THE GENOMIC ARCHITECTURE OF THE RUSSIAN POPULATION OF SAANEN GOATS IN COMPARISON WITH WORLDWIDE SAANEN GENE POOL FROM FIVE COUNTRIES

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A b s t r a c t

The Saanen goat breed is valued for its high milk productivity and good adaptive qualities, which contributed to its worldwide distribution outside Switzerland. In Russia, the Saanen is a popular breed that had been officially recommended for breeding and had a pedigree status. Breeding in local environments as well as regional specifics of the used breeding strategies can lead to a significant change in the allele pool of breeds, and therefore, it is relevant to conduct genomic studies of national populations of world breeds to establish their current genetic status. Here, for the first time we presented the results of whole-genome analysis of the Russian population of goats of the Saanen breed in comparative aspect with the original (Switzerland) and the world gene pool of the Saanen breed, represented by four countries. The aim of our work was to assess genetic diversity and to study population structure of the Saanen goats of Russian selection in comparison with representatives of this breed from five different countries (Switzerland, Italy, France, Argentina and Tanzania) whose whole-genome SNP-profiles were obtained from the database of the AdaptMap project. The studies were conducted on 21 goats of the Saanen breed (RUS), bred in one of the Russian breeding farms, in 2019-2020. DNA was extracted from the selected ear fragments using DNA Extran-2 kits (Syntol CJSC, Russia). Genotyping was performed using a GoatSNP50 BeadChip DNA chip (Illumina, Inc., USA) containing 53347 SNPs and providing coverage of the average interval between SNPs in 40 kb. To assess the genetic diversity and to perform comparative analysis of the Russian goat population with the representatives goats of this breed from five different countries, we used SNP-profiles of the Saanen goats bred in Switzerland (SWI, $n = 38$), Italy (ITA, $n = 22$), France (FRA, $n = 55$), Argentina (ARG, $n = 11$) and Tanzania (TNZ, $n = 8$), which were downloaded from the publicly available digital data repository Dryad and generated in within the AdaptMap project. The Swiss population of the Saanen breed was assumed as a sample of the original gene pool. Bioinformatic processing and visualization of whole-genome genotyping data was performed in the PLINK 1.90, Admixture 1.3, SplitsTree 4.14.5 software, in R packages "diveRsity" and "pophelper". The observed heterozygosity varied from 0.381 in SWI to 0.423 in FRA and was high in RUS (Ho = 0.418). In SWI, ITA, FRA populations the values of the inbreeding coefficient were close to zero level; RUS, ARG, and TNZ showed heterozygote deficiencies, which were 1.5%, 8.9, and 6.0%, respectively. Allelic richness was maximal in ARG, RUS, and FRA (Ar ≥ 1.979) and minimal in SWI (Ar = 1.934). The Principal component analysis and the phylogenetic tree showed a clear differentiation between the national and original populations of the Saanen breed. Analysis of population structure demonstrated

the presence of the genetic component of the SWI cluster in goats from the RUS group. RUS had the smallest genetic distances with FRA (F_{ST} = 0.02; R_{ST} = 0.189) and ITA (F_{ST} = 0.023; R_{ST} = 0.215); and RUS was highly differentiated from TNZ (F_{ST} = 0.054; R_{ST} = 0.311) and SWI (F_{ST} = 0.06; R_{ST} = 0.276). Thus, different selection strategies resulted in genetic differences between the national goat populations of the Saanen breed. However, genomic components of the original gene pool are still present in the Russian goat population of the Saanen breed.

More than 50 dairy goat breeds have been created over the history of domestic goat breeding worldwide [1], among which the Saanen breed is the most popular. The breed got its name from the Swiss Zaanental Valley, where it was bred using the method of long-term folk selection in the middle of the 19th century [2, 3]. Among goats, the Saanen breed is an analogue of the Holstein cattle breed, characterized by high milk productivity (from 300 to 2000 kg for 150-300 days of lactation) [3]. Goats of this breed are easily acclimatized to different conditions of keeping and feeding without significant loss of milk production. They were imported from Switzerland to most countries in Europe [3, 4], North [5] and South America [6], Australia [7], Asia [8], and Africa [9], where the use of their valuable gene pool significantly transformed the national dairy industry.

