in East Asia).

Some loci show occasional autocorrelation peaks at intermediate distances, which may be the signatures of other less important demographic processes. However, the overall pattern of variation of the 3 of 8 markers considered is clinal, with populations at the outermost of the geographical range (Europe and East Asia) showing the highest DNA divergence and intermediate samples showing intermediate characteristics with gradual changes of allele frequencies (Caucasus, Volga-Ural region, Central Asia and Siberia).



On the whole, allele frequency gradients spanning through Eurasia are evident and supported by patterns of genetic changes of PV92 and NBC148, and NBC182 to a lesser extent. Probably the 3 loci reflect the same and most likely simultaneous demographic events.

They are the main genetic consequences to be expected of a directional population expansion and migration. The pattern observed can be related to a directional gene flow and historical migrations through Eurasia. It can be suggested that these demographic processes are related to expansion and mass migration of numerous nomadic steppe tribes alongside the Eurasian steppe belt. Taking

into account some historical facts it's more likely that gene flow from East to West was in a greater extent than from West to East.

### Discussion

The most intriguing is the relatively low interpopulation differentiation of Central Asia populations. During many centuries Central Asia was a transit corridor for numerous population migrations and trading routes [27, 28]. Despite of Central Asia's cultural, religious, and lin-

guistic similarities, these populations were formed from different nomadic tribes united relatively recently into distinct nationalities [28].

In this context the surprising fact is the very low level of interpopulation differentiation of the Siberian populations. The fact that Kalmyks inhabiting the Lower Volga in the Caspian Steppe are genetically closely related to Yakuts and Evenks supports the hypothesis of their recent descent from Mongols. It is also evidence for the absence of mixture of Kalmyks with local populations since settling in this region.

Populations of Central Asia are genetically much closer to Siberian populations than to Volga-Ural or Caucasus populations despite of geographical distances between these populations. When the Central Asian and Siberian populations are treated as one dataset the  $G_{ST}$  value calculated for these two regions is 0.007 indicating the close genetic relationships supported by historical and demographical history of these two regions. Genetically, the Central Asian and Siberian populations can be considered as one community scattered over a huge geographic area.

Nogays (Kuban Nogays and Karanogays) which are remains of the Nogay Horde demonstrate a quite interesting genetic pattern. Despite of their recent common origin [29], Kuban Nogays are genetically and anthropologically [30] closer related to European and other Caucasus populations than Karanogays. Karanogays inhabiting the Nogay Steppe of Dagestan are genetically still closer to Central Asia populations. Obviously, the Karanogays are geographically isolated from other Caucasus populations and keep their original gene pool. Since their recent settling in Dagestan there is only a low level of admixture with the autochthonous Caucasus population.

The Volga-Ural populations demonstrate the highest level of interpopulation diversity among the regions analyzed. This is also supported by the high cultural and linguistic diversity of these populations. Some subpopulations of Bashkirs even have a distinct origin [24]. At the same time this region was the area of comings and goings of numerous different tribes during many centuries. Some tribes settled in this region relatively recently [24]. The current pattern of genetic diversity of Volga-Ural populations is formed by linguistic, cultural and religious differences developing which over time lead to less admixture and consequently more genetic divergence.

The close genetic relationship of Caucasus and European populations has been shown earlier [9], so the observed pattern on the PC plot was quite expected. On the other hand the genetic markers used could have a low

power of resolution unable to discriminate between European and Caucasus populations. In this context, two questions arise. (i) Was the gene pool of the Caucasus population intact after the beginning of the Neolithic expansion or was it influenced by a gene flow from the Near East? (ii) Has the gene pool of the Caucasus been influenced by Neolithic farmers to the same extent as the European populations? If this would indeed be the case, possibly Alu insertions as genetic markers cannot discriminate Europeans from Caucasus populations.

Thus, the geographic divide between Europe and Asia, e.g. the Ural Mountains and the Caspian Sea, can also be considered as a genetic boundary. None of the populations inhabiting Asia are genetically closely related to European populations and vice versa except for Karanogays population with a well-known history.

