THE YAKUT BRANCH OF Y-CHROMOSOME AS A PART OF THE HAPLOGROUP N-M2016

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http://doi.org/10.33384/26587270.2022.08.02.05e

Annotation. Based on the massive parallel sequencing, phylogenetic tree of the Y-chromosomal haplogroup N-M2016 was built. The branch N-M1982 of Yakut-Sakha men majority is located on the tree. The ages of tree branching nodes are estimated.

Time to the most recent common ancestor (TMRCA) 970 ± 210 years BP ("present" defined as AD 1950) of one of the main Yakut male lineages N-M1991 is confirmed by accelerator mass spectrometry dating of a sample of the ancient man Yana Young [1] who died about 766 yBP.

A sharp increase in the number of Yakut-Sakha ancestors observed on the Yakut branch N-M1982, began from 1320 ± 100 AD. Age of the population explosion is consistent with the radiocarbon dating of the Kulun-Atakh archaeological culture sites.

Keywords: Yakuts (Sakha), phylogenetic tree , Y-chromosome, haplogroup N-M2016, N-M1982, TMRCA

For citation: Adamov D.S. The Yakut branch of the Y-chromosome as part of the haplogroup N-M2016. 2022.2(8). P. 29 – 36. http://doi.org/10.33384/26587270.2022.08.02.05e

Received 30, September 2022, accepted for publication 19, November 2022, published 15, December 2022

Introduction. The Yakut-Sakha male population is unique in its homogeneity. Population genetics studies have revealed that about 90 % of men have a Y-chromosomes, which forms a separate cluster of Y-STR haplotypes inside the N-Tat/M178 haplogroup [2–9]. The cluster is marked with single nucleotide polymorphism (SNP) mutations M2019, M2118 [10-13].

In addition to the Yakuts, lineages of the haplogroup N-M2019/M2118 are observed with low frequency in other modern Eurasian populations [13, 14]. N-M2019/M2118 samples were found in the burials of ancient nomads in Mongolia [15, 16], Avars and early Hungarians in Hungary [17, 18]. According to Y-STR loci of ancient samples, the presence of the N-M2019/M2118 haplogroup is assumed among the Xiongnu [19] and the Khazars [20].

Due to the data obtained by massive parallel sequencing technology, it is possible to reveal the structure of the Yakut Y-chromosomal branch, as well as male branches of the Yakut closest relatives.

Materials and methods. One of the main sources of genetic information in the public domain is the HGDP database (Human Genome Diversity Project [21]). The database contains genetic samples from 1050 individuals from 52 populations. The Yakuts-Sakha is represented by samples of 18 men and 7 women. For further studies of the demography of human populations, establishing relationships and the origin of populations, genetic scientists carried out massive parallel sequencing of HGDP samples with high read quality using the Illumina X10 sequencer [21]. Out of 18 male Yakut-Sakha samples from the HGDP panel, 16 samples show the N-M2019/M2118 haplogroup.

We also used data published earlier in the scientific literature:

- Yakut samples YakK3, YakS8, YakM1, Even sample EvenS2 from [12];
- Evenk sample (SRR1822287) and Even sample (SRR1822619) from [22];
- two samples of Buryats from Hulun-Buir, Inner Mongolia Auton-

omous Region, China [23];

New samples used in the work: a sample of the Karakalpak from Uzbekistan and a sample of the author, tested in the FTDNA commercial laboratory.

To check correctness of the branch age estimations we used the data on the Y-chromosome and radiocarbon dating of the ancient Yana Young men published in [1].

Coverage of the Y-chromosome sequencing is presented in Table 1. The Table 1 also contains information about the length of the combBED ("combined BED") regions. To calculate the branch ages, reliable regions of the Y-chromosome nucleotide sequences were selected. The boundaries of the combBED regions include nucleotide sequences from the euchromatin X-degenerated and, to a lesser extent, ampliconic regions [24].

