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Mitochondrial DNA Variation in the Kets and Nganasans and Its Implications for the Initial Peopling of Northern Eurasia

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Abstract—Mitochondrial DNA (mtDNA) variation was studied in 38 Kets and 24 Nganasans, the indigenous inhabitants of the north of the Yenisey River Basin and the Taimyr Peninsula. The results were compared with the analogous data obtained for 59 Kondinski and 39 Sos'vinski Mansi. As a whole, mitochondrial gene pool of Mansi, Nganasans, and Kets was characterized by unique combination of European-specific (H, H2, H3, H8, U2, U4, U5, U7, J2, and W) and Asian-specific (A, C, D, and Z) mtDNA haplogroups. Specific features of the haplogroup geographical distribution along with the results of phylogenetic reconstruction favor the hypothesis of the genetic trace left in Trans-Urals and the adjacent Siberian territories by early migrations from the Near East.

INTRODUCTION

Archaeological evidence on the initial peopling of the territories eastward to the Urals by the nomadic groups hunting mammoths and other members of the Pleistocene fauna 40 000-45 000 years ago are well documented [1, 2]. The following migration waves took place during the period after the Ice Age (about 11 000 years ago), characterized by the changes in landscapes, flora, and fauna. At that time the Ob and Yenisei River basins were peopled by half-settled tribes of fishers and hunters. In the course of time they were either subjected to substantial assimilation, or displaced northward by the populations formed in climatically more favorable regions of South Siberia. To the time of the arrival of Russians to Siberia in the 16th century, only few populations of hunters-gatherers retained in the form of anthropological isolates. At present, these populations are at the stage of complete degradation and assimilation [2–5]. For these reasons, the remnants of their unique gene pools represent invaluable source of genetic information, important to study molecular evolution of north Eurasian populations, and also to reconstruct evolutionary history of *Homo sapience* [6].

Earlier we showed that mitochondrial gene pools of Siberian Eskimos and Aleuts of the Commander Islands are comprised of extremely small number of mtDNA haplotypes belonging to only one or two phyletic lineages, haplogroups (A and/or D respectively), from the four major haplogroups (A, B, C, and D), typical of Native Americans [7, 8].

Substantial genetic diversity was typical of Chukotka Chukchi (haplogroups A, C, and D), and Koryaks and Itel'mens from Kamchatka, who were characterized by the presence of haplogroups A, C, and D along with Asian-specific haplogroups G, Y, and Z [9]. Even higher diversity was revealed in Mansi from circumpolar Siberia [10]. It was shown, that 63.3% of mtDNA gene pool of Mansi was represented by European-specific haplogroups (clusters UK, TJ, and HV), while the proportion of Asian-specific haplogroups (A, C, D, F, G, and M) constituted only 36.7% [10].

It should be noted in this respect that the structure and origin of mtDNA haplogroups in Kets and Nganasans, indigenous populations of the north of the Yenisey River region, are still poorly studied. Our earlier data on mtDNA variation in Kets and Nganasans obtained by means of incomplete restriction analysis were found to be insufficiently informative [11] for testing the existing ecological, archaeological, and linguistic models of the early peopling of Northern Eurasia [2, 5].

In the present study new data on mtDNA variation in the Kets and Nganasans, most ancient inhabitants of the Yenisey River Basin and the Taimyr Peninsula are presented (Fig. 1). The results were compared with the analogous data obtained for Mansi, most ancient present-day inhabitants of the circumpolar Urals and the Lower Ob River region [10], and subjected to joint phylogenetic analysis.

MATERIALS AND METHODS

The Kets have been the inhabitants of the Yenisey River basin in its middle (Upper Kets) and lower (Lower Kets) parts during many centuries. Anthropologically, Kets belong to the mixed Mongoloid–Cauca-

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soid type. At present, the population number of Kets constitutes only several hundred individuals, which are at most assimilated by Russian settlers, or are merged with their western neighbors, Sel'kups, which are close to them in respect of their material culture but not the language. Though during the most part of their recent history Kets were anthropologically and linguistically isolated [3, 12]; their language has terms pointing to primary associations with the Uralic linguistic family [13].

Blood samples of Kets examined were obtained from 38 individuals. Of these, the samples from 21 Upper Kets from the settlement of Sulomai (Baikitskii raion, Krasnoyarsk krai) were collected in 1992. The samples of 17 Lower Kets were collected in the town of Turukhansk during planned exhibition to the lower Yenisei River region in August 2001 (Fig. 1). These individuals were born in the neighboring settlements (Maduika, Pakulikha, Kellog, Surgutikha, Bakhta, and some others), some of which do not exist any more.

