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HUMAN GENETICS

Polymorphism of the Y-Chromosome Diallelic Loci in Ethnic Groups of the Altai–Sayan Region

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Abstract—Using the data on five diallellic Y-chromosome loci (*DYS199*, *92R7*, *SRY1532*, *RBF5*, and *DYS287*) polymorphism, genetic structures of the five Turkic-speaking ethnic groups of the Altai–Sayan upland (Tuvinians, Sojots, Shorians, Khakassians, and Southern Altaians (Altai-Kizhi), were described. The gene pools of the populations examined were characterized by the presence of pronounced paleo-Caucasoid component (*92R7-T*-lineages). The frequency of this component increased westward, reaching more than 70% in Shorians and Southern Altaians. Haplotype *TAT*-C (*RBF5* locus) was observed in all populations, except Shorians, with the frequencies varying from 5.4% in Altai-Kizhi to 18.8% in Khakassians. The *Alu*-insertion in the *DYS287* locus was revealed only in the Altaian sample with the frequency of 3.3%. It was established that the Altai–Sayan populations studied split into two statistically significantly different groups. One of the groups was represented by Tuvinians, Sojots, and Khakassians, while another one was comprised of Shorians and Altaians.

INTRODUCTION

Ethnic groups of the Altai–Sayan region are different in respect of their anthropological features, though they share the prevalence of Turkic language and culture in their genesis. The formation of the indigenous anthropological type of the Altai–Sayan upland is traced back to the Neolithic and characterized by intense admixture of the European and Mongoloid groups. In most indigenous people of the region, namely, Southern Altaians, Tuvinians from the steppe regions, and some groups of Khakassians, the most Mongoloid, Central Asian type prevails. This type is a complex racial genetic structure, the origin of which traces back to the Mongoloid groups that underwent admixture at different periods of time (from the ancient times to the late Middle Ages). In respect of their anthropologic features, Shorians along with some Ugric and Samoyed peoples are typical representatives of the Uralic race. The features of the Uralic race, occupying intermediate position between large Mongoloid and Caucasoid races, can be also observed among Northern Altaians and some of the Khakassian groups [1–3].

Heterogeneity of anthropological composition of contemporary population of the Altai–Sayan uplands is the result of the complex history of peopling of the region and geographical closeness to the presumptive foci of Mongoloid and Caucasoid race origin [3]. To draw some conclusions about the origin and differentiation of the ethnic groups of the region, application of a complex approach including classic methods of anthropology, archaeology, linguistics, history, and ethnology along with modern methods of molecular genetic analysis of human populations seems useful.

One of the most promising approaches to infer genetic history of peoples is the analysis of variation in highly polymorphic genetic systems, which are inherited in one of the parental lineages and lack recombination. At present, the studies of such polymorphic systems as human mitochondrial DNA (mtDNA) and nonrecombining portion of the Y chromosome are most popular. Analysis of paternally inherited Y-chromosome variation is widely used to investigate genetic history of certain peoples and their communities [4].

The nonrecombining portion of the Y chromosome spans the region of about 60 kb. According to the modern data, it contains more than 250 polymorphic loci represented by slowly evolving diallelic markers [5–7], as well as by rapidly evolving microsatellite (STR) and minisatellite loci [8, 9].

The present study was focused on the description of the main male lineages in the gene pools of the Altai–Sayan ethnic groups. The choice of the *DYS199*, *92R7*, *SRY1532*, *RBF5*, and *DYS287* diallelic loci for investigation of Y-chromosome variation was based on evolutionary stability of their alleles, as well as on high effi-

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ciency of this marker set for the description of the genetic structures of different Eurasian ethnic groups [10–12].

MATERIALS AND METHODS

Variation of the five Y-specific diallelic loci was examined in 244 individuals representing five indigenous populations of the Altai–Sayan upland. Only the individuals who were paternally unrelated at least for two generations participated in the study.