To identify SNP mutations, data on the Y-chromosome nucleotide sequences call variants recorded in PILEUP or VCF files were used. Some of the samples were missing these files. In such cases, the BAM file was processed using the Samtools software package to create the corresponding PILEUP file. The BamView program was used to view BAM files.

Single nucleotide variants were processed using the method developed by the author together with the participants of the YFull project [24]. The method makes it possible to effectively identify true mutations among various call errors, mapping errors, and other failures.

The ages of individual branches were estimated using the method described in [24]:

$$T = \frac{N_{SNP}}{\mu B},$$

where T is the estimated age of the branch,

$N_{SNP} = \Sigma_i N_i$ – the total number of observed mutations formed since the split of the branch until the present, N_i – number of mutations in each sample i,

$B = \Sigma_i B_i$ – the total length of read nucleotide sequences of all samples within the borders of the combBED region [24]. B_i – length of read nucleotide sequences in each sample i,

μ – SNP mutation rate constant, taken equal $8.2 \cdot 10^{-9}$ mutations per year per base pair [24].

Age is counted in calendar years from present time, accepted according to international tradition as 1950, into the past. The HGDP panel specimens, which make up the majority of the sample, were collected in the 1990s, and the donors were born in the 1950s and 1960s.

Calculation of the age estimation error is based on assumption of the Poisson nature of the SNP mutation process [10]. The variance is calculated taking into account the covariance:

$$D = \frac{1}{n^2}[\Sigma_i N_i + 2\,\Sigma_i \Sigma_{j>i} N_{ij}],$$

where N_i – number of mutations in each sample i,

N_{ij} – number of mutations common for samples i and j,

n – number of samples per branch.

The relative standard deviation was estimated taking into account the calibration error of the mutation rate constant σ_μ =7.3%, carried out in [24]:

$$\sigma = \sqrt{\frac{D}{N_{SNP}^2} + {\sigma_\mu}^2}$$

Time to the most recent common ancestor (TMRCA) calculation based on a sample of Y-STR haplotypes, was carried out using the ASD_0 method with a preliminary determination of the ancestral alleles [26].

$$ASD_0 = \frac{1}{L}\sum_{j=1}^{L}\frac{1}{N}\sum_{i=1}^{N}\left(A_j(i) - A_j(0)\right)^2,$$

N – sample size, L – number of STR loci in the haplotype,

$A_j(i)$ – allele value (number of tandem repeats) at locus j of haplotype i,

$A_j(0)$ – ancestral allele value.

TMRCA estimation is carried out according to the formula

$$\tilde{T} = \frac{ASD_0}{\bar{\mu}},$$

where $\bar{\mu} = \frac{1}{L}\sum_{j=1}^{L}\mu_j$ mean mutation rate constant, μ_j – mutation rate constant at STR locus j.

The sample of 17 loci Y-STR haplotypes was composed of 237 Yakut samples (see Table S1 of the Supplement). The average value of the STR mutation rate constant was taken to be 0.0026 per locus per generation of 31.5 years [27, 28]. The ancestral haplotype in sequence of loci DYS19, DYS389I, DYS389B, DYS390, DYS391, DYS392, DYS393, DYS385a, DYS385b, DYS438, DYS439, DYS437, DYS448, DYS456, DYS458, DYS635, GATAH4 was defined as:

14-14-17-23-11-16-14-11-13-11-10-14-19-14-16-22-12.

Results. The phylogenetic tree of the Y-chromosome haplogroup, called N-M2016, was constructed from the data of massive parallel sequencing of 26 samples, in accordance with the hierarchy of observed SNP mutations. The tree of the haplogroup N-M2016 is presented in Fig. 1. The SNP mutations identified in the studied samples are summarized in Table S2 of the Supplement. All mutations that occurred in the Y-chromosome sites inside the combBED region [24], as well as part of mutations read outside the combBED region, are presented.