Nganasans are the direct descendants of the reindeer hunters from Northern Eurasia. They originate from two relative Uralic-speaking tribes, Avamskie and Vadeevskie Nganasans, indigenous inhabitants of the Taimyr Peninsula. During many centuries Avamskie Nganasans had matrimonial contacts with Yenisey Entsi, which were close to them in material culture and the language, and also with their eastern neighbors, the tribes of Vadeevskie Nganasans [14]. For instance, in the 1920s, 17 Entsi women and 16 Vadeevskie Nganasan women migrated with matrimonial purposes to the population of Avdeevskie Nganasans with the population number of about 550 individuals. The gene flow from Yenisey Entsi continued up to the early 1970s [15]. At present, the total population number of Nganasans does not exceed 500 individuals.

Blood samples of 24 Nganasans, settled in the city of Dudinka, were collected in September 2001. Potential donors were selected based on the pedigree data gathered in the mid-1970s with the purpose of obtaining a representative population sample from the main six Nganasan tribes and a number of Entsi tribes, merged with them [15].

DNA was extracted from buffy coats by use of standard procedures (QIAamp Blood Kit, QIAGEN, United States). MtDNA was amplified in the form of ten overlapping PCR fragments. Polymorphic sites were screened based of restriction fragment length polymorphism (RFLP) observed with 19 restriction enzymes, *Acc*I, *Alu*I, *Ava*II, *Bam*HI, *Bst*NI, *Bfa*I, *Dde*I, *Hae*II, *Hae*III, *Hha*I, *Hinc*II, *Hinf*I, *Hpa*I, *Mse*I, *Msp*I, *Mbo*I, *Nla*III, *Rsa*I, and *Taq*I. Restriction fragments were separated by electrophoresis in agarose gel (2.0–4.0%). Gels were stained with ethidium bromide and DNA fragments were visualized in the UV light. Polymorphism was scored by comparison with the published sequence [16]. Haplotype of each mtDNA was represented by a set of restriction polymorphic sites in association with a variant of control-region sequence. According to systematically updated nomenclature of mtDNA groups and subgroups [17–21], a set of mtDNA haplotypes in a combination with the nearest common ancestor, founder haplotype, was traditionally denoted as "mtDNA haplogroup," or "mtDNA lineage."

Fig. 1. Approximate positions of the Uralic-speaking populations (Saami, Mansi, and Nganasans), Kets, and Evenks.

Nucleotide sequences of mtDNA, including the regions of hypervariable segments I and II (HVSI and HVSII), were determined by use of fluorescent labeling of double stranded PCR products with Big Dye Terminators kit (ABI/Perkin-Elmler Cetus, United States) and subsequent fragments separation on ABI Prism 3100 automated sequencer. The data were treated by SEQUENCER (version 4.0.5, GeneCode Corp) software package.

Phylogenetic analysis was performed manually using the median network method [22].

RESULTS AND DISCUSSION

MtDNA haplotypes revealed in Kets and Nganasans are demonstrated in Table 1. Table 2 shows the data on the distribution of mtDNA haplogroups and their frequencies in both populations in comparison with Mansi in the west, and Evenks in the east. Unusually high frequency of haplogroup U mtDNA sublineages harboring the 12 308 transition in the coding region [17] deserves special interest. This first of all concerns haplogroup U4, distinguished by the 4643 *Rsa*I+ and 11 329 *Alu*I+ site gains in the coding region and the 16 356 transition