The sample of Southern Altaians (proper Altaians, or Altai-Kizhi; $N = 92$) was formed from the residents of the settlements of Kaisyn and Mendur-Sokkon, Ust'-Kansk raion of the Altai Republic. Tuvinian sample ($N = 64$) was represented by the residents of Bai-Taiga, Barun-Khemchinskii, Dzun-Khemchinskii, Kaa-Khemskii, Mongun-Taiga, Ovuyrskii, Tandinskii, Ulug-Khemskii, Chedi-Khol'skii, Erzya, and Kyzyl raions of the Tuva Republic. It was composed of the representatives of the main Tuvinian tribes, Irgit, Mongush, Ondar, Oorzhak, Oyun, Saaya, Sat, and Khertek. Khakassian sample ($N = 32$) was represented by the residents of the settlements of Askiz, Beisk, and Ordzhonikidze raions of the Khakassian Republic. The sample of Mountain Shorians ($N = 22$) was formed from the residents of the settlement of Orton, Tashtagol'skii raion of Kemerovo oblast. Sojot sample ($N = 34$) was represented by the inhabitants of Okinskii and Tunkinskii raions of the Buryat Republic.

Total DNA was extracted from the samples of biological tissues (blood and hair bulbs) using standard techniques [13].

Typing of the Y-chromosome polymorphic loci was carried out using polymerase chain reaction (PCR) in a UNOII (BOIMETRA) thermal cycler with subsequent restriction analysis of the DNA fragments obtained. In all cases PCR was performed using the PROMEGA buffer solution and *Taq* DNA polymerase (SibEnzyme, Novosibirsk, Russia).

Amplification of the *DYS287* (*YAP*) was carried out using the primers and reaction conditions described earlier [14]. The *YAP*(–) allele was represented by a fragment of 150 bp, and the *YAP*(+) allele was identified as a fragment of 455 bp in size.

The 709-bp DNA fragment containing Y-specific *92R7* locus [15] was obtained using the 5'-GACCCGCTGTAGACCTGACT-3' and 5'-GCCTATCTACTTCAGTGATTTCT-3' primers and the reaction conditions described in [16]. The *92R7C* allele was identified by the presence of the *Hind*III restriction endonuclease recognition site (the enzyme used was purchased from SibEnzyme, Novosibirsk). The allele was identified as a pair of DNA restriction fragments of 197 and 512 bp in size.

Amplification of the *RBF5* (*TAT*) locus was carried out using the primers and reaction conditions described in [17]. Polymorphic alleles were identified after digestion of PCR products with the *Hsp*92II restriction endonuclease (Promega) by the absence (the *TAT*-C allele), or the presence (the *TAT*-T allele) of the 83- and 29-bp DNA fragments.

The *DYS199* locus [18] was amplified using a modified primer [10] containing a recognition site for the *Mfe*I restriction endonuclease (the enzyme used was purchased from SibEnzyme, Novosibirsk) on the Y-specific C alleles.

The *SRY1532* locus containing the A–G transition [19] was amplified and analyzed as described earlier [10]. G allele was identified by the appearance of the *Dra*III restriction endonuclease (isoschisomer of the *Ade*I; the enzyme used was from Fermentas, Lithuania).

Y-chromosome haplotype diversity (h) was calculated according to the formula of Nei and Tajima [20]:

$$h = (1 - \sum x^2)N/(N - 1),$$

where x is the population frequency of each Y-chromosome haplotype and N is a sample size. Genetic similarity between the populations in respect of Y-specific haplotypes frequency distribution was determined using the r measure and the test of identity I [21].

RESULTS AND DISCUSSION

Distribution of Y-Specific Alleles and Haplotypes and Genetic Diversity of the Altai–Sayan Populations

Analysis of variation at diallelic loci on the nonrecombining portion of Y-chromosome (*DYS199, 92R7, SRY1532, RBF5* and *DYS287*) in 244 subjects representing five ethnic groups of the Altai–Sayan region (Altai-Kizhi, Khakassians, Shorians, Sojots, and Tuvinians) detected polymorphisms in four of the five loci examined (Table 1). In the Altai–Sayan populations tested the C–T transition in the *DYS199* locus typical to the indigenous ethnic groups of America and some Northern Asian populations [11, 18, 22] was not observed. The T–C transition in the *RBF5* locus (*TAT*-C allele) was observed in Tuvinians, Sojots, Altai-Kizhi, and Khakas with the frequencies of 14.1, 11.8, 5.4, and 18.8% respectively. Insertion of the *Alu* element in the *DYS287* locus (the *YAP*(+) allele) was revealed only in Altaians with the frequency of 3.3%. Polymorphisms at the *92R7* and *SRY1532* loci were detected in all five populations examined. The *92R7*-T allele differing from the ancestral variant by the absence of the *Hind*III recognition site was observed with maximum frequencies in Shorians (72.7%) and Altaians (70.7%). Lower frequencies of this allele were detected in Khakassians (37.5%) and Sojots (32.4%). Minimum frequency of the *92R7*-T allele was found in Tuvinians (15.6%). Maximum frequencies of the *SRY1532*-A allele, usually observed in association with the *92R7*-T allele, were found in Shorians and Altaians (54. 6 and 41.3% respectively). This allele was also detected in Khakassians and Sojots with similar frequencies of 25 and 26.5% respectively. At the same time, Tuvinian popula-

