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# The Effect of Marriage Migration on the Genetic Structure of the Taimyr Nganasan Population: Genealogical Analysis Inferred from MtDNA Markers

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**Abstract**—The marriage structure of Nganasans during the time period from 1796 to 1991 and genealogy of carriers of mitochondrial DNA haplotypes was studied in a sample of 280 individuals. It was shown that, from the beginning of its formation to the late 1970s, the population exhibited high endogamy (1976, 83.8%; 1926, 88.4%; 1976, 74.3%). The main source of traditional marriage migration (preferentially female) was populations of Entsy and, indirectly, Nentsy. Intense assimilation of Nganasans by the immigrant population, and to a lesser extent, by Dolgans, in the second half of the 20th century resulted in a reduction of endogamy index in Avam Nganasans to 42.5% by 1991. Assimilation by the immigrants was predominantly paternal, promoting preservation of the historically formed genetic diversity of the Nganasan mitochondrial gene pool. Genealogical analysis of mtDNA haplotypes showed that a relatively high total frequency of Western Eurasian mtDNA haplogroups (20.4%) in the Mongoloid (according to anthropological type) Nganasan population is explained not only by the common ethnic origin with Entsy and Nentsy, but also by direct marriage migration from the Entsy population and indirect marriage migration, from the Nentsy population. This migration led to accumulation of Entsy–Nentsy maternal lineages in the genealogy of Avam Nganasans (38.9 in 2000 of the total number). Of all mtDNA haplotypes, seven (of 21) were introduced to Avam Nganasans by female Entsy and Nentsy, whereas the total frequency of these haplotypes was 0.204. Genetic diversity of mitochondrial DNA haplotypes was 0.935.

## INTRODUCTION

Nganasans are the northernmost Eurasian ethnic people, which colonized the hard-accessible and climatically severe tundra zone of the Taimyr Peninsula. This is a unique population of the aboriginal inhabitants of Siberia, which has completely formed about 300 years ago. Up to the mid-1970s, this ethnic group was in essence an anthropological isolate. In 2000, the total size of the Nganasan population was 855 (according to the Regional Statistical Department, Taimyr Autonomous Region, town of Dudinka), including 671 individuals living in settlements of Ust'-Avam, Volochanka, and 74, in the settlement of Novaya. The brief history of the development and the genetic and demographic population structure of the Nganasan population in the 1970s, were described earlier [1–10]. Based on the data on polymorphism of blood groups, isozymes, serum proteins, and immunoglobulin (Gm) allotypes, it has been shown that the Nganasan population, being virtually devoid of Caucasian components, displays high frequencies of North Mongoloid haplotypes *Ns*, *cDE*, *Gm* (*za*;...; *b035st*), and alleles *Hpa*<sup>2</sup> and *Fy*<sup>a</sup> [1, 2, 6, 10, 11]. However, a recent discovery in Nganasans of a unique combination of Western and Eastern Eurasian mtDNA hap-

logroups [12, 13] motivated an in-depth analysis of their genetic structure. The aim of the present study is examining the effect of marriage migration and ethnic history on the genetic structure of the Nganasan population inferred from mtDNA markers.

## MATERIALS AND METHODS

The demographic data were collected by T.V. Goltsova during expeditions to Taimyr (settlements of Ust'-Avam and Volochanka in 1974 through 1976, and in 1991; Novaya settlement, in 1978). The main methods of collecting data were interviews of the family members, analysis of archive data of management accounts for 1954–1978, 1991 and the census of 1796 [14]. For each family, in which at least one of the spouses was a Nganasan, the following information was recorded: place of birth and residence; routes of migrations of ancestors; ethnic and kin attribution; relatives in ascending and lateral lineages; adopted and illegitimate children; earlier marriages of the spouses. The index of metisation was estimated from the pedigree as the total probability of inheriting by the probands of the arbitrary gene for “ethnicity” from immigrant ancestors of

another (not Nganasan) ethnic group. The index was computed as follows: the values of  $\alpha_i = (1/2)^n$  (where  $n$  is the number of steps in the pedigree from the immigrant ancestor to the probands and  $i$  is the number of immigrant ancestors of the proband) were calculated for all immigrant ancestors in the proband's pedigree and then summed over all  $i$ 's. In addition, the data on the marital structure in Nganasans and Entsy from works by Dolgikh [15] were analyzed. Osipova and Karafet collected 280 blood samples during an expedition of 2000 in Ust'-Avam, Volochanka, and Dudinka (Taimyr Autonomous Region). Sampling of peripheral venous blood was conducted after filling out a questionnaire and giving a written informed consent by the subjects examined. Analysis of pedigrees three to four generations in depth identified 107 subjects not related maternally, while a further increase of depth of the analysis up to four–seven generations allowed combining the initially independent maternal lineages into nuclear families, thereby limiting their number to 54. Children of recent mixed marriages of Nganasans with Dolgan women were excluded from analysis of mtDNA haplotype distribution. The genealogical stage of analysis is of key significance for population-genetic studies, because it permits maximum validity of estimating (reconstructing) the historically formed genetic diversity of Nganasans along the maternal lineage and in this connection estimate the contribution of traditional marital migrants before the assimilation of Nganasans by other aboriginal peoples and immigrant populations in the second half of the 20th century.