Samples of Yakuts, Evens, and Evenks form a separate N-M1982 branch [12] within the N-M2016 haplogroup. This unambiguously confirms the founder effect, which

Sample ID	n	Reference	Mean coverage, X times	Average combBED area size, Mbp
HGDP009XX (кроме HGDP00951)	15	[21]	17	8.4
HGDP00951	1	[25]	22	8.4
YakM1, YakS8, YakK3, EvenS2	4	[12]	>40	8.4
SRR1822287, SRR1822619	2	[22]	19	8.4
HLB-061, HLB-102	2	[23]	9	6.2
YF01684	1	present study	48	7.8
496828	1	present study	50	7.3
Yana Young (ERR3351001)	1	[1]	~1	not available

Table 1. Quality of Y-chromosome reading.

was previously suggested based on the data on Y-STR haplotypes [3, 4, 7]. Separate branches include samples of the Buryat from Hulun Buir (N-F23218) and the Karakalpak (N-BY178126).

TMRCA of the main nodes of the phylogenetic tree was estimated from the number of mutations in the combBED areas. The results are presented in Table 2.

Discussion. The haplogroup N-M2016 arose as a result of the split of the haplogroup N-M2058 (this is the main branch of the haplogroup N-M2019/M2118) into two parallel branches: the studied N-M2016 and the fraternal N-B508/A9408 ([13], not indicated in Fig. 1). Haplogroup N-B508/A9408 is rare, but widespread along the western and eastern Eurasian steppe and in China. The age of the N-M2016 branch is estimated to be 3440 ± 630 yBP. The obtained date corresponds to the time of the transition of the Mongolian steppe hunter-gatherers to dairy breeding in the process of cultural transmission from more western nomads [30].

Approximately 2840 ± 540 yBP the branch N-BY178126, represented by a specimen from the Karakalpak Kandekli tribe (Karakalpakstan, Uzbekistan), separated from the parental branch N-M2016. This branch demonstrates a characteristic combination of tandem repeats 10-13 in the double Y-STR locus DYS385, while in other related branches of the N-M2019/M2118 haplogroup, an ancestral state 11-13 is commonly observed. The branch has not been identified in Europe, it is observed in Central Asia among the Mongols of Outer and Inner Mongolia, the Kazakh tribe Zhalair, the Hazaras, and the Uighurs. Apparently, haplogroup N-BY178126 is of Mongolian origin. Data on Y-STR haplotypes are in Table S1 of the Supplement.

The N-M1982 and N-F23218 branches formed as part of the N-M1987 haplogroup 2270 ± 450 yBP (Table 2, Fig. 1). The branch N-F23218 is represented on the phylogenetic tree (Fig. 1) by two samples of Buryats from Hulun Buir (Inner Mongolia, China). The authors of [31], who published the Y-STR haplotypes of these samples, call the Buryats, apparently, the New Barguts of Khulun Buir. The branch is very rare at present. A thorough search of Y-STR haplotype variants in the scientific literature and worldwide databases has identified several specimens presumably belonging to the N-F23218 branch (Table S1 of the Supplement). The discussed branch is closest to the Yakut branch N-M1982. The branches split time falls on the beginning of the Xiongnu era.

The Yakut samples form a separate branch marked by the M1982 mutation. The N-M1982 branch also contains Y-chromosome samples of the Evenks, Evens, and Dolgans [29, 32-34].

The Yakut haplogroup N-M1982 has been studied in sufficient detail to date. Time to the most recent common ancestor of the Yakut-Sakha Y-chromosome N-M1982 is evaluated at the split point into the haplogroups N-M1991 and N-M1933. Based on the number of SNP mutations in 23 samples, TMRCA is estimated to be 1270 ± 250 yBP (Table 2). Calendar date is 680 ± 250 AD. The estimated time interval includes the Rouran Khaganate, the Turkic Khaganates, and the Uighur Khaganate.

S.A. Fedorova et al. estimated TMRCA of the Yakut branch using 6 loci Y-STR haplotypes at approximately 1600 years [29]. B. Packendorf's group estimation, based on 9 STR haplotypes, is about two times younger [4]. The present study calculation based on 17 STR haplotypes is between these dates: 1300 ± 500 yBP.