In conclusion, our analysis of 8 Alu insertion loci indicates that the populations of the two boundary regions between Europe and Asia, the Volga-Ural region of Russia, and populations of the North Caucasus are more similar to European than to Asian populations. Siberian and Central Asian populations are genetically closely related to each other. Finally the fact that populations of the 4 regions analyzed fit the genetic variation throughout Eurasia attests that they were involved in the same major demographic processes that took place within the continent no matter what genetic differences or similarities the populations demonstrate.

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## References

- 1 Batzer MA, Arcot SS, Phinney JW, Alegria-Hartman M, Kass DH, Milligan SM, Kimpton C, Gill P, Hochmeister M, Ioannou PA, Herrera RJ, Boudreau DA, Scheer WD, Keats BJ, Deininger PL, Stoneking M: Genetic variation of recent Alu insertions in human populations. *J Mol Evol* 1996;42:22–29.
- 2 Perez-Lezaun A, Calafell F, Mateu E, Comas D, Ruiz-Pacheco R, Bertranpetit J: Microsatellite variation and the differentiation of modern humans. *Hum Genet* 1997;99:1–7.
- 3 Richards M, Macaulay V, Hickey E, Vega E, Sykes B, Guida V, Rengo C, Sellitto D, Cruciani F, Kivisild T, Villems R, Thomas M, Rychkov S, Rychkov O, Rychkov Y, Golge M, Dimitrov D, Hill E, Bradley D, Romano V, Cali F, Vona G, Demaine A, Papiha S, Triantaphyllidis C, Stefanescu G: Tracing European founder lineages in the Near Eastern mtDNA pool. *Am J Hum Genet* 2000;67:1251–1276.
- 4 Hammer MF, Karafet TM, Redd AJ, Jarjanazi H, Santachiara-Benerecetti S, Soodyall H, Zegura SL: Hierarchical patterns of global human Y-Chromosome diversity. *Mol Biol Evol* 2001;18:1189–1203.
- 5 Underhill PA, Passarino G, Lin AA, Shen P, Mirazon ML, Foley R, Oefner PJ, Cavalli-Sforza LL: The phylogeography of Y chromosome binary haplotypes and the origins of modern human populations. *Ann Hum Genet* 2001;65:43–62.
- 6 Forster P: Ice Ages and the mitochondrial DNA chronology of human dispersals: A review. *Phil Trans R Soc Lond B* 2004;359:255–264.
- 7 Batzer MA, Stoneking M, Alegria-Hartman M, Bazan H, Kass DH, Shaikh TH, Novick GE, Ioannou PA, Scheer WD, Herrera RJ, Deininger PL: African origin of human-specific polymorphic Alu insertions. *Proc Natl Acad Sci USA* 1994;91:12288–12292.
- 8 Stoneking M, Fontius JJ, Clifford SL, Soodyall H, Arcot SS, Saha N, Jenkins T, Tahir MA, Deininger PL, Batzer MA: Alu insertion polymorphisms and human evolution: Evidence for a larger population size in Africa. *Genome Res* 1997;7:1061–1071.
- 9 Nasidze I, Risch G, Robichaux M, Sherry ST, Batzer MA, Stoneking M: Alu insertion polymorphisms and the genetic structure of human populations from the Caucasus. *Eur J Hum Genet* 2001;9:267–272.
- 10 Watkins WS, Ricker CE, Bamshad MJ, Carroll ML, Nguyen SV, Batzer MA, Harpending HC, Rogers AR, Jorde LB: Patterns of ancestral human diversity: An analysis of Alu-insertion and restriction-site polymorphisms. *Am J Hum Genet* 2001;68:738–752.
