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DATING THE TIME TO THE MOST RECENT COMMON ANCESTOR OF THE SAKHA (YAKUTS) WITH Y CHROMOSOMAL HAPLOGROUP N3A2-M1982: NEW ETHNOGENETIC RECONSTRUCTIONS

Time to the most recent common ancestor (TMRCA) of Sakha men with haplogroup N3a2-M1982 of the Y chromosome was evaluated by 23 STR markers using the mutation rate constant of Y-STR loci that we had previously calculated. The obtained TMRCA values indicate a period of ~1300-1400 years ago (VI-VII centuries AD), associated with the primary expansion of the population. Based on genetic data and analysis of texts from ancient Chinese chronicles, a hypothesis has been put forward about the connection of the ancestral Sakha population with the Yuzhe people, who supplied mammoth ivory to China

Keywords: TMRCA, STR, Y-chromosome, Yakuts, haplotypes

Introduction. The most striking feature of gene pool of the Yakut ethnos is the dominance of men with the rare haplogroup N3a2-M1982 of the Y chromosome (>80%) due to the founder effect. When using a panel of 17 STR loci, carriers of three STR haplotypes - Ht1, Ht2 and Ht3 - stand out among them [20, 43]. Haplotype Ht1, otherwise called the "Tygyn Darkhan/Elley lineage", has higher frequencies in the Yakut population. The carriers of this lineage are the majority of men - 33% of Central, 40% of Northern and 13% of Vilyui Yakuts [20, 21, 43]. Ht2 conventionally called the "Omogoy lineage" takes a second place, distributed to a greater extent in central Yakutia (30%), to a lesser extent in Vilyui (8%) [20, 43], among the Northern Yakuts it is found with a frequency of 3% [19]. Haplotype Ht3 is more typical for the Vilyui Yakuts (20%), in central and northern Yakutia its frequencies are 4% and 5%, respectively [20, 43].

Determining the TMRCA (time to the most recent common ancestor) for men with haplogroup N3a2-M1982 is of great interest for ethnogenetic reconstructions, because it is associated with the beginning of the formation of the Yakut gene pool characteristics, distinguishing it from other ethnic groups. The period during which all the observed diversity of N3 haplotypes of the Yakuts arose, calculated in the study of B. Pakendorf, based on the mutation rate of 9 STR markers and was initially estimated at ~880±440 years ago [34]. Much larger TMRCA values were proposed by V.N. Kharkov using 7 STR markers ~4.45 ± 1.96 thousand years ago [17] and S.A. Fedorova using 6 STR markers ~1540 ± 580 years ago [19, 27] . It should be noted that such strong differences in the ages of "Yakut" N3 haplotypes in the early studies of geneticists were determined mainly by the use of different sets of STR markers and different mutation rate constants in STR loci. Average STR mutation rate in the Y chromosome in the study of B. Pakendorf was taken to be ~0.003 mutations per locus per generation (according to Kayser et al., 2000 [29]), and in the studies of V.N. Kharkov and S.A. .Fedorova ~0.00069 (according to Zhivotovsky et al., 2004 [42]).

The value of Y chromosomal STR mutation rate constant, in turn, depends on the length of a male generation, which in early studies was taken to be 25 years [17, 19, 27, 42]. Meanwhile, the size of the intergenerational interval can vary greatly due to differences in marriage traditions and demographic parameters among different peoples. Therefore, the value of this indicator for the Yakut population was clarified based on the genealogical data of 712 families, reconstructed from revision tales from 1768, 1795, 1816, 1858, and church registers for the period from 1768 to 1918, and materials from the 1917 census [9]. The length of a male generation among the Yakuts turned out to be on average 35.7 years, which is much higher than the average general population values previously used in genetic studies when calculating the time of genetic divergence of the Y chromosome [9].

To estimate the mutation rate of at Y-STR loci in the Yakut population more accurately, we also used a rare approach based on constructing a phylogenetic tree of the N3a2-M1982 Y chromosome relying on the massively parallel sequencing data, which has become more accessible in the last decade [2]. The mutation rate of 23 STR markers of the Y chromosome was calibrated using radiocarbon dating of an ancient sample with the "Yakut" N3a2-M1982 haplogroup, found in the lower reaches of the Yana River in the Arctic zone of Yakutia. A bone specimen of this medieval male Yana Young, ~800 years old, was found by local residents during the mining of the Yana Mammoth Cemetery [46]. Our adjusted estimate of the STR mutation rate constant for 23 marker STR haplotypes of Yakuts turned out to be equal to 0.0024 mutations per locus per generation [2], which is much different from the values of this indicator used in earlier publications [17, 19, 34].