Table 1. Polymorphism of mtDNA in Kets and Nganasans

Haplo-group	RFLP	HVSI (–16000)	HVSII	Sample	
				Kets	Ngana-sans
U2	**+5424q + 12308g + 15907k**	**051** 086 **129C 183C 189** 256 **362** 365 519	**73** 152 200 217 263		1
U4	**+4643k + 11329a + 12308g**	134 **356** 519	**73** 152 195 198 263		2
	+4643k + 11329a + 12308g	134 **356** 519	72 **73** 152 195 263	8	
	+4643k + 11329a + 12308g	311 **356** 519	**73** 146 152 **195** 263	1	
	+626e + **4643k** – 11326c + **11329a + 12308g**	189 **356** 519	**73** 195 263		3
	+626e + **4643k** – 11326c + **11329a + 12308g**	111 189 **356** 390 519	**73 195** 263	2	
U5a	**+12308g**	**192 256 270** 399	**73** 146 263	2	
H	**–7025a – 14766u**	crs	152 263	1	
	–7025a – 14766u	519	263	3	
	+6514i **– 7025a – 14766u**	crs	199 263		1
H8	**–7025a** + 8198a **– 14766u**	**162** 519	73 263		1
W*	**5046 12414**	153 **223** 319	**73** 152 189 199 263	1	
A	**+663e**	**223** 242 **290** 293C **319**	64 73 146 263	2	
	+663e	189 **223 290 319** 362 519	97T 105–110(6 bp del) 150 152 235 263	1	
F	+4732k – 10226c **– 12406h/** –12629b + 15907k	172 179 183d 189 193+C 232 249 **304** 311	73 152 204 **248d** 263	9	
C	**+10394c + 10397a – 13259o/**	093 **223 298 327** 519	73 **248d** 263		1
	+10394c + 10397a – 13259o/	171 **223 298 327** 344 357 519	73 **248d** 263	5	
	–7497e **+ 10394c + 10397a – 13259o/**	**223** 259 + A **298** 311 **327** 519	73 146 **248d** 263		1
	+3397k **+ 10394c + 10397a – 13259o/**	145 171 **223 298 327** 344 357 519	73 **248d** 263		1
	–1715c + 3397k **+ 10394c + 10397a – 13259o/**	148 **223** 288 **298 327** 519	73 **248d** 263		2
	–1715c + 3397k **+ 10394c + 10397a – 13259o/** 9bp ins	148 **223** 288 **298 327** 519	73 **248d** 263		1
	+1718e + **10394c + 10397a – 13259o/** +15847a	148 **223** 288 **298 327** 519	64 73 152 **248d** 263		1
	+1718e + 3397k + **10394c + 10397a – 13259o/** +15847a	148 **223** 288 **298 327** 519	64 73 152 **248d** 263		1
	+8249b/ + **10394c + 10397a – 13259o/**	**223 298 327** 519	73 146 263	1	
Z	**+10394c + 10397a**	129 **185 223** 224 **260 298** 519	73 151 152 **248d** 263	1	
	–7497e **+ 10394c + 10397a**	129 185 **223** 224 260 **298** 519	73 151 152 248d 263		1
D	**–5176a** – 10180l **+ 10394c + 10397a** +15437e	**223** 319 **362**	73 239 263 197		4
	–5176a + 10394c + 10397a	**223 362** 519	73 263		2
	–5176a + 5823a + **10394c + 10397a** – 15530u^{het}	**223** 291 311 **362** 519	73 152 263	1	
	–5176a + 10394c + 10397a + 10646k	093 **223** 232 290 **362** 471	63 64 66T 73 195 263		1
			Total	38	24

Note: Diagnostic sites are boldfaced. Mutations are the transitions regarding the Cambridge Reference Sequence [16]. Transversions are denoted; d, deletion. Restriction enzymes are denoted by single-letter code: a, *Alu*I; b, *Ava*II; c, *Dde*I; e, *Hae*III; f, *Hha*I, g, *Hinf*I; h, *Hpa*I; i, *Hpa*II; j, *Mbo*I; k, *Rsa*I; l, *Tag*I; m, *Bam*HI; n, *Hae*II; o, *Hinc*II; q, *Nla*III; r, *Bfa*I; s, *Acc*I; t, *Bst*NI; u, *Mse*I. The simultaneous presence/absence of associated restriction sites determined by a single nucleotide substitution is denoted by "/." 9bp ins is the 9bpCOII/tRNALys triplication. Coordinates of the HVSI and HVSII sequencing are 16013–16520 and 30–300 bp, respectively.

* See the text for explanations.

in control region. In addition, in the sample of Nganasans the mtDNA haplotype (5424 *Nla*III+ and 15 907 *Rsa*I+ site gains, the 16 129C and 16 183C transversions, and the 16 051, 16 189, 16 362, 152, and 217 transitions) from a rare haplogroup U2 [20, 23] was revealed. In two Kets the mtDNA haplotype distinguished by the 16 192, 16 256, and 16 270 transitions, signature mutations for haplogroup U5a, was observed. Note unexpectedly high frequency of haplogroup U4 in Nganasans (20.8%), and especially in Kets (28.9%). These high frequencies are comparable with that revealed in Mansi (16.3%), while in the present-day populations of Northern Europe, including Saami and Finns, which similarly to Nganasans, and Mansi belong to the Uralic linguistic family, haplogroup U4 is extremely rare, or not detected [23, 24].