TMRCA of the dominant Yakut branch N-M1991 is estimated 970 ± 210 yBP. There are unique data on the ancient Yana Young sample published in [1]. The sample was found on the Yana River by local residents digging the Yana Mammoth Cemetery for commercial purposes. The age of the Yana Young sample was

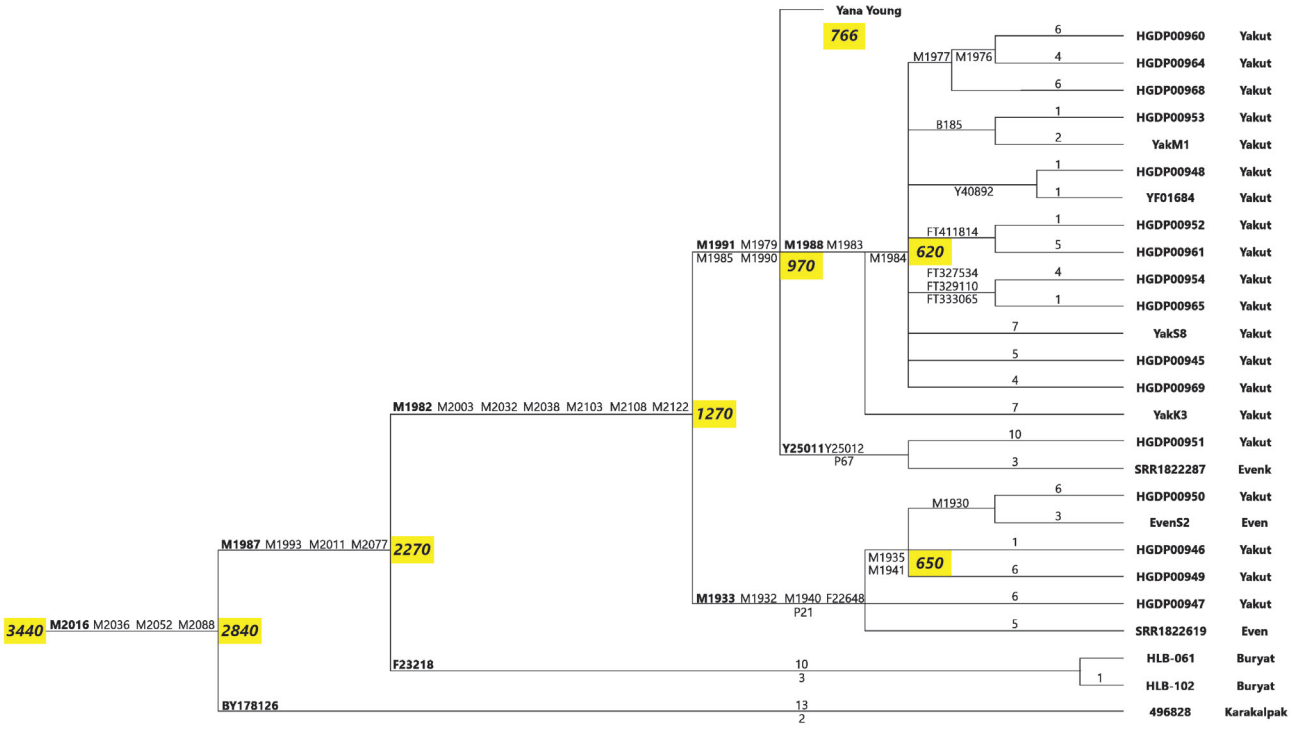

Fig.1. Phylogenetic tree of the haplogroup N-M2016.
Constructed from data on massive parallel sequencing of the Y-chromosome. Branch ages in years BP are highlighted in yellow. Mutations that fall within the combBED regions are indicated above the lines; mutations outside the combBED region are indicated below the lines. In the private branches, only numbers of detected mutations are indicated.

evaluated by the accelerator mass spectrometry (AMS) method as 14C 862 ± 26 years. Taking into account a calibration table, the authors determine the sample age of about 766 AD. The Y chromosome of the Yana Young man belongs to the N-M1991 branch, which is dominant among modern Yakuts [1].