The purpose of this study was to clarify the time to the most recent common ancestor for the "Yakut" N3a2-M1982 haplotypes using recalculated mutation rate constant for 23 marker Y-STR loci and to reconstruct the genetic history of the Sakha people using updated data.

Materials and methods. To calculate TMRCA, 51 samples of men with hap-

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logroup N3a2-M1982, residents of Yakutia, were selected from previously published works. Of these, 29 samples had data on 23 STR markers: [25] – 16, [37] – 5, [26] – 4, [39] – 2, [49] – 1, [3] – 1. In 22 samples from [45], 21 STR loci from the PowerPlex Y23 panel were genotyped; they lack data for loci with relatively low mutation rates DYS549 and DYS643.

The age of the most recent common ancestor *T* was calculated using the ASD (average squared distance) method, or determining the average root-mean-square distance [25, 30] using the formula:

$$T = \frac{1}{L\bar{\mu}}\sum_{k=1}^{L}\frac{1}{N_k}\sum_{i=1}^{N_k}\left[A_k(i) - A_k(0)\right]^2,$$

where $L = 23$ is the number of STR loci in the sample of haplotypes;

$\bar{\mu}$ is mutation rate constant per locus, averaged over all STR loci;

N_k is number of samples in which alleles at STR locus k are known;

$A_k(i)$ is value of the STR allele of locus k in sample i;

$A_k(0)$ is value of the ancestral allele of STR locus k.

The mutation rate constant for 23-marker PowerPlex Y23 haplotypes, calibrated in [2] using radiocarbon dating of a sample of the ancient man Yana Young, ~800 years before present, is equal to 0.0024 mutations per locus per generation. The average interval of one male generation, previously calculated basing on an analysis of the genealogical data of the Yakuts of the 18th-19th centuries, was taken to be 35.7 years [9]. A description of the method for calculating the uncertainty of the TMRCA estimate is given in the Appendix.

The age of the recent common ancestor was also estimated by constructing a phylogenetic network of the generated sample of haplotypes (n=51) using the ρ-statistics method. TMRCA calculation is built into the program for constructing phylogenetic networks using the median-joining algorithm [28] Network v.10.2.0.0. The weight for all STR loci was set to 10, with the parameter ε = 0.

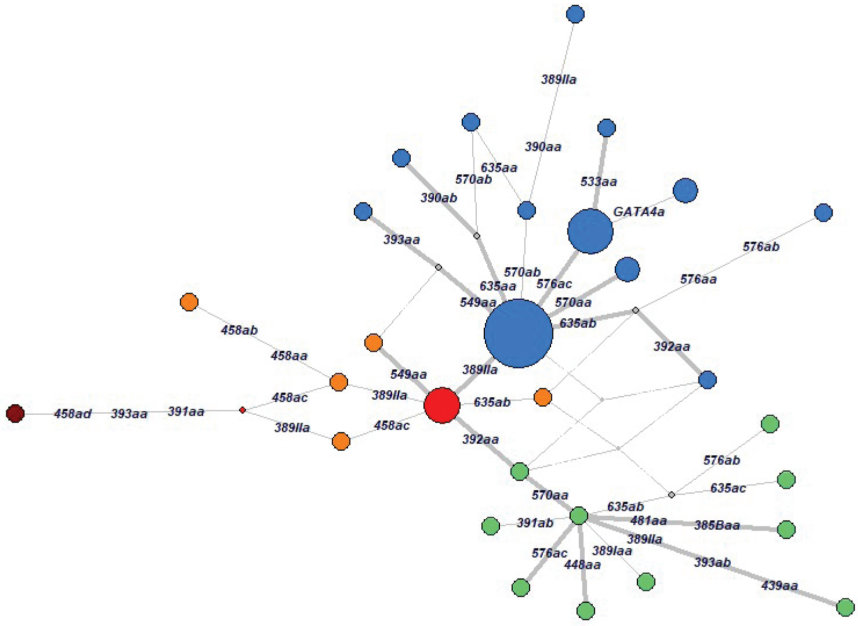
Results and Discussion. Time to the most recent common ancestor of men in the studied sample, calculated by the ASD method, is 1380 ± 460 years BP or before 1950 (Note: 1950 is chosen for the “present time” date in the sciences that using radiocarbon dating. The donors of the DNA samples used to calculate the TMRCA were born in the second half of the twentieth century, so a small correction for recalculation to 1950 can be neglected).