- 11 Watkins WS, Rogers AR, Ostler CT, Wooding S, Bamshad MJ, Brassington A-ME, Carroll ML, Nguyen SV, Walker JA, Prasad BVR, Reddy PG, Das PK, Batzer MA, Jorde LB: Genetic variation among world populations: inferences from 100 Alu insertion polymorphisms. *Genome Research* 2003;13:1607–1618.
- 12 Romualdi C, Balding D, Nasidze IS, Risch G, Robichaux M, Sherry ST, Stoneking M, Batzer MA, Barbujani G: Patterns of human diversity, within and among continents, inferred from biallelic DNA polymorphisms. *Genome Res* 2002;12:602–612.
- 13 Bakunin VM: Description of Kalmyk People, especially of Torgouts, and the Acts of Their Khans and Masters. Elista, Kalmyk publishing house, 1995.
- 14 Smirnov P: Travel Notes on Kalmyks' Steppe of Astrakhan Province. Elista, Kalmyk publishing house, 1999.
- 15 Sambrook J, Fritsch EF, Maniatis T: Molecular Cloning: A Laboratory Manual. Cold Spring Harbor, Cold Spring Harbor Laboratory Press, 1989.
- 16 Arcot SS, Adamson AW, Lamerdin JE, Kanagy B, Deininger PL, Carrano AV, Batzer MA: Alu fossil relics – distribution and insertion polymorphism. *Genome Res* 1996;6:1084–1092.
- 17 Arcot SS, Adamson AW, Risch G, LaFleur J, Lamerdin JE, Carrano AV, Batzer MA: High-resolution cartography of recently integrated chromosome 19-specific Alu fossils. *J Mol Biol* 1998;281:843–855.
- 18 Arcot SS, DeAngelis MM, Sherry ST, Adamson AW, Lamerdin JE, Deininger PL, Carrano AV, Batzer MA: Identification and characterization of two polymorphic Ya5 Alu repeats. *Mutat Res Genomics* 1997;382:5–11.
- 19 Carroll ML, Roy-Engel AM, Nguyen SV, Salem AH, Vogel E, Vincent B, Myers J, Ahmad Z, Nguyen L, Sammarco M, Watkins W, Henke J, Makalowski W, Jorde L, Deininger P, Batzer M: Large-scale analysis of the Alu Ya5 and Yb8 subfamilies and their contribution to human genomic diversity. *J Mol Biol* 2001;311:17–40.
- 20 Nei M: Molecular Evolutionary Genetics. New York, Columbia University Press, 1987.
- 21 StatSoft Inc: STATISTICA (data analysis software system), version 6, 2001. www.statsoft.com.
- 22 Guo S, Thompson E: Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics* 1992;48:361–372.
- 23 Rosenberg MS: PASSAGE. Pattern Analysis, Spatial Statistics, and Geographic Exegesis. Version 1.1. Department of Biology, Arizona State University, Tempe, AZ, 2001.
- 24 Kuzeev RG: The People of the Central Volga Region and Southern Ural. Moscow, Nauka, 1992.
- 25 Khusnutdinova EK, Khidiatova IM, Viktorova TV, Galeyeva AR, Mustafina OE: Analysis of the genetic differentiation of Bashkirs and Ethnoses of the Volga-Ural region from data on polymorphic markers of the nuclear genome. *Genetika* 1999;35:707–712.
- 26 Bermisheva M, Tambets K, Villems R, Khusnutdinova E: Diversity of mitochondrial DNA haplotypes in ethnic populations of the Volga-Ural region of Russia. *Mol Biol (Mosk)* 2002;36:990–1001.
- 27 Akhmedov BF: The State of Nomadic Uzbeks. Moscow, Nauka, 1965.
- 28 Tolstov SP: People of Central Asia and Kazakhstan. Moscow, USSR Academy of Sciences Publishing House, 1962–1963, Vol 1, 2.
- 29 Lavrov LI: Historical and Ethnographical Sketch of Caucasus. Leningrad, 1978.
- 30 Kereitov RKh: Ethnical History of Nogays. Stavropol, 1999.