According to official data [10], pedigree dairy goat breeding in Russia is represented by four foreign breeds: Alpine (since 2015), Saanen (since 1993), Murciano Granadina (since 2019), and Nubian (since 2018). Nevertheless, according to data for 2018, the Saanen breed is the most numerous [11]. The breeding stock of goats of the Saanen breed is concentrated in three stud farms, six breeding reproducers, and one gene pool enterprise and amounts to 12.3 thousand heads. The average milk yield in herds varies from 822 kg per 305 days of lactation in the breeding reproducer KH Rus-1 LLC (Stavropol Province, Budyonnovsky District, Pokoynoye village) to 961 kg per 305 days of lactation in the gene pool enterprise LLC "Berezka" (Kursk Province, Kursk District, Petrovskoye village) [4].

Along with the use of pure-bred Saanen goats for dairy production, their crossings with local goat populations are promising [1, 12]. Therefore, goat sires of the Saanen breed are a high-quality improving material that allows for short term conversion of mongrel low-productive groups of goats (with a milk yield of 200-250 kg for 305 days of lactation) into reliable milk producers with a milk yield of up to 663 kg for 305 days of lactation [1, 12].

Genomic studies of domestic goats were not as common as those of other livestock species [13]. In 2013, three large scientific groups conducting projects to search for single nucleotide polymorphisms (SNPs) joined into the International Goat Genome Consortium (IGGC) to create a DNA chip [14]. As a result of the SNP selection, 53347 SNPs were included in the final set in the Goat SNP50 BeadChip chip (Illumina, Inc., USA).

The development of this DNA chip has led to increased interest in studies of the genome organization of domestic goats. For example, L. Nicoloso et al. [15] investigated the genetic diversity of 14 Italian goat breeds based on genome-wide data. Mdladla et al. [16] demonstrated the applied value of a whole-genome SNP analysis in their studies of indigenous goat breeds in South Africa. Using Goat SNP50 BeadChip, Rahmatalla et al. [17] identified the genes associated with the growth and development of bones and the formation of the immune system in Sudanese goats. Brito et al. [18] studied genetic diversity in more than 1000 goats from nine popular commercial breeds.

Numerous scientific works resulted in the generation of SNP profiles of

goat breeds from different countries around the world (3171 goats from 117 populations), which were collected in the AdaptMap project database [19, 20] and were used to identify runs of homozygosity [20], establish historical goat migration routes [21], and search for loci under pressure of selection [22]. In addition, the creation of publicly accessible databases of SNP profiles allows for the study of breeds imported to various countries to assess their discrepancy or similarity with the original gene pool.

Here, we present the first reported genome-wide analysis of the Russian population of Saanen goats, for which a comparative assessment was performed with the original (Switzerland) and the world gene pool of the Saanen breed, which was represented by four countries.

Our aim was to evaluate the genetic diversity and establish the structure of the Russian population of the Saanen breed in comparison to the gene pool of goats of this breed from five different countries (Switzerland, France, Italy, Argentina, and Tanzania), whose genome-wide SNP profiles were obtained from the AdaptMap project database.

Material and methods. The studies were performed in 2019-2020 on goats (*Capra hircus*) of the Saanen breed ($n = 21$, RUS) bred at one of the breeding reproducers in the Russian Federation. DNA was isolated from selected fragments of the auricle using DNA Extran-2 kits (Syntol CJSC, Russia). Genotyping was performed using a GoatSNP50 BeadChip DNA chip (Illumina, Inc., United States) containing 53347 SNPs and providing an average 40 kb spacing between SNPs [14]. Reading of DNA chips was performed on an iScan Reader System (Illumina, Inc., USA), and the raw data were loaded into GenomeStudio 2.0 (Illumina, Inc., USA) to call genotypes.