Ancestral haplotype selected as an average 23-marker variant, in the format of recording loci DYS19, DYS385a, DYS385b, DYS389I, DYS389B, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS448, DYS456, DYS458, DYS481, DYS533, DYS549, DYS570, DYS576, DYS635, DYS643, GATA H4 matches the Ht3 haplotype and looks like this:

14-11-13-14-17-23-11-16-14-14-11-10-19-14-16-20-11-12-19-16-22-12-12.

Figure shows the median network built using 51 samples of haplogroup N3a2-M1982. Three samples of N-F23218 Buryats from Hulun Buir (China, [41]) were added as outliers to determine the root of the phylogenetic tree. The TMRCA estimate based on the median network using the ρ-statistics method was 1260 ± 460 BC. (Note: The lower TMRCA value using this method compared to ASD is due to the fact that Network does not account for back mutations at the DYS389II locus in the two samples, HGDP00945 and HGDP00969).

According to the phylogenetic network (Figure) structure and TMRCA calculations (Table 1), during the period of the primary increase in population size ~ 1300-1400 years ago from the MRCA lineage (Ht3) more widespread in Vilyui, a lineage had occurred leading to the Ht2 haplotype, characteristic to the Central Yakuts. The secondary increase in population size began much later, ~900 years ago, apparently due to another influx of migrants from the southern regions [2, 3, 21]. At the same time, further splitting of Ht3 occurred into a lineage leading to Ht1. Thus, in VI-VII centuries AD in the ancestral population there were obviously men with haplotypes Ht3 and Ht2, while the dominant modern haplotype Ht1 (“Elley’s lineage”) arose much later, in the ~11th century, and its divergence began during a period of sharp increase in population size starting from ~14th century [3, 21]. The territorial distribution of evolutionarily more ancient haplotypes Ht3 and Ht2 may indicate the initial settlement of the Vilyuy region and then central Yakutia by the ancestors of the Yakuts, which corresponds to the concept of the famous Yakut historian and ethnographer G.V. Ksenofontov [12, 13]. However, archaeological findings in recent years indicate that pastoral groups appeared on the Olekma River in Southern Yakutia in the 3rd-4th centuries [4], therefore, the settlement of the Lena-Amga interfluve could also occur through Olekma. Resolving this issue requires additional archaeological researches and phylogeographic studies of haplotype frequencies distributions in modern and ancient populations. Dating ~1300-1400 years BP does not contradict archaeological materials, according to which groups of southern pastoralists appeared on the territory of Yakutia in the



Phylogenetic median network of 23-marker STR haplotypes of men (n=51) with haplogroup N3a2-M1982. The ancestral haplotype is highlighted in red, Ht1 and its derivatives in blue, Ht2 and its derivatives in green, Ht3 derivatives in orange, and the 17-marker STR haplotype of the Buryats from Hulun Buir (China) in brown. The branches of the phylogenetic tree of haplogroup N3a2-M1982 reconstructed on complete sequencing data of 23 male samples in [2], are highlighted in bold.

3rd-4th centuries AD [4], because indicates the most probable time of appearance of the most recent common N3a2 ancestor at the period of primary expansion of the Sakha people.

The obtained TMRCA values of the most recent common N3a2-M1982 ancestor in comparison with data of other authors are shown in Table 1. Taking into account the confidence intervals, the TMRCA estimates in this paper are consistent with the results of studies [3, 19, 26, 27, 34] and the YFull group [48]. In general, it should be noted that TMRCA values calculated in recent years from samples of haplotypes with a large number of STR loci and expanded fully sequenced samples almost all indicate a time interval of ~1300-1400 years BP. A slight overestimation of TMRCA in [26, 33] is partly explained by the use of other Y-SNP mutation rate constants – $0.74 \cdot 10^{-9}$ and $0.76 \cdot 10^{-9}$, instead of $0.82 \cdot 10^{-9}$ per site per year in [3] and YFull calculations [48].

