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HUMAN GENETICS

Haplotypes at Two Diallelic Y-Chromosome Loci in the Indigenous and Migrant Populations of Siberia

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Abstract—Two diallelic Y-chromosome markers, the Y *Alu* polymorphism (*YAP*) and the T–C transition (*Tat*), were analyzed in the indigenous (Tuvinian, Buryat, Northern Altaian, and Tatar) and migrant (Slavic) populations of Siberia. A high frequency of the allele *C* was revealed in several indigenous populations (25–55%) and in Russians (20.8%). The *YAP*+ allele occurred at a surprisingly high frequency (31.4%) and was completely linked with the *C* allele in Buryats. The *YAP*+ chromosome was also found in the Tuvinian population (1.5%). The two diallelic loci showed a marked linkage disequilibrium (D' = 92.4%) in the total sample. The *YAP–/T* and *YAP–/C* haplotypes prevailed in both indigenous and migrant populations: their respective frequencies were 80.4 and 19.6% in the Slavic population and 71.8 and 19.9% in the indigenous one. The *YAP+/C* (7.8%) and *YAP+/T* (0.5%) haplotypes were found only in the indigenous population. An appreciable heterogeneity in haplotype frequency distribution between regional subpopulations was revealed in Russians, Tuvinians, and Buryats. The origin and evolution of Y-chromosome lines in Northern Asia are considered.

INTRODUCTION

The Y chromosome has recently become one of the major subjects in studies of human population genetics and evolution [1, 2]. It was long believed that the Y chromosome is significantly less polymorphic than the autosomes and mtDNA [3–7]. However, many polymorphic markers, including diallelic polymorphisms and microsatellite markers, have been found in the Y chromosome during recent years, thereby putting into question our view of its low variation. The Y chromosome displays several unique properties, in particular, paternal inheritance and no recombination in the region lacking a homologous X-chromosome counterpart. This makes it possible to infer a paternal lineage from the Y-chromosome haplotypes, which form a unique record of mutations that arose in earlier generations. Since the effective size of the Y-chromosome pool in a population is low (four times lower than that of the autosomes), the Y chromosome is more significantly affected by genetic drift and displays a higher interpopulation variation as compared to the autosomes and mtDNA. Analysis of Y-chromosome haplotypes facilitates elucidation of a wide variety of problems in population genetics and evolution, from characterization of the world gene pool to a high-resolution discrimination between closely related populations [8–12]. As a subject of population genetic studies, the Y chromosome is to a certain extent similar to mtDNA. However, the Y chromosome is far more promising, as its size is estimated at approximately 60 Mb, whereas the mitochondrial genome is of about 16.5 kb and actually acts as a single locus.

An appreciable number of polymorphic diallelic markers have recently been reported for the Y chromosome [1, 13–17]. Insertion of an *Alu* element in the *DYS287* locus of region Yq11 (Y *Alu*-polymorphism or *YAP*) is among the first found and best studied markers [13, 18]. The frequency of the *Alu* insertion (the *YAP*+ chromosome) markedly varies in human populations from various regions. The *YAP*+ frequency is rather high (60–95%) in Africans [14, 19, 20–24] and moderate (approximately 50%) in Bushmen and Hottentots [19]. The *YAP*+ chromosome occurs at a low frequency (less than 11%) in only few populations from Europe, Asia, and the New World [14, 21–27]. In Asia, a high frequency of *YAP*+ has been detected only in the Japanese (33–56% [18, 28]) and Tibet (36–53% [29, 30]) populations. The *Alu* insertion has also been found in 1.3–3% of Mongols, Altaians, and Koreans [29, 31].

Another diallelic marker recently found in the Y chromosome is the T–C transition (*Tat* mutation) which results in a loss of the *Hsp*92II site and produces a *Mae*II site [32]. Preliminary data suggest that the distribution of this transition is restricted to Northern Eurasia. Allele C is rarer on average but occurs at a high frequency in Yakuts (86%), Buryats (58%), and in Finno-Ugric people: Finns (52%), Estonians (47%), and Maris (38%) [32].