For parameters characterizing reading quality (GenCall, GC) and clustering of SNP markers (GenTrain, GT), cutoffs were set to 0.5 [23]. In PLINK 1.90 [24], we selected SNP markers with a minor allele frequency (MAF) more than 5% that did not deviate from Hardy-Weinberg equilibrium at $p < 10^{-6}$, were in linkage equilibrium, and were located only on autosomes.

To assess the genetic diversity and perform comparative analysis of the Russian goat population with the global gene pool, we used SNP profiles of Saanen goats bred in Switzerland (SWI, $n = 38$), Italy (ITA, $n = 22$), France (FRA, $n = 55$), Argentina (ARG, $n = 11$), and Tanzania (TNZ, $n = 8$), which were obtained from the Dryad publicly available digital data repository [25] and generated within the AdaptMap project [20, 21]. The Swiss population of the Saanen breed was chosen as the original gene pool.

Observed heterozygosity (H_o), unbiased expected heterozygosity (uH_e), allelic richness (Ar), inbreeding coefficient F_{is} (with a confidence interval of 95%), pairwise F_{ST} [26], and R_{ST} (Reynolds distance) values [27] were calculated in the R package "diveRsity" [28].

Principal component analysis (PCA) was performed in PLINK 1.90 with subsequent plotting in the R package "ggplot2" [29]. A NeighborNet graph based on the matrix of pairwise F_{ST} values was visualized in SplitsTree 4 software [30].

The population structure and genetic homogeneity of the Russian and other national groups of Saanen goats were established in Admixture 1.3 software [31] with a graphical representation using the R package «pophelper» [32]. The most probable number of ancestral clusters (K) was determined by calculating values of the cross-validation error (CV error) for K from 1 to 7 in Admixture 1.3 software.

Bioinformation processing and data visualization were performed using the R Project for Statistical Computing software environment [33].

Results. An analysis of genetic diversity (Table 1) showed that the observed heterozygosity ranged from 0.381 in SWI to 0.423 in FRA. The H_o value in RUS (0.418) was ranked second after the maximum. In three populations (SWI, ITA, FRA), the inbreeding coefficient was insignificant, which could indicate a state close to genetic equilibrium in these groups. In the RUS group, a small deficit of heterozygotes was noted (1.5%). The ARG and TNZ groups were characterized by more significant heterozygote deficiencies of 8.9% and 6.0%, respectively.
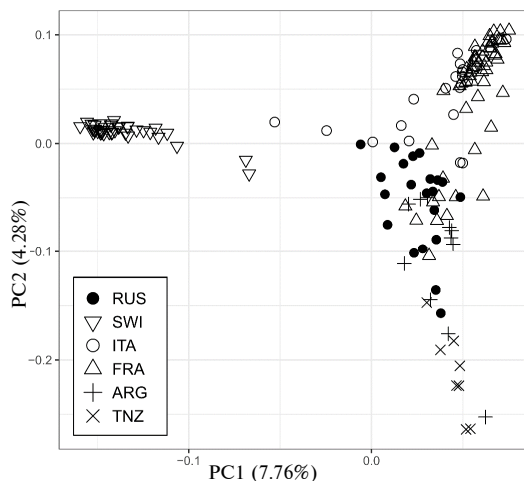
1. Characterization of the genetic diversity of the Russian and five national populations of goats (*Capra hircus*) of the Saanen breed, evaluated using the GoatSNP50 BeadChip DNA chip (2019-2020)

Group	n	H_o	uH$_e$	uF$_{is}$	Ar
RUS	21	0.418	0.424	0.015 (0.013; 0.017)	1.979
SWI	38	0.381	0.380	−0.002 (−0.003; −0.001)	1.934
ITA	22	0.417	0.418	0.002 (0; 0.004)	1.975
FRA	55	0.423	0.422	−0.002 (−0.003; −0.001)	1.979
ARG	11	0.386	0.426	0.089 (0.086; 0.092)	1.980
TNZ	8	0.388	0.414	0.06 (0.057; 0.063)	1.970