Table 1

Summary data of Y chromosomal haplogroup N3a2-M1982 TMRCA

TMRCA, years	Genetic markers	n	Age estimation method	Ref.
1380 ± 460	23 STRs	51	ASD	This study
1260 ± 460	23 STRs	51	ρ-statistics	This study
1300 ± 500	17 STRs	237	ASD	[3]
880 ± 440	9 STRs	162	ρ-statistics	[34]
4450 ± 1960	7 STRs	97	ASD	[17]
1540 ± 580	6 STRs	215	ASD	[19, 27]
1270 ± 250	SNPs in combBED region (8.5 Mbp)	23	Y-SNP mutations counting	[3]
1350 95 % CI 900-1800	SNPs in combBED region (8.5 Mbp)	17	Y-SNP mutations counting	[48]
1737 95 % CI 919-2609	SNPs in 6.2 Mbp region	4	Y-SNP mutations counting	[33]
1589 95 % CI 821-2580	SNPs in 9.8 Mbp region	4	Y-SNP mutations counting	[26]

Table 2

Information from the Chinese chronicles of the Tang Dynasty about the countries that supplied the khutu horn (gǔduō骨咄)

Source	Year of publishing	juàn	Country of gǔduō 骨咄 origin	Notes
Tongdian	801	200	Юйчжэ	
Tanhuiyao	961	98	Юйчжэ	written gǔtǔ 骨吐
Taiping Huanyuji	976-983	198	Юйчжэ	
Taiping Huanyuji	976-983	199	Кыргызы	
Cefu Yuangui	1005-1013	961		no information about 骨咄
Xin Tangshu	1060	217b	Кыргызы	
Xin Tangshu	1060	39	Мохэ	written 骨骨出

The age we calculated for the most recent common ancestor of the Yakuts based on the N3a2 chromosome data corresponds to the periods of the First and Second Turkic Khaganates, the nomadic states of the Orkhon Turks (or Kok-Turks), which existed in 552 - 744 AD. The main policy of the Turks at that time was to conquer the zone of the Eurasian steppes and control the routes of the Great Silk Road [18]. To north of territories of the Kok-Turks, numerous Tele tribes roamed. In translation of a fragment of the “Xin Tangshu” (1060) text made by Iakinf Bichurin, it is noted that “They [Tele] were considered subjects of the Tukyue House. The people of Tukyues were heroic with their forces in the deserts of the north” [6], i.e. it is implied that Kok-Turks hired the Tele to represent their interests in the north. The text of the later Chinese historical encyclopedia “Wenxian Tongkao” (1273-1317) records that “When the Tujue state conducted punitive campaigns to the east and west, [it] always used their [Tele] services to curb the northern steppe” [14]. (The mentioned texts of Chinese chronicles are publicly available on the sites https://chinesenotes.com/xintangshu/xintangshu217a.html, https://ctext.org/wiki.pl?if=gb&chapter=681264&remap=gb, their modern translation shows that it was really about bribery or hiring). The northernmost of the Tele tribes were the Kurykans. B.B. Dashibalov supposed that “...through the Kurykan the Turks carried out extortions from the taiga population of Eastern Siberia, the Kurykans were suppliers of furs, livestock, and iron” [8].

It is curious that a bone sample of a medieval man Yana Young, ~800 years old, a carrier of the “Yakut” N3a2-M1982 haplogroup, was found by local residents during the mining of the Yana mammoth cemetery. Analysis of SNP mutations on the Y chromosome showed that the Yana Young lineage is located on the branch of Ht1, which is dominant among the male lineages of modern Sakhas, but evolutionarily arose earlier than the “Elley lineage” [2, 3, 46]. More recent mutations (M1988 and Y25011) are absent in the ancient Yana Young sample [2, 3]. The Yana Young man Y-chromosome lineage has not been preserved in the modern population. The mitochondrial DNA of this medieval man belongs to the branch of haplogroup D4o2 [47], which is often found today among the Central Yakuts [27], the age of this branch according to YFull MTree is ~1350 years (95% CI 3800-325 years). In PC analysis of SNP data, the Yana Young sample is located into the cluster of modern Yakuts [32]. Genome-wide analysis using the ADMIXTURE algorithm (K=7) also showed the genetic proximity of the Yana Young person to modern Yakuts [44]. Thus, the results of genome-wide studies showed that the ancient man Yana Young, found in a mammoth cemetery, was not genetically different from modern Yakuts. Accordingly, it can be assumed that the Sakha have long been suppliers of mammoth ivory to China and medieval Muslim countries [1, 7, 23]. The world's main reserves of fossil mammoth ivory are located in Yakutia; the total resources are estimated from 34,000 up to 450,000 tons [16]. In this regard, it was interesting to trace Referencess to mammoth ivory and the countries from which it was supplied, in ancient manuscripts.