Genotyping of mtDNA haplotypes was performed at Estonian Biocenter (Tartu) by S.I. Zhadanov. Genomic DNA was extracted from a suspension of cell elements by phenol–chloroform procedure after incubation with proteinase K [16]. The primary nucleotide sequence was determined for I (16024–16383) hypervariable segment of the control mtDNA region HVS-1 using ABI 377A Automated DNA Sequencer (Applied Biosystems) and fluorescence terminating kit DYE-namic ET (Amersham Pharmacia Biotech). To amplify these segments and sequence the amplified DNA fragments, primers of the complementary sequence were used both for light and heavy mtDNA strands. Mitochondrial haplogroups were identified by restriction mapping of informative polymorphic mtDNA sites after their amplification in PCR [17–19]. Genetic diversity of mtDNA types was estimated as  $H = (1 - \sum x_i^2)N/(N - 1)$  [20], where  $x_i$  is the population frequency of the mtDNA haplotype and  $N$  is the sample size.

*History of the Nganasan population.* Ethnographic studies [21–24] indicate that the Nganasan population has formed as a result of assimilation of Paleoasian people by Samodians (including the ancestors of Tundra Entsy) coming from the south and Tunguses. According to these sources, five major ancestral Nganasan groups formed prior to the 17th century: Kuraks (Kosterkins) and Pyasid Samoyeds (Momde), who are

descendants of the Paleoasians assimilated by Samodians arrived from the south; Tavgi (Chunanchar and Porbins) and Vanyadyrs (the future Vadey Nganasans) resulting from the Tungus assimilation of Paleoasians; and Tidirises (Turdagins)—descendants of Tunguses assimilated by Kuraks, Pyasid Samoeds, and ancestors of Tundra Entsy. Paleoasian and Tungus languages were lost, and Nganasans adopted Samodian as their language [21].

Yenisei Nentsy and Entsy, western neighbors of Nganasans, are closest to the latter in language and ethnic origin [24]. Nentsy, Entsy, and Nganasans have a common anthropological type with Mongoloid features increasing in this series [25]. The evidence on anthropological similarity of these three ethnic groups is in good agreement with the results of analysis of genetic distances between 28 Siberian populations at 62 diallelic markers of nonrecombining Y-chromosomal regions [26], which showed that similarity of Nentsy, Entsy, and Nganasans are most similar to one another.

For better understanding of the modern ethnic history of Nganasans and estimating the contribution of neighboring ethnic groups to their gene pool, including mitochondrial one, the marriage structure of Nganasans should be examined.

## RESULTS AND DISCUSSION

### *Dynamics of Marriage Structure in Nganasans*

Inhabiting extensive territories of Taimyr tundra from the Yenisei River shores at the west to the Kheta and Khatanga rivers at the east, Nganasans from the ancient times have been migrating in small groups on parallel routes southward and back following wild reindeer [21]. This nomadic life created intrapopulation isolation, which was counterbalanced by marital migration, caused by traditional taboo on marriages between close relatives up to second cousins [5]. Although the migration territory considerably reduced in the mid-20th century, the character of spreading of the Avam and Vadey Nganasans was largely preserved: the descendants of the Avam Nganasans migrating by western routes predominantly inhabit the settlement of Ust'-Avam, and descendants of those migrating by central routes, in Volochanka, while the Vadey Nganasans traditionally inhabit the easternmost areas (Novaya).

Table 1 presents the dynamics of the Nganasan traditional marriage structure over the period of two centuries. The Entsy population was virtually a single source of marital migrants (mainly women) for Nganasans from the late 18th century to the 1920s. This is in good agreement with the data by Dolgikh [15]. Predominantly Avam Nganasans contracted marriages with Entsy women, which is supported by the results of the estimation of Nganasan metisation index (our data of 1976) as an indicator of migration gradient of the "Entsy genes" to three Nganasan subpopulations. As seen from Table 2, metisation index significantly