N o t e. n — sample number; H_o — observed heterozygosity, uH$_e$ — unbiased expected heterozygosity, uF$_{is}$ — inbreeding coefficient, Ar — rarified allelic richness. In parentheses, magnitude of the F_{is} variability is given at a confidence interval of 95%. The arithmetic mean error for the parameters H_o, uH$_e$ and Ar is ±0,001. Groups of goats of the Saanen breed: RUS — Russian; SWI — Swiss; ITA — Italian; FRA — French; ARG — Argentinean; TNZ — Tanzanian.

The highest allelic richness was found in the ARG (Ar = 1.980), RUS (Ar = 1.979), and FRA (Ar = 1.979) populations. For the SWI group, it was minimal (Ar = 1.934).

Principal component analysis (Fig. 1) showed that the first principal component, responsible for 7.76% of genetic variation, separated the SWI group from the remaining five populations, including RUS. The second principal component, corresponding to 4.28% of genetic variability, separated SWI, ITA, and partially FRA from RUS (some of which were located almost on the axis), ARG, and TNZ (located in the most distant sector of the PCA-plot) populations.
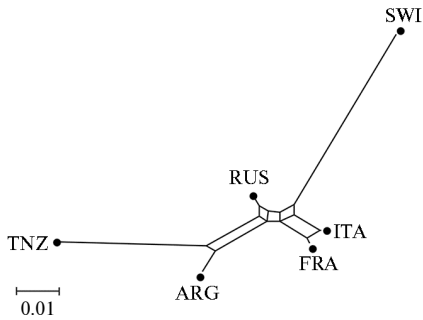

Fig 1. Results of principal component analysis (PCA) for Russian and five national goat populations (*Capra hircus*) of the Saanen breed based on SNP profiles obtained using the GoatSNP50 BeadChip DNA chip (2019-2020)**.** Groups of goats of the Saanen breed: RUS — Russian; SWI — Swiss; ITA — Italian; FRA — French; ARG — Argentinean; TNZ — Tanzanian.

There were two distinguished clusters in the structure of the genetic network, demonstrating the relationships between the Russian and five national populations of goats of the Saanen breed (Fig. 2). The first included a long isolated SWI branch, an ITA + FRA subcluster adjacent to it, and a more distant short RUS branch (at the junction of clusters). The second cluster was formed by separate branches of ARG and TNZ.

F_{ST} and R_{ST} values were calculated to achieve a better understanding of genetic differentiation between the studied goat populations. Their values (Table 2) were maximal between the SWI and TNZ groups (F_{ST} = 0.109; R_{ST} = 0.374), as

well as between SWI and ARG (F_{ST} = 0.078; R_{ST} = 0.321). Minimal differentiation was observed between ITA and FRA (F_{ST} = 0.008; R_{ST} = 0.154).

Fig. 2. NeighborNet graph based on pairwise F_{ST} values demonstrating relationships between the Russian and five national populations of goats of the Saanen breed based on SNP profiles obtained using the GoatSNP50 Bead-Chip DNA chip (2019-2020)**. Groups of goats of the Saanen breed: RUS — Russian; SWI — Swiss; ITA — Italian; FRA — French; ARG — Argentinean; TNZ — Tanzanian.

By studying the genetic relationships of RUS with the populations from other countries, we observed minimal genetic distances between RUS and the FRA and ITA groups (F_{ST} = 0.02; R_{ST} = 0.189 and F_{ST} = 0.023; R_{ST} = 0.215), and the greatest differentiation was with the TNZ and SWI groups (F_{ST} = 0.054; R_{ST} = 0.311 and F_{ST} = 0.06; R_{ST} = 0.276, respectively).