The extensive historiography about medieval European unicorn legends mentions a bone of unknown origin called a "khutu horn" [31]. In the Middle Ages, “khutu horn” (ختو, khutū, khutuw, chutww, etc.) was highly valued among the Turkic peoples, in the Muslim East and in China [22, 35], because it was rare and was used in the manufacture of prestigious items - knife handles, sheaths, caskets, belt linings, etc. It was believed to has the ability to detect and neutralize poisons. Due to the high price, the “khutu horn” became an attribute of diplomatic gifts between the rulers of Central Asia [38]. In the ideas of the medieval Turks, reflected by Mahmud Kashgari in “Divan lugat at-Turk” (1074), “khutu horn” is a bone (horn, whisker) of a sea fish or a tree root brought from China [15, 30, 31]. Following this narrative, the great polymath Biruni inquired its origins ambassadors from the Khitan Liao Empire (circa 1027). The ambassadors replied, “This is the frontal bone of a bull; the same is said in the books, but with the addition that this bull is found in the land of the Khirkhiz” (Yenisei Kyrgyz) [1]. Obviously, the ambassadors referred to Chinese written publications of that time. The word “khutu” itself, being Siberian in origin, came to Muslims through the Chinese characters gǔduō 骨咄 (pronounced in Russian transcription as “kuto”). The use of hieroglyphs gǔduō to denote this ornamental material has been noted since the Chinese Tang Dynasty (VII-X centuries). Table 2 provides information about the countries that supply gǔduō.

Sung scholars began compiling the collection “Xin Tangshu” in 1044, that is, after Biruni’s meeting with the Khitan ambassadors. However, the text about the country of the Kyrgyz, which mentions the khutu beast, was known earlier. From the surviving documents, the same entry is contained in the Taiping Huanyuji encyclopedia, compiled in 976-983, which also reproduces an older text about the country of Yuzhe, as a supplier of the bone. Thus, the information from Taiping Huanyuji occupies an intermediate position in ideas about the origin of gǔduō in the 10th century. In the later encyclopedia “Tsefu Yuangui” (1005-1013), the mention of gǔduō is already excluded from the description of the country of Yuzhe. It should be noted here that trade and other ties of the Yenisei Kyrgyz began to expand after the defeat of the ancient Uyghurs in 840. The strategically advantageous geographical location of the Kyrgyz territory at the junction of the steppe and the Siberian taiga allowed them to intercept from the Kurykans access to northern riches, including mammoth ivory. Judging by the data of Chinese chronicles, starting from the 10th century, the Kyrgyz played a role of key intermediaries in the supply of mammoth raw materials, in particular ivory, and before that date the source of bone was the country of Yuzhe (Table 2).

The earliest information about gǔduō is contained in the “Tongdian” encyclopedia (801). This message is in the “Taiping Huanyuji” encyclopedia translated by N.V. Küner looks like this: “The state of Yujia is located east of the state of Ju, 15 days' drive. This country is vast and densely populated. The customs are the same with Bayegu. Few cows and horses, many sables and gutu” [14]. The same thing is written in “Tang Huiyao” (961), but khutu is designated somewhat differently (gǔtǔ 骨吐) [14]. A message about the country of Yuzhe is included in the “Tongdian” encyclopedia from an unknown road guide of the mid-7th century, the original of which has not survived [10].

The countdown of the days of travel from China to the northern countries of Yuzhe, Ju, Damo, Gushi began from the lands of the Bayirku, one of the Tele tribes. According to the monuments of the Darasun culture, the country of Bayirku was located in the southern part of Transbaikalia and northern Mongolia and called Bayegu [11]. The Ju country of reindeer herders was located northeast of the Bayegu country, and Yuzhe was located 15 days' journey east of the Ju country [14]. But in determining the distance from the Bayegu country to the Ju country, sources differ: “Tong Dian” and “Tang Huiyao” give 6 days of travel (500 li), and “Taiping Huanyuji” - 50 days of travel. North in Chinese sources is shifted to the northwest [5], due to the orientation towards sunrise in the summer. Taking this into account, the country of the Ju reindeer herders, according to the “Taiping Huanyuji”, was located somewhere in the lower reaches of the Olekma and correlates with the ancestors of the Evenks, and the country of Yuzhe is in Central Yakutia and is possibly associated with the ancestors of the Sakha.