Table 3 provides information about the alleles of the Yana Young sample at the positions of Y-SNP polymorphism, determined from BAM file.

We can see from the data in Table 3, that the Yana Young sample has mutations at the M1991 level. At the same time, younger mutations of the M1988 and Y25011 levels, which characterize the two modern male lineages of the Yakut-Sakha, are absent in the ancient sample. Note that radiocarbon dating indicates the date of death of the Yana Young man. The TMRCA value, according to genetic data, on the contrary, refers to meiosis, i.e. the moment of birth. The Yana Young man was born around 1150 AD. Thus, date of the split of the N-M1991 haplogroup into branches N-M1988 and N-Y25011 (970 ± 210 yBP) is in perfect agreement with the life time of Yana Young (800 yBP). Obviously, the Yana Young man belonged to one of the extinct branches of the haplogroup N-M1991. The vast majority of ancient male lineages did not survive to the present. There are three main reasons for the elimination of male lineages. The first is the so-called "bottlenecks", sharp short-term population declines associated with epidemics, wars, hunger and other cataclysms. The second reason is global in nature and operates constantly. The probability of having a girl instead of a boy is close to 0.5. Mathematical models based on the theory of branching processes predict a high probability of elimination of most male lineages. In addition, there is directed, social selection. Modern men are the descendants of a limited number of the most successful or "lucky" ancient men. The comparative analysis of the results of two methods - radiocarbon dating and the method of molecular genetic clocks - gives reason to believe that the TMRCA calculations based on Y-SNP polymorphism carried out in the present study are correct.

A characteristic feature of the constructed phylogenetic tree (Fig. 1) is a sharp increase of genetic diversity in the N-M1984 and N-M1935 branches of the N-M1982 haplogroup. TMRCA of the N-M1984

Branch	n	TMRCA, years BP	Estimates from other papers, years BP
N-M2058	26	3340±630	
N-M2016	26	2840±540	
N-M1987	25	2270±450	
N-M1982	23	1270±250	~1600 [29] 880±440 [4]
N-M1991	17	970±210	
N-M1984	14	620±100	~900 [29]
N-M1935	4	650±170	~900 [29]

Table 2. TMRCA of the branches of the N-M2016 haplogroup phylogenetic tree according to the data on Y-chromosome SNP polymorphism.

branch is estimated from 14 samples to be 620 ± 100 yBP. The split of the N-M1935 branch, the most numerous in the N-M1933 haplogroup, occurred 650 ± 170 yBP. Within one sigma, the Y-chromosome lineages N-M1984 and N-M1935 ages are in good agreement with each other. The increase in genetic diversity reflects rapid population growth. It is reasonable to assume that the increase in the number of men with mutations M1984 and M1935 occurred simultaneously, within the same ethnic community of Yakut-Sakha ancestors. Based on this assumption, the population sharp increase date should be counted as arithmetic average, i.e. 630 ± 100 yBP. Calendar date is 1320 ± 100 AD.

For the first time, a sharp increase in the number of the Yakut-Sakha ancestors was discovered by S.A. Fedorova et al. [29]. According to the Yakut geneticists, the increase in the number of the Yakut-Sakha ancestors ("the second expansion") began about 900 years ago, coinciding "with the estimated time of the migration of the last, most extensive wave of the Turkic-speaking ancestors of the Yakuts into the Middle Lena basin" [35].

The dating of a sharp increase in the population of Yakut Sakha ancestors with the Y-chromosome haplogroup N-M1982, carried out in this work, corresponds to the time of the Kulun-Atakh archaeological culture [36]. Radiocarbon dating of the sites of the Kulun-Atakh culture according to the cultural layer of the third excavation site of the Kulun-Atakh settlement is 1415 ± 40 AD, according to the cultural layer of the Uganya settlement is 1370 ± 50 AD [36]. The dates obtained by two different methods - the radiocarbon method and the molecular genetic clock method do not contradict each other. The time resolution of the phylogenetic tree nodes is determined by the average time interval for occurrence of one SNP mutation. For the method used in this work, the resolution is about 150 years or 5 male generations. A lot of male lineages have formed during the Yakut-Sakha ancestor five generations. The most of them have been eliminated to present. How many lineages survived is still unknown.