**Table 1.** Matrix of the traditional marriage structure of Nganasans in 1796, 1926, 1976–1978, and 1991

Marriage type	Frequency of marriage types in subpopulations (% of the total marriage number)					
	Avam Nganasans				Vadey Nganasans	
	1796* <i>n</i> = 117	1926** <i>n</i> = 114	1976*** <i>n</i> = 170	1991*** <i>n</i> = 188	1926** <i>n</i> = 33	1978*** <i>n</i> = 33
Between Nganasans from one subpopulation	78.6	71.1	48.8	38.3	27.3	36.4
Between Nganasans from different subpopulations	5.2	14.0	21.8	4.2	72.7	57.6
Nganasans–Entsy	16.2	14.9	7.7	3.7	0.0	0.0
Nganasans–Nentsy	0.0	0.0	2.4	1.6	0.0	0.0
Nganasans–Dolgans	0.0	0.0	10.0	16.0	0.0	3.0
Nganasans–Immigrants	0.0	0.0	9.4	31.9	0.0	3.0
Other marriages	0.0	0.0	0.0	4.3	0.0	0.0
Total	100.0	100.0	100.0	100.0	100.0	100.0
Endogamy index for Avam and Vadey Nganasans	83.8	85.1	70.6	42.5	100.0	93.9
Endogamy index for Nganasans in total	1926—88.4; 1976–1978—74.3					

Note: *n*, the number of marriages.

\* Estimated by us based on the 1796 census of Avam Samoyeds (Nganasans) [14].

\*\* Estimated by us using the data of Table 4 in Dolgikh's article [15].

\*\*\* Our data.

**Table 2.** Mean Nganasan–Entsy metisation index ( $\bar{x} \pm s_x$ ) by the paternal and the maternal pedigree lineages in settlements of Ust'-Avam, Volochanka, and Novaya (1976–1978)

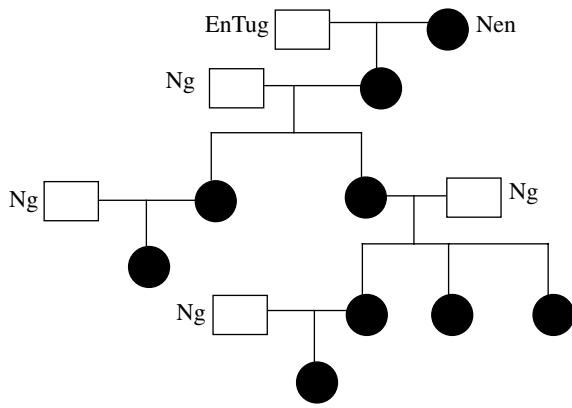
Parameters	Avam Nganasans from two settlements		Vadey Nganasans, Novaya settlement	Total
	Ust'-Avam	Volochanka		
<i>n</i>	225	350	119	694
$\bar{x} \pm s_x$	0.270 ± 0.014	0.138 ± 0.009	0.021 ± 0.005	0.163 ± 0.007

Note: *n*, the number of people for which metisation index was calculated; differences between settlements significant at  $P < 0.001$ .

declines from 0.270 to 0.021 from the west eastwards—from Ust'-Adam and Volochanka (Avam Nganasans) to Novaya (Vadey Nganasans). A decrease in frequency of mixed marriages with Entsy was caused by a reduction in the migration territory of Nganasans and an increase in their distance from the Entsy migration routes, which resulted from the construction of Soviet collective farms, settlements and partial settling of Nganasans in the mid-20th century. Female Nentsy proved to be founders of 4.1% of maternal lineages in Nganasan pedigrees in 1976 and of 5.9%, in 1991, which is probably explained by stepwise marriage migration of women in the Nentsy–Entsy–Nganasans series. This suggestion is based on Dolgikh's data that in 1926, the Yenisei Nentsy population had 65 families that were not assimilated by Dolgans and Russians, in which the proportion of marriages of Entsy men with Nganasan women was 20%, and with Nentsy women, 26.2% [15]. Although when Nganasan men chose wives outside their population, they preferred Entsy women, who are closest to them in language and life

style, the presented data on the marriage structure among Entsy indicate that the future wife could be the Entsy–Nentsy metis, as shown in the pedigree in Fig. 1. Another variant of Nentsy contribution to the Nganasan population is a rare practice of adoption of Nentsy orphans by Nganasan families. An example is a founder of a maternal lineage, Nentsy woman Biyuptar, an adopted daughter from the Nganasan family of Turdagins. The process of partial mutual assimilation of Entsy and Nentsy has started as early as in the 17th century, which, in particular, resulted in the formation of Entsy clans originated from Nentsy—Tadobe (Sovalovs) and Bunalya (Tuglakovs), whose women married Nganasans [24].