Conclusion. Thus, the obtained TMRCA dating for the “Yakut” N3a2-M1982 haplotypes of ~1300-1400 years allows us to take a new insight at the information from the Tang chronicles of the 7th-10th centuries about the Yuzhe people. The Yuzhe people were engaged in breeding horses and cattle, had similar customs with one of the Tele Bayirku tribe, and there was a lot of diāoshǔ (sable) and gǔduō (mammoth ivory) on their land. Extraction of tusks from mammoth cemeteries could have been a traditional trade for the ancestors of the Yakuts since the 7th century AD. A small clan or tribe in which the most recent common ancestor of the Yakut branch N3a2-M1982 was born may have belonged not to the Baikal Kurykans, but to the people called “Yuzhe” in Chinese ancient chronicles.

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The authors declare that they have no conflict of interest.

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Appendix

Contribution of covariance to the error of TMRCA estimation using the ASD method. STR mutations are assumed to occur randomly according to a Poisson distribution. For simplicity, let’s consider the case of single-marker haplotypes, i.e. one STR locus. In the stepwise mutational model (SMM) the contribution of covariance to the total variance of the TMRCA estimate using the average squared distance (ASD) method is described by the formula:

$$D_{cov} = \mu\bar{t} + 2\mu^2\overline{t^2}, \qquad (1)$$

where μ – is the mutation rate constant; $\bar{t}$ – is the average age of shared branches for all pairs of the studied sample of STR haplotypes, i.e. average time interval from the most recent common ancestor of the entire sample to the common ancestor of a randomly selected pair of haplotypes; t^2 - is the average squared age of shared branches for all pairs of the studied sample of STR haplotypes.

As a rule, the value of $\bar{t}$ is significantly less than the estimated age of the most recent common ancestor T, and the quadratic term in formula (1) can be neglected. For this case

$$D_{cov} \cong \mu\bar{t} = \frac{2\mu}{N(N-1)} \sum_i \sum_{i<j} (T - T(i,j)), \quad (2)$$

T(i,j) – is age of the common ancestor of a pair of haplotypes i and j, *N* is sample size. Summation is performed over all pairs of haplotypes, there are $N(N-1)/2$ pairs in total.

Let us introduce a notation for the average age of the common ancestor of a randomly selected pair of STR haplotypes:

$$T^* = \frac{2}{N(N-1)} \sum_i \sum_{i<j} T(i,j). \quad (3)$$

Estimator for the age of a pair of hplotypes for the ASD method [24, 40] is

$$T_{ij} = \frac{(A(i)-A(j))^2}{2\mu}, \quad (4)$$

where *A(i), A(j)* – are allele values of STR haplotypes *i* and *j*, respectively. Then

$$T^* = \frac{1}{\mu N(N-1)} \sum_i \sum_{i<j} (A(i) - A(j))^2 =$$
$$= \frac{1}{\mu N(N-1)} \sum_i \sum_{i<j} [(A(i) - \bar{A}) - (A(j) - \bar{A})]^2,$$

where $\bar{A} = \frac{1}{N}\sum_i A(i)$ is average STR allele value for the sample. Taking into account its properties,

$$T^* = \frac{1}{\mu N} \sum_i (A(i) - \bar{A})^2. \quad (5)$$

Substituting the resulting expression into formula (2), we finally obtain:

$$D_{cov} = \mu(T - T^*) = \frac{1}{N}\sum_i (A(i) - A(0))^2 -$$
$$- \frac{1}{N}\sum_i (A(i) - \bar{A})^2, \quad (6)$$

where *A*(0) – is an ancestral allele value.

Total relative error of the TMRCA estimation by the ASD method is calculated as:

$$\frac{\sigma}{\mu T} = \sqrt{\frac{1+2\mu T}{N\mu T} + \frac{T-T^*}{\mu T^2}}. \quad (7)$$