Here, we report the distribution of haplotypes at the *YAP* (*DYS287*) and *Tat* loci in 318 men from the indigenous (Tuvinian, Buryat, Northern Altaian, and Tatar) and migrant (Slavic) populations of Siberia. We also characterize the inter- and intrapopulation diversity and the association between the *YAP* and T–C transition.

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The results obtained are discussed in the context of the evolution of the Y chromosome in Northern Asia.

MATERIALS AND METHODS

We analyzed 318 paternally unrelated men. A sample from the indigenous Siberian population included individuals of four ethnic groups of the Altaic linguistic family: Tuvinians (n = 129), Buryats (n = 48), North Altaians (n = 20), and Tatars (n = 9). A sample from the migrant Slavic population included Russians (n = 101) and Ukrainians and Belarussians (n = 11). All individuals were selected so that their lineage involved no interethnic marriages in at least the last two generations.

We analyzed three geographically distant rural subpopulations from the southeastern (village Kungurtug, $n = 49$), northeastern (village Toora-Khem, $n = 35$), and western (village Teeli, n = 45) regions of the Tuva Republic. Buryats were also from three geographically distant subpopulations: from Ulan-Ude (n = 20), the village Kurumkan (n = 22) located in Northern Buryatia, and the village Khuromsha (n = 6) located approximately 30 km to the west of Ulan-Ude. Data on Tuvinians and Buryats were collected from 1993 to 1998 during expeditions of the Institute of Medical Genetics, Tomsk Research Center, Russian Academy of Medical Sciences [33]. Blood specimens of North Altaians (Kumandinians, Chelkanians, and Tubalars) were collected in the town of Gorno-Altaisk; those of Tatars were collected in Tomsk.

Russians were from two subpopulations: Tomsk ($n = 47$) and the village of Kargala (n = 54), which is located approximately 80 km to the north of Tomsk. Ukrainians and Belorussians, who were included in the total sample from the Slavic population, were born in Ukraine and Belarus, respectively; their blood specimens were collected in Tomsk.

DNA was isolated from peripheral blood lymphocytes according to the standard procedure. The *DYS287* (*YAP*) locus was PCR-amplified with primers described earlier [28]. The products of 455 and 150 bp, which corresponded to the *YAP*+ and *YAP*– alleles, respectively, were separated in 2% agarose gel. To identify the *Tat* alleles, a 112-bp fragment was amplified with primers Tat1 and Tat3, which were described by T. Zerjal *et al.* [32]. The PCR products were digested with *Hsp*92II (Promega). Generation of fragments of 83 and 29 bp indicated the presence of the *Hsp*92II restriction site corresponding to the allele *T*.

Gene diversity, which is equivalent to the expected heterozygosity estimated for markers present on both homologs, was obtained as $H = n/(n-1)(1-\Sigma p^2)$, where n is the sample size and p is the frequency of a given haplotype [34]. Gametic disequilibrium was inferred from the coefficient D and the standardized coefficient $D' = D/D_{\max}$ [35].

RESULTS

The *YAP* and *Tat* allele and haplotype frequencies and data on gene diversity in the ethnoses studied are summarized in the table.

The *C* allele occurred at a high frequency in the indigenous Mongoloid populations (24.8% in Tuvinians, 41.7% in Buryats, and 55.5% in Tatars). The frequency of this allele in Russians was lower (20.8%). The small samples of North Altaians and Ukrainians were monomorphic and had only the *T* allele. Surprisingly, the Y chromosome with the *YAP*+ allele was detected at a high frequency in Buryats (in 15 out of 48 individuals, i.e., 31.4%). The *YAP*+ allele was completely linked with the *C* allele in the Buryat population ($D/D_{\max} = 1$). Two (1.5%) out of 129 Tuvinians also carried the *YAP*+ chromosome. Only the *YAP*– allele was detected in all other populations. The two diallelic loci displayed a marked linkage disequilibrium in the pooled sample (D' = 92.4%). The *YAP–/T* and *YAP–/C* haplotypes prevailed in both indigenous and migrant populations of Siberia: their frequencies were 80.4 and 19.6%, respectively, in the Slavic population and 71.8 and 19.9%, respectively, in the indigenous population. The *YAP+/C* (7.8%) and *YAP+/T* (0.5%) haplotypes were found only in the indigenous population.