The marriage structure of Nganasans significantly changed in the second half of the 20th century because of assimilation by immigrants and by Dolgans. According to Simchenko [22], in 1966 mixed marriages with these groups constituted less than 1%. Our data show that marriages with Dolgans accounted for 10.0% of the total marriage number in 1976 and 16.0% in 1991



**Fig. 1.** Pedigree of haplotype *U2e*: 051, 086, 129C, 183C, 189, 256, 362, 365 carriers (descendants of a Nentsy woman) in the Nnganaskan population. Nen, Nentsy; Ng, Nnganaskan; EnTug, the Entsy man Tuglakov. Here and in Figs. 2, 3, maternal offspring are designated by dark color.

(Table 1). Particularly interesting for reconstructing the Nnganaskan mitochondrial gene pool is analysis of the marriage dynamics with immigrant (Caucasoid) people. The data presented in Table 1 show that the frequency of this marriage type increased from 9.4% in 1976 to 31.9% in 1991 in places of dense Nnganaskan dwelling. As demonstrated by Dolgikh [15], Nnganaskans contracted marriages with immigrants since the second half of the 19th century. In 1795 through 1902, eleven Nnganaskan men registered their marriage with Russian women in church and one Nnganaskan man contracted marriage with a Dolgan woman [15]. These were poor Nnganaskan men, who had left their population and lived in the vicinity of Russian settlements, working as hired hands. They were often baptized Christians and gradually assimilated by the Russian population or, together with Russians and Yakuts, adopted Yakut language and joined the nascent Dolgan ethnic group. The offspring of these marriages did not return to their population. Only one marriage of a Nnganaskan from the Ngomde clan with the Russian Zatundrin peasant woman Barkhatova (contracted in 1856) is known, by which a woman, who was officially recognized as a Russian, joined the Nnganaskan community. However, this woman, as all Zatundrin peasants, could be a metis with a Tungus, Yakut, and (or) Nnganaskan admixture [15]. Based on genealogical analysis, we failed to reveal representatives of immigrant Caucasoids among the ancestors of Nnganaskans inhabiting the traditional territories.

As seen from Tables 3 and 4, Nnganaskan women contracted mixed marriages with immigrants far more frequently than men: the frequency of their marriages increased from 8.8% in 1976 to 30.3% in 1991. During this time, Nnganaskan men contracted very few marriages with Russian women: 0.6% in 1976 and 1.6% in 1991; their allegedly “Russian wives” proved to be illegitimate daughters of Nnganaskan women by Russian men.

Thus, based on ethnographic studies, census data, and our demographic–genealogical evidence, we showed that prior to 1991, Nnganaskan assimilation was biased with regard to sex (marriages with Russian women were virtually absent). This suggests that inflow in the Nnganaskan gene pool of Western Eurasian genes, characteristic of the modern immigrants, occurs mainly by paternal lineage. As to mixed marriages of Nnganaskans with Dolgans, the inflow of “Dolgan genes” in the Nnganaskan population by the maternal lineage remains insignificant.

This permits a correct reconstruction of the maternal gene pool structure of Nnganaskans before the assimilation processes started in the 20th century and assessment of the effect of traditional marriage migration from populations of Entsy and Nentsy inferred from mtDNA genetic markers.

#### *Distribution of mtDNA Haplogroup and Haplotype Frequencies*

In Table 5, frequencies of main Western and Eastern Eurasian mtDNA haplogroups and haplotypes are presented. As expected, Nnganaskans exhibit a high frequency of Eastern Eurasian mtDNA haplogroups (0.796). However, our results support the earlier evidence [12, 13] on a relatively high frequency of Western Eurasian haplogroup *U* and, in particular, its sub-haplogroup *U4*, which, according to our estimates, reaches a frequency of 0.130.

The total frequency of Western Eurasian mtDNA haplogroups in the Nnganaskan population was 0.204, which is considerably lower than the corresponding frequency (0.334) presented by Derbeneva *et al.* [12]. This discrepancy can be explained by either mixed composition of the sample (Entsy and Nnganaskans) or its small size ( $N = 24$ ) in [12]. In addition, the number of generations in pedigree analysis was not given in this publication. In another study of the same Nnganaskan sample [13], the pedigree analysis involved only three generations. Because of this, maternal lineages, which would be grouped in one nuclear family in deeper analysis, were considered independent (see Materials and Methods of the present article).