Haplogroup H, found in the European populations with an average frequency of about 40.0% [25], was detected in four Kets (10.8%) and two Nganasans (8.4%). In addition, in one Nganasan individual a rare mtDNA haplotype harboring the 16 162 transition, a signature mutation of haplogroup H8 [23], was observed. Contrary to Mansi, Nganasans and Kets lacked mtDNA haplotypes from cluster TJ, widely distributed in the present-day European populations [24, 25].

Unusual mtDNA haplotype (crs; G16153A-C16223T-G16319A; A73G-T152C-A189G-T199C-A263G) detected in one Ket individual did not conformed to the generally accepted classification [18, 20]. Because of this, its complete nucleotide sequence was determined. Among the mutations revealed in the coding region (G709A, C739T, A750G, A1438G, T1633C, A2706G, A4769G, G5046A, C7028T, T7581C, A8860G, A10841G, C11674T, G11719A, T11722C, G12192A, T12414C, C12705T, C14766T, G15106A, and A15326G), three (G5046A, C11674T, and T12414C), were typical of haplogroup W [21, 23].

With respect to Asian-specific haplogroups found in the indigenous populations of the north of the Yenisey River Basin, it should be noted that Kets and Nganasans possess identical mtDNA haplotype of haplogroup Z. This haplogroup was first identified in Koryaks and Itel'mens from Kamchatka [9]. Furthermore, in the population of Upper Kets (the settlement of Sulomai) haplogroup F was detected. It was shown that all nine Kets carrying haplogroup F had one mtDNA haplotype (Table 1), i.e., the probability of the founder effect was close to 100%. It cannot be excluded that haplogroup F appeared in Kets only recently as a result of recent marriages with their neighbors, western Evenks, where this haplogroup is found with low frequency [26]. It is more likely, however, that haplogroup F was purchased from the Sayan–Altai region, the territory of presumptive origin of one of the Kets' ancestors [12]. The discovery of two similar to Kets F mtDNA haplotypes in four Tofalars (13%), the contemporary inhabitants of Eastern Sayans, favors this proposal (our unpublished data).

Table 2. Frequencies of mtDNA haplogroups (in %) in indigenous populations of Siberia

Haplogroup	Mansi (N = 98)	Kets (N = 38)	Nganasans (N = 24)	Evenks (N = 51)
U2	–	–	4.2	–
U4	16.3	28.9	20.8	–
U5a	2.0	5.3	–	–
U5a1	2.0	–	–	–
U7	5.1	–	–	–
K	3.1	–	–	–
J1b1	2.0	–	–	–
J2	10.2	–	–	–
T	4.1	–	–	–
T1	3.1	–	–	–
H	–	10.5	4.2	–
H2	3.1	–	–	–
H3	6.1	–	–	–
H8	–	–	4.2	–
H*	5.1	–	–	–
V	1.0	–	–	–
W*	–	2.6	–	–
A	3.1	7.9	–	3.9
F	1.0	23.7	–	2.0
C	17.3	15.8	33.3	84.3
Z	–	2.6	4.2	–
D	8.2	2.6	29.2	9.8
G	6.1	–	–	–
M*	1.0	–	–	–

Note: Haplogroup frequencies in Mansi and Evenks were taken from [8, 26], respectively.

The discovery of "Early Paleolithic" haplogroups U4 and U7 in Mansi led to a suggestion that these mtDNA lineages represent a genetic trace left in the region between Ob and Yenisey Rivers by the migrations of proto-Eurasians formed in the Near East [10]. Indeed, a remarkably higher than in all other populations frequency of haplogroup U4 [23, 24] was found not only in Mansi, Kets, and Nganasans (Table 2), but also in Northern Altaians (18.5%) (our unpublished data). High intragroup diversity of clusters H and U (Table 2) typical of Kets and other Uralic-speaking populations also favors the hypothesis of proto-Eurasian trace. Moreover, according to some estimates, founder haplotypes of haplogroups H and U arose in the Near East 23 000 and 52 000 years ago [25, 27].