Analysis of haplotype frequency distribution revealed a heterogeneity of the regional subpopulations of the indigenous Siberian ethnic groups. A significant difference was detected between the three Tuvinian subpopulations (χ^2 = 28.3, d.f. = 2, $P < 0.001$) and between the three Buryat populations (χ^2 = 15.9, d.f. = 2, $P < 0.001$). A difference in haplotype frequency distribution between the Russian subpopulations from Tomsk and Kargala was nearly significant (χ^2 = 3.7, d.f. = 1, $P < 0.1$).

Differentiation of the populations under study was assessed according to Nei [34]; the method consisted in estimating contributions of individual differences within a population and interpopulation differences to the total genetic diversity (table). The coefficient of gene differentiation between the urban Russian population from Tomsk and the rural Russian population from the village Kargala was 3.7%. Previously, gene differentiation between these two populations was estimated at approximately 0.6%, based on the analysis of polymorphic autosomal *Alu* repeats [36]. The essential difference in the extent of differentiation between the autosomal and Y-chromosome gene pools seems natural, as the latter has a smaller effective size and, therefore, the variants of the Y chromosome are geographically clustered [2].

A higher differentiation was characteristic of the regional subpopulations from the Tuva Republic (G_{st} = 4.3%) and from Buryatia (G_{st} = 13.5%). In total, the interpopulation difference contributed 14.3% to the total gene diversity of the indigenous Siberian ethnic groups.

Allele and haplotype frequency distribution in ethnic groups of the Slavic and indigenous populations from Siberia

Population	Sample size *n*	*YAP*		*Tat*		Haplotypes				*H*	G_{st}, %
		YAP–	*YAP+*	*T*	*C*	*YAP–/T*	*YAP–/C*	*YAP+/T*	*YAP+/C*		
Russians											
Tomsk	47	47	0	40	7	40	7	0	0	.2591	
Kargala	54	54	0	40	14	40	14	0	0	.3910	
Total	101	101	0	80	21	80	21	0	0	.3377	3.7
Ukrainians and Belarussians	11	11	0	10	1	10	1	0	0	.1818	
Total for the Slavic population	112	112	0	90	22	90	22	0	0	.3186	–*
Tuvinians											
Kungurtug	49	48	1	45	4	44	4	1	0	.1900	
Teeli	45	45	0	33	12	33	12	0	0	.4003	
Toora-Khem	35	34	1	19	16	19	15	0	1	.5361	
Total	129	127	2	97	32	96	31	1	1	.3917	4.3
Buryats											
Ulan-Ude	20	8	12	7	13	7	1	0	12	.5421	
Khuromsha	6	4	2	4	2	4	0	0	2	.5330	
Kurumkan	22	21	1	17	5	17	4	0	1	.3848	
Total	48	33	15	28	20	28	5	0	15	.5630	13.5
North Altaians	20	20	0	20	0	20	0	0	0	0	
Tatars	9	9	0	4	5	4	5	0	0	.5554	
Total for the indigenous population	206	189	17	149	57	148	41	1	16	.4404	
Total	318	301	17	239	79	238	63	1	16	.4000	8.5

* G_{st} was not calculated for Ukrainians and Belorussians because of the small sample size.

DISCUSSION

Origin of the C Allele and Russian Gene Pool

It is commonly assumed that most polymorphic Y-chromosome point nucleotide substitutions, which have been detected in modern populations, originated from unique mutations that arose in an ancestral chromosome and were distributed as a result of genetic drift and migration [1, 37, 38]. Zerjal *et al.* [32] made this assumption for the T–C transition that they discovered. We detected the allele *C* on both *YAP*– and *YAP*+ chromosomes, suggesting either a recurrent T–C mutation or a deletion of the *Alu* element from the chromosome carrying the allele *C*. The latter seems less probable: insertion of the *Alu* repeat in a given locus is a unique event with the known initial (without *Alu*) and final (with *Alu* insertion) states, and precise deletion of *Alu* is virtually impossible [39]. The initial and final states of the *YAP* polymorphism have been verified by analysis of this locus in primates: only the YAP^- allele has been found in the chimpanzee and gorilla genomes [14]. The initial and final states of the T–C transition are also known, as chimpanzee and orangutan carry only the *T* allele [32]. In our sample, the Y chromosomes with the *C* allele possibly represented two separate lines. One of them, *YAP–/C*, is distributed among modern Turkic ethnic groups and, at a lower frequency, among Russians. The other, *YAP+/C*, is almost completely restricted to Buryats. The variant *YAP+/C* seems to be evolutionarily younger, as the region of its distribution is smaller. Modern Buryats and Mongols separated from their common ancestral group only recently. Hence, the Mongol gene pool can be expected to include *YAP+/C*. Indeed, a low frequency of the *YAP*+ and *C* alleles has been reported for Mongols [29, 32]. However, the two loci were studied independently from each other and in rather small samples.