As shown in Table 6, in 1976 Entsy women founded 29.6% maternal lineages in the Nnganaskan pedigrees in total, including 32.5% in the Avam Nnganaskans and 7.1%, in Vadey Nnganaskans. These data are in a good agreement with the value of metisation index (Table 2), estimated for the part of the Nnganaskan population that was not mixed with Dolgans and immigrants. As noted above, 4.1% of maternal lineages in 1976 and 5.9% in 1991 were of the Nentsy origin. The proportion of the Entsy contribution in the Nnganaskan pedigrees is more significant than supposed on the basis of the frequency of mixed marriages with Entsy (Tables 1, 3, 4), which is probably explained by accumulation of Entsy mater-

**Table 3.** Marriage structure of Avam Nganasans (total for Ust'-Avam and Volochanka), 1976 (marriage proportion \* in the total number, %)

Husband (ethnicity)	Wife (ethnicity)					Total ( <i>n</i> = 170)
	Nganasans	Entsy	Nentsy	Dolgans	immigrants	
Nganasans	70.6	5.3****	1.2**	4.7	0.6***	82.4
Entsy	2.4****	0	0	0	0	2.4
Nentsy	1.2**	0	0	0	0	1.2
Dolgans	5.3	0	0	0	0	5.3
Immigrants	8.8	0	0	0	0	8.8
Total	88.2	5.3	1.2	4.7	0.6	100.0

\* Including marriages (and women with illegitimate children) with first-generation Entsy–Nganasans, Dolgans–Nganasans, Nentsy–Nganasans metises.

\*\* All Nentsy (four individuals) are offspring of one man; of them, three are full sibs by Nganasan mother and Nentsy father, and one is a half-sib by father (with a Nentsy mother).

\*\*\* A single short marriage of a Nganasan man with a Russian woman. After divorce, the woman left the region with the single child of this marriage.

\*\*\*\* 13 individuals attributed to Entsy are representatives of nine paternal Entsy lineages and nine maternal lineages; of the latter, six are Entsy and three are Nganasan.

**Table 4.** Marriage structure of Avam Nganasans (total for Ust'-Avam and Volochanka), 1991 (marriage proportion\* in the total number, %)

Husband (ethnicity)	Wife (ethnicity)					Total ( <i>n</i> = 188)
	Nganasans	Entsy	Nentsy	Dolgans	immigrants	
Nganasans	42.5	1.6	0.5	5.9	1.6**	52.1
Entsy	2.1	0.0	0.0	0.05*	0.0	2.6
Nentsy	1.1	0.0	0.0	0.0	0.0	1.1
Dolgans	10.1	0.05*	0.05*	0.0	0.0	11.2
Immigrants	30.3	1.6*	0	1.1*	0	33.0
Total	86.2	3.25	0.55	7.05	1.6	100.0

\* Including marriages (and women with illegitimate children) with first-generation Entsy–Nganasans, Dolgans–Nganasans, Nentsy–Nganasans metises.

\*\* Illegitimate daughters of Nganasan women by immigrant men.

nal lineages in the Nganasan pedigrees owing to permanent marriages with Entsy women in the past.

It is of interest to compare frequencies of mtDNA haplogroups in Nganasan proper (the lineages whose founders were Nganasans) and Entsy–Nentsy (the founder was a Entsy or a Nentsy woman) maternal Nganasan lineages (Table 5). The frequency of Western Eurasian haplogroups in the Nganasan lineages proper was 0.152, whereas in the Entsy–Nentsy lineages, it was almost twofold higher (0.286). The greatest contribution in these differences was made by subhaplogroups *U2*, *U5*, and haplogroup *T*, which are completely absent in the Nganasan maternal lineages. The frequencies of the Eastern Eurasian mtDNA haplogroups in the both lineages are slightly different (0.848 and 0.714, respectively). However, the differences between individual haplogroups are more pronounced. Subhaplogroup *D4* occurred only in the Entsy (0.238) lineages and haplogroup *A*, only in Nganasan (0.121)

lineages. All these differences are statistically nonsignificant because of the small sample size. However, this sample is based on blood specimens of 280 Nganasans from the settlements of Ust'-Avam and Volochanka, including children from these settlements living in a boarding school in the town of Dudinka. In all, this sample represents 41.7% of all Nganasans living in these settlements and covers 87.1% of maternal lineages, for which at least one descendant was alive by 2000. Thus, using traditional methods of mathematical statistics in small isolated populations, in which individuals are related in many generations, is not efficient and leads to a contradiction: the deeper the pedigree analysis, the higher the significance of identification of independent (unrelated) maternal lineages, but the smaller the sample size (the number of maternal lineages). In view of this, we considered the differences detected as being worth further examination and con-