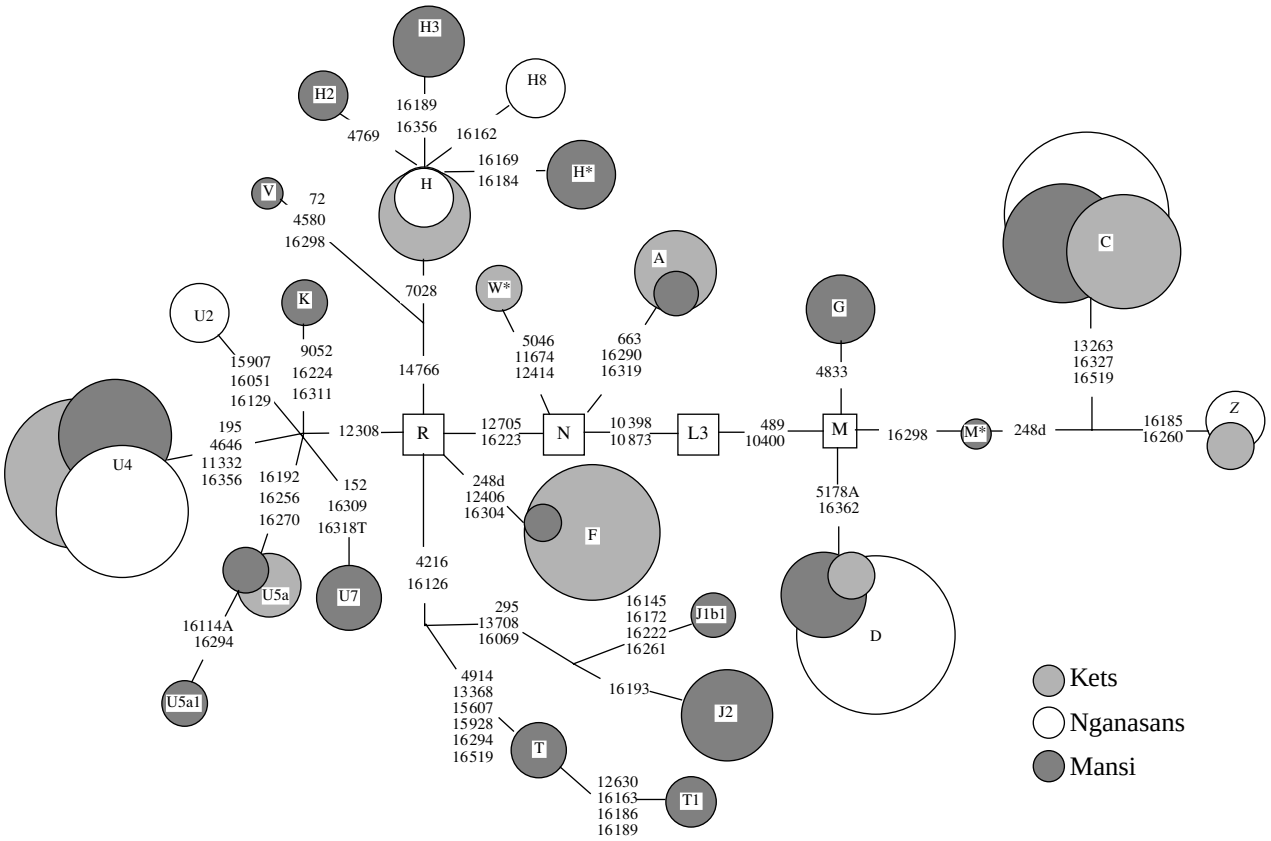

Fig. 2. Phylogenetic reconstruction of mtDNA haplogroups from Mansi, Kets, and Nganasans. The areas of circles are proportional to the number of individual mtDNAs. Mutations are transitions, unless the base change is explicitly indicated. Root macrogroups, R, N, L3, and M, are designated by square boxes [30].

Thus, mitochondrial gene pool of the ancient populations of West and Middle Siberia is distinguished for unique combination of European-specific (H, H2, H3, H8, U2, U4, U5, U7, J2, and W) and Asian-specific (A, C, D, and Z) mtDNA haplogroups, originating from the ancestor Eurasian haplogroup L3. The results of phylogenetic analysis (Fig. 2) are consistent with the idea of Bunak [28] on the "independent Eurasian formation," which was developed as a result of early expansion from the Near East rather than due to late displacements of ancient Caucasoids and Mongoloids [29].

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