Table 1. Frequencies of Y-specific diallelic loci alleles in populations of the Altai–Sayan region

Population	*N*	Allele frequencies (%)								
		TAT-C	*TAT*-T	*92R7*-T	*92R7*-C	*SRY1532*-A	*SRY1532*-G	*YAP*(+)	*YAP*(–)	*DYS199*-C
Tuvinians	64	14.06	85.94	15.63	84.37	10.94	89.06	0	100.0	100.0
Sojots	34	11.76	88.24	32.35	67.65	26.47	73.53	0	100.0	100.0
Shorians	22	0	100.0	72.73	27.27	54.55	45.45	0	100.0	100.0
Khakassians	32	18.75	81.25	37.50	62.50	25.00	75.00	0	100.0	100.0
Altai-Kizhi	92	5.44	94.56	70.65	29.35	41.30	58.70	3.26	96.74	100.0

Note: *N*, sample size.

tion was characterized by minimum frequency of this Y-specific allele (10.9%).

We showed that in the populations examined five Y-specific haplotypes, determined by the combinations of different alleles, were present (Tables 2 and 3). Ancestral Y-specific haplotype is characterized by the *TAT*-T/*YAP*(–)/*92R7*-C/*SRY1532*-G/*DYS199*-C allele combination (haplotype 1). Among the populations tested it was widely distributed only in Tuvinians (70.3%) and Sojots (55.9%). In the remaining populations its frequency varied from 20.7% in Altaians and 27.3% in Shorians to 43.8% in Khakassians. The haplotype differing from the ancestral one by the C–T transition in the *92R7* locus (haplotype 4) was discovered with maximum frequency in Altaians (29.4%). The frequencies of this haplotype in Khakassians and Shorians were 12.5 and 18.2% respectively. Minimal frequencies of this haplotype were observed in Tuvinians and Sojots (4.7 and 5.9% respectively). The Y-chromosome type differing from the above mentioned by the G–A mutation in the *SRY1532* locus (haplotype 5) was found in all populations tested with the frequencies corresponding to those of the *SRY1532*-A allele (Tables 1 and 3).

All Altai–Sayan populations examined were characterized by high levels of genetic diversity, maximum values of which were observed in the populations of Altaians and Khakassians (Table 3). Though the gene pools of the populations studied were represented by the sets of virtually the same Y-chromosome haplotypes, population of the Altai–Sayan region cannot be considered as genetically homogenous (Table 4). The test for identity I showed that the populations examined split into two statistically significantly different groups ($0.001 < P < 0.01$). One of the groups was represented by Tuvinians, Sojots, and Khakassians, while the other was comprised of Shorians and Altaians. The genetic differences of Shorians and Altaians from the other populations examined can be for the most part explained by maximum frequencies of the *92R7*-T and *SRY1532*-A alleles and, hence, haplotypes 4 and 5, observed in the gene pools of these populations (Table 1 and 3).

Paleo-Caucasoid Component in the Gene Pools of Altai–Sayan Ethnic Groups

The *92R7*-T allele is the marker defining a group of male lineages widely distributed among the population of Eurasia and indigenous populations of America. Recent studies on Y-chromosome lineage diversity in different populations of the world showed that the *92R7*-T-derived haplotypes represent the ancient paleo-Caucasoid component, which by its origin is associated with the population of Central Eurasia [10]. High frequencies of the most ancient haplotype, defined by the *92R7*-T/*SRY1532*-G allele combination (haplotype 4 in the present study, haplotype 1C in [11], haplotype HG1 in [12], and haplotype 10 in [10]), were observed in the populations from different geographic areas, namely, India (21.7%), Europe (37%), Ireland (98.5%, nearly fixation level), Western Siberia, including Kets (83.3%) and Sel'kups (76.2%), and also in the indigenous populations of America (35.2%) [10–12]. One of the derivatives of this central haplotype is defined by an additional mutation in the *DYS199* locus (variant *DYS199*-T), which was found only among the indigenous populations of America [11, 18, 22]. Another haplotype was defined by the *92R7*-T/*SRY1532*-A allele combination (haplotype 5 in the present study, haplotype 1D in [11], haplotype HG3 in [12], and haplotype 32 in [10]). It was practically absent from the populations of Africa, Eastern Asia, and America. At the same time, high frequencies of this haplotype were observed in the populations of Central and Eastern Europe (up to 50% in Russians, Poles, and Slovaks), Southeastern Asia (up to 32% in