**Table 5.** Distribution of mtDNA haplotype and haplogroup frequencies in the Avam Nganasan population, 2000

Haplogroup	Haplotype (HVS-I)	Number of maternal lineages ( <i>n</i> = 54)	Haplotype frequency	Haplogroup frequency		
				population in total ( <i>n</i> = 54)	Nganasan maternal lineages ( <i>n</i> = 33)	Entsy and Nentsy maternal lineages ( <i>n</i> = 21)
Western Eurasian (total)		<b>11</b>		<b>0.204</b>	<b>0.152</b>	<b>0.286</b>
<i>U</i>		9		0.167	0.121	0.238
Including: <i>U4</i>		7		0.130	0.121	0.143
	<i>I34, 356</i>	4	0.074			
	<i>I89, 356</i>	3	0.056			
<i>U2e</i>		1	0.018	0.018	0.000	0.048
<i>U5</i>		1	0.018	0.018	0.000	0.048
<i>T</i>	<i>I26, I63, I86, I89, 261, 294</i>	1	0.018	0.018	0.000	0.048
<i>H</i>	<i>CR5</i>	1	0.018	0.018	0.030	0.000
Eastern Eurasian (total)		<b>43</b>		<b>0.796</b>	<b>0.848</b>	<b>0.714</b>
<i>C</i>		18		0.333	0.394	0.238
Including:		5	0.093			
	<i>093, 223, 298, 327</i>	2	0.037			
	<i>I48, 223, 288, 298, 327</i>	9	0.167			
	<i>223, 260insA, 298, 311, 327</i>	1	0.018			
	<i>I45, I71, 223, 298, 327, 344, 357</i>	1	0.018			
<i>Z</i>	<i>I29, I85, 223, 224, 260, 298</i>	2	0.037	0.037	0.000	0.095
<i>D</i>		15		0.278	0.242	0.333
Including:		7	0.130	0.167	0.212	0.095
	<i>223, 362</i>	1	0.018			
	<i>223, 362, 368</i>	1	0.018			
	<i>I70, 223, 362</i>	1	0.018			
<i>D4</i>		5		0.093	0.000	0.238
	<i>223, 319, 362</i>	4	0.074			
	<i>093, 223, 239, 243, 319, 362</i>	1	0.018			
<i>D5</i>		1	0.018	0.018	0.030	0.000
	<i>I72, I82C, I83C, I89, 223, 266, 362</i>	3	0.056	0.056	0.061	0.048
<i>G2a</i>	<i>086, I72, 223, 227, 278, 362</i>	4	0.074	0.074	0.121	0.000
<i>A</i>	<i>223, 227C, 230, 256, 290, 311, 319</i>	1	0.018	0.018	0.030	0.000
<i>Y</i>	<i>I26, I89, 231, 266</i>	1	0.018	0.018	0.030	0.000

**Table 6.** Distribution of maternal lineages in the population of Avam (Ust'-Avam, Volochanka) and Vadey (Novaya) Nganasans according to ethnicity in 1976–1978 (%)

Maternal lineages (from pedigrees)*	Avam Nganasans (n = 83)	Vadey Nganasans (n = 28)	Total for population (n = 98)
Nganasan	63.9	89.3	66.3
Entsy	32.5	7.1	29.6
Nentsy	3.6	3.6	4.1
Entsy + Nentsy	36.1	10.7	33.7
Lineages descending from immigrants	0.0	0.0	0.0
Total	100.0	100.0	100.0

\* Dolgan maternal lineages are not included, because marriages of Nganasans with Dolgan women were extremely rare before 1966, constituting 4.7% and 5.9% of all Nganasan marriages respectively in 1976 and 1991, respectively.

ducted genealogical analysis of individual carriers of HVS-1 mtDNA haplotypes.

#### *Genealogical Analysis at Individual mtDNA Haplotypes (HVS-1)*

It was established that out of seven maternal lineages carrying the most common Western Eurasian haplogroup *U4*, only three (with mtDNA haplotypes *U4: 189, 356* and *134, 356*) ascend to Entsy. Both haplotypes occur both in Entsy and in Nentsy lineages, which is confirmed by the absence of differences in the *U4* subhaplogroup frequency between them (Table 5). Apparently, this is explained by an ancient origin of this subhaplogroup and its wide distribution not only among Samodians but also in other peoples, primarily in those belonging to the Ural linguistic family [27, 28]. This does not permit to differentiate the effect of relatively late Entsy migrations from other events preceding the ethnic history of Nganasans. At the same time, haplotype *U4: 134, 356* occurs not only in Nganasans, but also in Dolgans (our unpublished data), which, at the first glance, is not consistent with the late onset of the aforementioned Nganasan mixing with Dolgans (second half of the 20th century). However, ethnographic sources recorded a practice of marrying Nganasan young women to Zatundrin peasants as well as residence of Nganasan orphans in their families, which, in their turn, since the late 18th century participated in forming the Dolgan ethnic group [15]. For instance, in the 1796 census record of Avam Samoeds (Nganasans), we have found an item on two young women from Nganasan families that were married to the Zatundrin peasant Andreyan Turkin and bourgeois Gavrila Aksenov. These family names are currently quite common in Dolgans, including those in mixed marriages with bourgeois. Thus, the observed similarity with Dolgans in haplotype *U4: 134, 356* may be explained by a unidirectional in the past migration of Nganasan young women and girls to the Dolgan ancestors.