In order to analyze the population structure of the studied groups of goats, we assessed the most probable number of clusters (Fig. 3, A). The lowest cross-validation error was identified at K = 3 and amounted to 0.64445. At K = 2, the SWI group formed its own isolated cluster (see Fig. 3, B). At K = 3, the ITA and FRA groups showed a similar population structure. Furthermore, the FRA population consisted of heterogeneous individuals, most of which were highly consolidated in their cluster, and the second part (about 30% of the animals) showed the presence of other genomic components. The TNZ group formed its own cluster. The RUS and ARG populations were characterized by the presence of all three identified genetic components, while RUS retained the largest share of the original element (SWI).

2. Genetic differentiation between the Russian and five national populations of goats (*Capra hircus*) of the Saanen breed, estimated using the F_{ST} and R_{ST} indicators based on genome-wide genotyping data using the GoatSNP50 BeadChip DNA chip (2019-2020)

Group	RUS	SWI	ITA	FRA	ARG	TNZ
RUS		0.276	0.215	0.189	0.254	0.311
SWI	0.060		0.275	0.276	0.321	0.374
ITA	0.023	0.059		0.154	0.263	0.327
FRA	0.020	0.065	0.008		0.248	0.316
ARG	0.029	0.078	0.035	0.035		0.318
TNZ	0.054	0.109	0.066	0.065	0.044	

N o t e. The pairwise F_{ST} values are presented below the diagonal, the Reynolds distances R_{ST} are above the diagonal. Groups of goats of the Saanen breed: RUS — Russian; SWI — Swiss; ITA — Italian; FRA — French; ARG — Argentinean; TNZ — Tanzanian.

Highly productive livestock breeds that are attractive for breeding are widespread outside of their original breeding area. In cattle breeding, such breeds include Holstein and Simmental; in pig breeding, this includes Landrace, Duroc, and Large White; in sheep breeding, this includes Rambouillet and Romney Marsh; and in goat breeding, the world leader is the Saanen breed. In exporting countries, the breeding process of imported genetic material begins. Thus, the assessment of the identity of national populations to the original gene pool is of practical importance because it helps to determine the general direction of selection and allows breeders to make possible adjustments to achieve the aimed goal [34]. Therefore, a comparative analysis of the SNP profiles of Simmental cattle of German-Austrian and Russian breeding revealed genomic regions with a high frequency of identical haplotypes, despite certain differences for breeding pur-

poses in the studied populations [34].
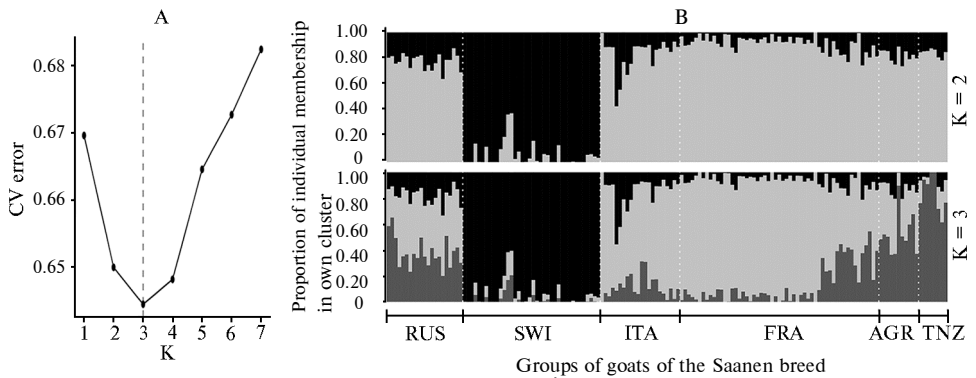
Fig. 3. Comparison of the population structure and analysis of the genetic homogeneity of the Russian and five national populations of goats (*Capra hircus*) of the Saanen breed using the GoatSNP50 BeadChip DNA chip (2019-2020): A — a graph showed cross-validation errors (CV error), calculated by testing the number of ancestral clusters (K) from 1 to 7 (the dashed line indicates the number of clusters for which the cross-validation error was the lowest); B — structure of the studied populations with the number of clusters equal to two and three. Groups of goats of the Saanen breed: RUS — Russian; SWI — Swiss; ITA — Italian; FRA — French; ARG — Argentinean; TNZ — Tanzanian.