The founder effect is also confirmed by the autosomal data of the Yakuts. According to the calculations of the authors of [37], the increase in the number of Yakuts began 19 ± 1 generations BP, i.e. around 1400 AD.

The bone of the ancient Yana Young man directly indicates the presence of men with the Y-chromosome of the Yakut lineage N-M1991 in the territory of Yakutia as early as the 12th century AD, two centuries before the expansion of the Kulun-Atakh culture. New radiocarbon dating of samples of the Kulun-Atakh culture by the AMS method made the initial stages of the Kulun-Atakh culture older [38]. The calendar age of a sample of food soot from the settlement of Uganya was determined with a probability 95.4% in the interval 962–1289 AD, the settlement of Neleger I - in the interval 1040–1253 AD. It can be assumed that due to some events, the small population of the ancestors of the Yakut-Sakha experienced a population explosion. Demographic boom materially based on rapid occupation by the Yakut-Sakha ancestors of empty hayfields ("kystyk") and

Branch	SNP mutation ID	Yana Young observed allele
N-M1991	M1991	derived
	M1979	derived
	M1985	derived
	M1990	no call
N-M1988	M1988	ancestral
	M1983	ancestral
	BY83221	ancestral
N-Y25011	Y25011	no call
	Y25012	ancestral
	P67	no call
	MF256101	ancestral
N-M1984	M1984	ancestral

Table 3. Y-chromosome alleles of the ancient sample Yana Young.

pastures ("sayylyk") in the alaases (thermokarst depressions) and along river valleys. The breeding of horses and cattle was a more progressive productive method of housekeeping by the ancestors of the Yakuts-Sakha compared to the appropriating method of the earlier inhabitants. The folk legends about Elley speak about new techniques applied by him in the management of domestic animal husbandry.

The genetic continuity of the Kulun-Atakh culture population and modern Yakut-Sakha has been convincingly proven in the works of the joint French-Russian group of geneticists [39-41]. Table S1 of the Supplement contains also data on Y-STR haplotypes of samples from the Early Yakut burials. Archaeological dates are from the review article by Bravina and Dyakonov [42]. Comparison of Y-STR alleles of ancient samples and modern samples of the Yakut-Sakha demonstrates that at the XV-XVII centuries AD the same two main male lineages, N-M1991 and N-M1933, dominated in the genetic pool of the Yakut-Sakha ancestors. The conclusion is based on the fact that, as a rule, there are 16 tandem repeats in DYS392 locus in the N-M1991 haplotypes, and 15 repeats in the N-M1933 haplotypes.

Conclusions. Based on massive parallel sequencing of samples of the Y-chromosome haplogroup N-M2016, the following conclusions can be drawn.

1. Three main branches are observed on the phylogenetic tree built in accordance with the hierarchy of SNP mutations (Fig. 1):

1) the Yakut branch N-M1982;

2) branch N-F23218, closest to the Yakut branch;

3)Mongolian branch N-BY178126, with 10 tandem repeats in the Y-STR locus DYS385a.

The Yakut branch N-M1982 dominates in Yakut-Sakha men, the other two branches are very rare.

2. Correctness of the method applied to dating the nodes of the phylogenetic tree is confirmed comparing the TMRCA of the N-M1991 branch 970 ± 210 yBP with genetic data of an ancient human sample of Yana Young man [1], who died about 766 years BP (determined by AMS).

3. The phylogenetic tree clearly presents a sharp increase in the number of the Yakut-Sakha ancestors, primarily in the N-M1984 and N-M1935 branches. Growth began from 1320 ± 100 AD. The dating is consistent with the age of the Kulun-Atakh archaeological culture sites, measured by the radiocarbon method [36, 38].

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