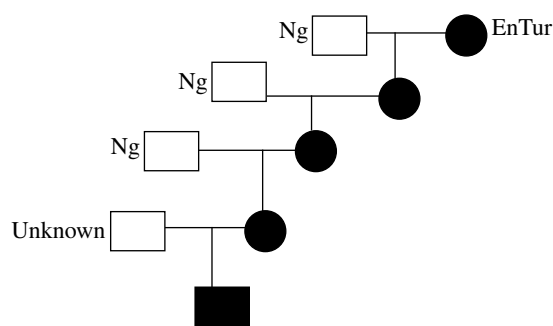
Haplotype *U2e: 051, 086, 129C, 183C, 189, 256, 362, 365* is represented in Nganasans by a single mater-

nal lineage ascending in generation 5 (late 19th century) to a Nentsy woman (Fig. 1). Her daughters from the marriage with the Tundra Entsy Tuglakov, which were considered Entsy by their father, married Nganasan men. The pedigree of this maternal lineage demonstrates a pathway of indirect transfer of the given Western Eurasian mtDNA haplotype from the Nentsy population via the Entsy one, in which the Nentsy woman married a Entsy man, to Nganasans, where her daughter married a Nganasan in the late 1930s and her granddaughters also married Nganasan men.

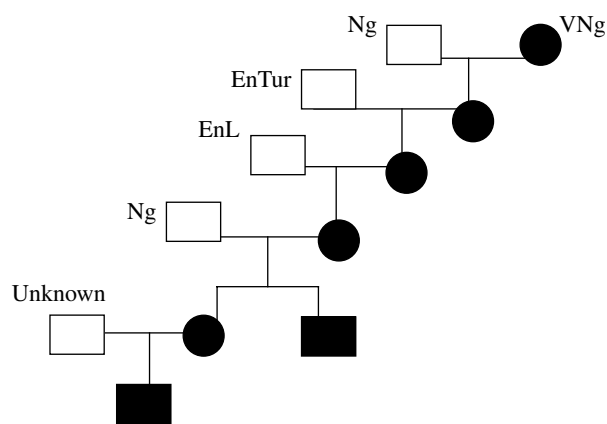
The presence of a single carrier of haplotype *U5: 172, 189, 270* is related to a single migration in the 1950s of the Entsy (by both parents) man Mirnykh Denchuda to the settlement of Volochanka, where he married a Nganasan; although he has six children and five grandchildren, this haplotype will be lost from the population. The pedigree of the single carrier of haplotype *T: 126, 163, 186, 189, 261, 294* ascends to a Forest Nentsy woman Turutina (Fig. 2), who at the brink of the 20th century married a Nganasan. A single maternal lineage bearing haplotype *H: CRS* found in Nganasans could be explained by a sporadic entry of Europeans in the Nganasan population, as was described above on example of the marriage of the Russian woman Barkhatova with a Nganasan. Nevertheless, we could not find Russian ancestors in the pedigree of the carrier of this haplotype (Fig. 3), and this lineage was founded in the sixth generation by a Vadey Nganasan woman.

Thus, the results of the genealogical analysis suggest that the diversity of mtDNA haplotypes, belonging to Western European haplogroups and subhaplogroups *U2, U5, and T* in modern Nganasans, is associated with marriage migration from the Entsy population.

As to the Eastern Eurasian mtDNA haplogroups, the main contribution to the differences between Nganasan and Entsy maternal lineages is made by haplotype *D: 223, 319, 362* (subhaplogroup *D4*), recorded only in Entsy–Nentsy maternal lineages, as well as haplotype *D: 172, 182C, 183C, 189, 223, 266, 362* (subhaplogroup *D5*) and haplotype *A: 223, 227C, 230, 256, 290*,



**Fig. 2.** Pedigree of haplotype *T*: 126, 163, 186, 189, 261, 294 carriers. EnTur, the Entsy woman Turutina; Ng, Nagnasan; unknown, father unknown.



**Fig. 3.** Pedigree of haplotype *H*: CRS carriers. EnTur, Entsy man Turutin; EnL, the Entsy man Ledovaiko; VNg, Vadey Nagnasan woman; Ng, Nagnasan; unknown, father unknown.

311, 319, which are present only in Ngnasan maternal lineages.