Table 2. Y-chromosome haplotype structures

Haplotype	*TAT*	*92R7*	*SRY1532*	*YAP*	*DYS199*
1	T	C	G	–	C
2	T	C	G	+	C
3	C	C	G	–	C
4	T	T	G	–	C
5	T	T	A	–	C

Table 3. Y-chromosome haplotype frequency distribution patterns and genetic diversity of the Altai–Sayan populations

Population	Haplotype frequency (%)					*h*
	1	2	3	4	5	
Tuvinians	70.31	0	14.06	4.69	10.94	0.479
Sojots	55.89	0	11.76	5.88	26.47	0.619
Shorians	27.27	0	0	18.18	54.55	0.623
Khakassians	43.75	0	18.75	12.50	25.0	0.718
Altai-Kizhi	20.65	3.26	5.44	29.35	41.30	0.704

Table 4. Genetic differences between populations of the Altai–Sayan region

Populations	1	2	3	4	5
1. Tuvinians		3.883	29.535***	7.009	60.879***
2. Sojots	0.978		13.487**	1.852	23.492***
3. Shorians	0.775	0.874		14.034**	8.104
4. Khakassians	0.959	0.986	0.865		16.252**
5. Altai-Kizhi	0.798	0.882	0.943	0.914	

Note: Above diagonal, identity indices *I*; below diagonal, similarity indices *r* [21]. ** $P < 0.01$, *** $P < 0.001$.

the populations of India, Pakistan, and Iran), and Altai (55%) [10–12, 23]. This wide distribution of Y-specific *92R7*-T haplotypes can be explained by ancient migrations from Central Eurasia to Europe and America, and also by relatively recent (about 7.5 thousand years ago) migrations of the representatives of the mound culture from the Central Asia to the Indian subcontinent, Europe, and Siberia [10, 12, 23].

Our findings point to the prevalence of the *92R7*-T lineages in the gene pools of indigenous populations of the Altai–Sayan region (Table 3). Taking into consideration the presence of paleo-Caucasoid Y-chromosomal component in the gene pools of Kets and Sel'kups [11], it should be recognized that the area of its distribution in Siberia is rather wide. Our results are thus consistent with paleoanthropological data [3] on the prevalence of the complex of Caucasoid traits in populations of the Altai–Sayan region, which can be traced back to the Neolithic and the Bronze Age. Extensive and gradual dispersal of Mongoloids from the east to the west, i.e., from the Middle Asia to Siberia, Central Asia, and further, to the southern Russian steppe and Northern Caucasus, having began in the 1st millennium BC, finally resulted in the prevalence of the Mongoloid traits in the anthropological composition of contemporary population of Southern Siberia [1–3].

Table 5. Percentage of Caucasoid lines in gene pools of the Altai–Sayan ethnic groups

Population	RFLP markers of mtDNA*	Diallelic Y-chromosomal loci
Tuvinians	5.6	15.6
Sojots	5.9	32.4
Shorians	35.7	72.7
Khakassians	18.5	37.5
Altai-Kizhi	23.9	70.7

* Data from [25].

Our data on polymorphism of the maternally inherited mtDNA in populations of the Altai–Sayan region [24, 25] suggested the prevalence of Mongoloid component in the gene pools of these populations (Table 5). The frequency of the Caucasoid lineages is minimal in Tuvinians and Sojots (about 6%). Other populations examined demonstrate an increase of Caucasoid lineage frequency from 18.5% in Khakassians to 23.9% in Altaians, and 35.7% in Shorians. Note that in these populations the frequency distribution patterns of male Caucasoid lineages (haplotypes 4 and 5) were very similar to those mentioned above. Therefore, the distributions of mtDNA and Y-chromosome lineages display the following geographic trend: in western regions of Altai–Sayan upland the proportion of Caucasoid component increases with the increasing distance from the areas of intense formation of the Mongoloid race [1, 3], reaching its maximum in the gene pools of Shorians and Altaians (Table 5).