The Saanen breed was involved in the development and testing of the GoatSNP50BeadChip DNA chip; therefore, the differentiations between the national populations of the Saanen breed would be completely determined by their genetic differences and would not depend on possible errors caused by the intraspecific biases in the polymorphic loci. For example, the Angora goat breed was not included in the initial list of breeds for the development of a DNA chip; thus, Lashmar et al. [35] preliminarily evaluated the informativeness of the GoatSNP50BeadChip for this breed.

Comparing the genetic diversity indicators calculated in our work for national populations of goats of the Saanen breed, high values were found in all groups, except for the original Swiss one. Burren et al. [36] investigated the genetic diversity in 10 local Swiss goat breeds, in which the observed heterozygosity ranged from 0.369 (Appenzell and Toggenburg) to 0.401 (Grisons striped and Peacock goat), and allelic richness varied from 1.531 (Stifelges) to 1.941 (Chamois colored). The observed heterozygosity was 0.385, 0.384, 0.338, 0.379, and 0.353 for the Alpine, La Mancha, Nubian, Saanen, and Toggenburg breeds, respectively, of the Canadian selection. In addition, in all the listed breeds, a minor deficiency of heterozygotes was recorded [18]. The Ho and Ar values in local Swiss goats and dairy breeds of Canadian selection corresponded to those evaluated for the original SWI group and were a bit inferior to those estimated for the RUS, ITA, FRA, ARG, and TNZ populations.

Like the Saanen, the Angora breed, originating from Turkey, is widespread in many countries of the world. C. Visser et al. [37] used the Goat SNP50 BeadChip to study the degree of geographical isolation and genetic variability in three populations of the Angora goat breed from South Africa, France, and Argentina. Among the national populations of the Angora breed, a difference in the expected and observed heterozygosity was recorded ($H_e = 0.371$-0.397; $H_o = 0.365$-0.414), which is comparable with the difference calculated in our research ($H_e = 0.380$-0.424; $H_o = 0.381$-0.423).

By summarizing the PCA results and the structure of the phylogenetic tree, we revealed a clear differentiation between the national (except for ITA and FRA) and the original populations of goats of the Saanen breed. Visser et al.

[37] also reported that the national populations of the Angora goats were very clearly separated from each other. The F_{ST} value between Angora populations was 0.120, while in our research the maximum F_{ST} value was 0.109 between TNZ and SWI. This might indicate that the populations of the Saanen breed did not move as far away from the original Swiss group as in the case of the Angora goats.

Interestingly, in accordance with the F_{ST} values, the greatest differentiation was found between RUS and SWI, while according to R_{ST} values, the RUS group was most isolated from TNZ, which was confirmed by the position of the corresponding groups on the PCA plot. According to Laval et al. [38], the calculation of Reynolds distances is the best method for estimating the divergence between closely related groups, which is consistent with our data. In addition, analysis of the population structure provided evidence of the conservation of the genomic components of SWI in goats of the RUS group.

Thus, the whole-genome study of the Russian population of goats of the Saanen breed showed that this group exceeds the original Swiss population by the values of genetic and allelic diversity indices and corresponds to those estimated in the French and Italian groups. The results of our work confirmed that various breeding strategies had led to genetic differences between national populations of the Saanen breed, including the Russian one. Nevertheless, the Russian population of the Saanen breed retains the genomic components inherent in the original gene pool, which, although it creates the necessary variability for selection, it also leaves the possibility of returning to the original type of the Swiss breeding.

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