Haplotype *A*: 223, 227*C*, 230, 256, 290, 311, 319, found in four Ngnasan maternal lineages, seems to be unique for Siberian peoples. In general, haplogroup *A* ubiquitously occurs in Mongoloid Siberian populations [29–33]. To establish its origin in Ngnasans, further study of mtDNA is required in the Vadey Ngnasans and Dolgans, as well as in Western groups of Evenks—descendants of Tunguses who have contributed to the formation of Ngnasans and Dolgans. Haplogroups *D* and *C* in Ngnasans are characterized by higher haplotype variety, which is in a good agreement with the data on other Siberian populations: Evenks [29], Tuvinians [30], Khakasses [31], Yakuts [32], and Altaians [33, 34]. The most common haplotypes in Ngnasans are *C*: 148, 223, 288, 298, 327 (frequency 0.167). Interestingly, the maternal lineages with these haplotypes were founded by Ngnasan women as well as by Entsy and Nentsy ones. This indirectly testifies to the existence of a common ethnogenetic substrate for the three Samodian ethnic groups. As to the other *D* and *C* haplotypes, they are distributed among Entsy and Ngnasan women in the following way. Haplotype *C*: 223, 260*insA*, 298, 311, 327 ascends to the Forest Entsy woman Silkina, and haplotype *C*: 145, 171, 223, 298, 327, 344, 357, to the Vadey Ngnasan woman Kyntuna. Of particular interest are haplotypes *D*: 223, 319, 362 and *D*: 093,

223, 239, 243, 319, 362 (subhaplogroup *D4*). Five maternal lineages were found, all of which ascend to the Entsy women Turutins, who married Ngnasan men in the late 19th century. Thus, the source of these haplotypes in the modern Ngnasan population is exactly Forest Entsy women. The total frequency of haplotypes introduced by marriage migration of Entsy and Nentsy women and characteristic only of Entsy–Nentsy maternal lineages (*U2e*: 051, 086, 129*C*, 183*C*, 189, 256, 362, 365; *U5*: 172, 189, 270; *T*: 126, 163, 186, 189, 261, 294; *D*: 223, 319, 362; *D*: 093, 223, 239, 243, 319, 362; *C*: 223, 260*insA*, 298, 311, 327; *Z*: 129, 185, 223, 224, 260, 298) was 0.204, and their number (seven haplotypes) constituted 28.6% of all mtDNA haplotype number in the Ngnasan population.

Index of genetic diversity estimated for the Ngnasan population from mtDNA haplotype frequencies was 0.935. This value is higher than in Chukchi, Eskimos [35] and Itelmens [36], but lower than in other ethnic groups of Northeastern Asia and those from the Turkic linguistic family [32].

The significance of Entsy–Nentsy marriage migration for the formation of the Ngnasan gene pool is confirmed by some results of genealogical analysis of car-

**Table 7.** Frequencies of classical Caucasoid and Mongoloid traits in the populations of Ngnasans, Entsy, and Nentsy

Genetic markers	Forest Nentsy	Tundra Nentsy	Entsy	Ngnasans	Reference
Europeoid					
<i>Gm</i> ( <i>f</i> , ...; <i>b</i> )	0.074		0.032	0.008	[7, 9, 39]
<i>cde</i>	0.068	0.083	0.056	0.021	[8, 37, 40]
Mongoloid					
<i>Gm</i> ( <i>za</i> ; ...; 035 <i>st</i> )	0.199		0.276	0.486	[7, 9, 39]
<i>Ns</i>	0.487	0.622	0.593	0.702	[11, 37, 38]
<i>Fy<sup>a</sup></i>	0.809	0.752	0.732	0.906	[11, 37, 38]
<i>Hp<sup>2</sup></i>	0.610	0.654	0.717	0.767	[11, 37, 38]



riers of classical Caucasoid genetic markers (Table 7). The table shows that, as compared to Nentsy and Entsy, Nganasans have the lowest total frequencies of Caucasoid and the highest frequencies of Mongoloid genetic markers. Earlier, it was demonstrated that a low frequency (0.008) of the "Caucasoid" genotype *Gm* (*f*; ...; *b*) in the Nganasan population was fully explained by the presence of two families carrying this *Gm* haplotype (one of the families was founded by a Entsy, and the other, by a Nentsy woman) [7, 9]. It was also shown that the descendants of the Entsy woman Pil'ko (Fil'ko) were carrying both the Western Eurasian mtDNA subhaplogroup *U4* and haplotype *Gm*(*f*; ...; *b*).

Thus, the results of the integral demographic, genealogical, and molecular-genetic analysis suggest that the mitochondrial gene pool of Nganasans was influenced not only by different ethnic components involved in the population formation, but also by direct or indirect marriage migration of women from neighboring populations of Entsy and Nentsy. Apparently, this explains the relatively high genetic diversity of mtDNA in the Nganasan population. The results of studying the assimilation dynamics of Nganasans by the immigrant populations showed that, in spite of a sharp increase in intensity of this process since the second half of the 20th century, it involves mainly male lineages and thus does not disturb the historically formed genetic diversity of the Nganasan mitochondrial gene pool.

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