The frequency of the allele *C* in Russians was relatively high: approximately 21% in our sample and 15% in a small sample (20 individuals) analyzed by Zerjal *et al.* [32], suggesting an appreciable contribution of Finno-Ugric or Turkic ethnoses to the formation of the modern Russian ethnos. The *C* allele was combined only with *YAP*– in the Russian population, suggesting that the contribution of Mongols was insignificant, since *C* was associated with *YAP*+ in Buryats. To more exactly estimate the contribution of the Ugric, Turkic, and Mongolian components to the Russian male gene pool, it is possible to use compound haplotypes including diallelic and microsatellite loci of the nonrecombinating region of the Y chromosome. Such an analysis is currently being carried out in our laboratory.

The Origin of YAP+

Our data on the high frequency of the *YAP*+ chromosome in the Buryat population are of interest with respect to the origin of this allele. M.F. Hammer [18] analyzed the *YAP*+ distribution in various geographic regions and assumed an African origin of the *Alu* insertion in the *DYS287* locus. This assumption explained the fact that the *YAP*+ frequency is high in Africans and gradually becomes smaller in populations from Northern Africa, Asia, Europe, the New World, and Oceania. Further analysis of haplotypes at three polymorphic point nucleotide sites (PN1, PN2, PN3), which are located in proximity to the *YAP* locus [34], and transition G–A at position 4064 of the *SRY* gene [24, 40] revealed a high frequency of several *YAP*+ haplotypes in Asian populations. Moreover, a variation in the *DYS19* microsatellite locus on the *YAP*+ chromosome with haplotype 3 in the Asian population was higher than in the African one. These data suggested a significant contribution from Asian populations to the African Y-chromosome pool. Proceeding from this, Altheide and Hammer [40] advanced an alternative hypothesis that *YAP*+ originated in Asia. With either origin, the same number of evolutionary events was required for the generation and distribution of *YAP*/*SRY* haplotypes.

A weak point in the hypothesis of an Asian origin of the *Alu* insertion in *DYS287* is the low frequency of *YAP*+ haplotypes in the modern Asian population. Theoretically, a wider distribution is expected for an ancestral haplotype than for its derivatives resulting from more recent mutations [41]. Hence, new data on a high *YAP*+ frequency in an Asian population (such as our finding that the frequency of the *Alu* insertion is high in Buryats) strengthen the hypothesis of the Asian origin of this allele.

The polymorphic *Alu* insertion in the Y chromosome is also of interest concerning the question of the peopling of Japan and the origin of the Japanese. A high *YAP*+ frequency in the Japanese has been associated with the first wave of migration (the Jomon culture) that resulted in the peopling of Japan more than 10 000 years ago [28]. A *YAP*+ frequency of approximately 40–50% in the Tibetan population [29, 30] favors Nei's hypothesis that the Japanese originated from Northeastern Asia [42]. Moreover, the *Alu* insertion in *DYS287* and point mutations in *DYS199* and *DYS271* are involved in the same haplotype in the Tibetan and Japanese populations, suggesting a common origin of the Y chromosome in both populations [30].

The high *YAP*+ frequency in Buryats also supports the hypothesis that this allele of modern Asian ethnic groups originated from Northern Asia. Most likely, all three Asian populations with high frequency of *YAP*+ received this variant of the Y chromosome independently of each other, as a result of migration from a common source located in Northern Asia. A detailed analysis with other Y-chromosome markers and in other modern populations from Northern and Central Asia will provide for a better understanding of these problems.

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