Other Components in the Gene Pools of the Altai–Sayan Ethnic Groups

It should be noted that *YAP*(+) haplotype (haplotype 2), found only in 3.3% of Altaians, along with haplotype 1, an ancestral type for all five loci, can be arbitrarily referred to as the Mongoloid component in the gene pools of the populations examined. A set of markers used in the present study is insufficient for detailed differentiation of Y-specific lineages, grouped in haplotype 1. Analysis of the literature data, however, shows that the RPS4Y and M9 lineages, distributed predominantly in Mongoloid populations, may belong to haplotype 1 [11, 12].

Haplotype 3, defined by the *TAT*-C allele and found in 14.6% of Tuvinians, 5.4% of Altaians, 11.8% of Sojots, and 18.8% of Khakassians, cannot be unambiguously attributed to either Mongoloid or Caucasoid lineages. It is established that *TAT*-C allele of the *RBF5* locus is distributed predominantly in Northern Eurasia. Maximum frequencies of this allele were observed in Yakuts (86%), Buryats from Mongolia (52%), and also in such Finno-Ugric peoples as Finns (61%), Estonians (37%), and Maris (33%) [12, 17]. The *TAT*-C allele was also found in populations of the Volga–Ural region with the frequencies varying from 9% in Mordovians to 68% in Udmurts [26]. Zerial *et al.* suggested that this mutation first arose in the populations of Asia and then dispersed over the territory of Northern Europe reaching Finland, which can indicate substantial genetic contribution of Mongoloids to the development of Northern European peoples [17]. These authors also advanced an alternative hypothesis concerning the origin of the *TAT*-C allele. Specifically, high frequency of the ancestral, in respect of the *TAT*-C allele, Y-chromosome variant *LLY22g*-A (17%) revealed in Maris is considered to be the evidence of the emergence of the *TAT*-C allele in this particular population [12]. The presence of the *TAT*-C allele in the Russian gene pool with frequencies varying from 15 to 21% is explained by the presence of considerable proportion of the Finno-Ugric and/or Turkic admixture in the modern Russians [17, 27].

Since in Tuvinians the tribe attribution is determined down the male lineage, it is thus possible to correlate the information on the origin of certain tribal groups with the Y-chromosome variants. For instance, the carriers of the *TAT*-C allele in Tuvinian population are the representatives of the Irgit tribe. This allele was found in the five of six members of the tribe examined. In addition, this allele is a marker for Y chromosomes in the representatives of three other tribes, namely, the Turkic by its origin Oorzhak tribe and two Mongolian tribes (Salchak and Mongush). Thereby, *TAT*-C haplotype in the Tuvinian gene pool may be either of Turkic, or of Mongolian descent. Some authors also suggest the Samoyedic origin of the Irgit tribe [28]. This in turn can serve as a confirmation of the Finno-Ugric origin of the *TAT*-C allele. The use of a combined approach based on the analysis of Y-chromosome diallelic and microsatellite loci variation along with the inclusion in the analysis of other Turkic and Finno-Ugric populations would provide detailed estimation of the contributions of different by the descent components to the gene pool of the present-day population of the region examined.

In the present study other examples of congruence between certain family names and Y-chromosome variants have been also established. For instance, in Shorians all males with the family name of Kiskorov are characterized by the presence of haplotype 5. At the same time, individuals with one family name can carry either evolutionary related Y-chromosome variants (for instance, haplotypes 4 and 5 in the Kirsanov males), or phylogenetically different haplotypes (Tuvinian males from the Oorzhak tribe carry three different haplotypes 1, 3, and 5). Thereby, analysis of Y-chromosome lineage variation in the carriers of one family name can serve as a source for obtaining the information on the specific features of the development of genetic structure of the male lineages in the peoples characterized by patrilinearity.

In general, the analysis of Y-chromosome diallelic loci variation provided identification of the main male lineages in the gene pools of the Altai–Sayan ethnic groups. Our findings show that the gene pools of the populations examined were characterized by the presence of strong paleo-Caucasoid component, the proportion of which increased westwards, reaching the value of more than 70% in Shorians and Southern Altaians. It is likely, that Mongoloid component, most pronounced in the gene pools of Tuvinians, Sojots, and Khakas, is of a Central Asian descend. Receiving the detailed information on the structure and diversity of this component requires extension of the set of diallelic markers along with the inclusion in the analysis of the number of Y microsatellite loci. Utilization of the gene geographic approach for the analysis of Y chromosome polymorphism also requires examination of the greater number of the samples representing different ethnic groups from the neighboring territories.

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