Original Article

Characteristics of the Allele Pool and the Genetic Differentiation of Goats of Different Breeds and their Wild Relatives by Str-Markers

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Abstract

Based on 16 STR-loci, the allele pool and interbreed differentiation of goat breeds of Russian and foreign breeding were investigated in this study. These breeds included Karachai (KRCH-K, n=73, mountain zone; KRCH-Z, n=33, foothill zone), Dagestan Downy (DAGD, n=30), Dagestan Wool (DAGW, n=30), Soviet Wool (SOVW, n=30), Saanen (SAAN, n=34), Murciano-Granadina (MURS, n=37), as well as wild goats, represented by three species of mountain goats (n=52): Siberian Capricorn (Capra sibirica) of Altai (CSIB-S, n=6), Tajikistan (CSIB-T, n=4), Kyrgyzstan (CSIB-K, n=6), and the Himalayas (CSIB-H, n=4); Bezoar goat (Capa aegagrus) of Turkey (CAEG, n=3) and Pakistan (CAEG-S, n=3); West Caucasian tur (*Capra caucasica*): western Caucasian (Kuban, CCAU-K, n=10), central Caucasian (CCAU-M, n=8), and eastern Caucasian (Dagestan, CCAU-D, n=8). The highest genetic diversity was observed in the North Caucasus breeds, such as Karachai, Dagestan Downy, and Dagestan Wool. The mean numbers of alleles per locus and allelic diversity were 7.385-9.154 and 7.353-7.713, respectively. The genetic proximity of Caucasian breeds was confirmed by cluster analysis, and they formed a common branch with the highest genetic affinity, while the Orenburg and Soviet Wool breeds formed another branch, and the third branch with the least affinity was the dairy breed of foreign selection.The analysis of the phylogenetic tree of domestic and wild species established the formation of three clusters formed by the subspecies of the West Caucasian tur, Siberian ibex, and breeds of domestic goats. At the same time, populations of the Bezoar goats were localized at the root of the last cluster, which confirmed their role as the ancestors of domestic goats.

Keywords: Goat, Wild Species, Breed, Genetic Diversity, Microsatellites, Genetic Differentiation

1. Introduction

Goats (*Capra hircus*) were domesticated about 10,500 years ago in the Fertile Crescent region (1-3)[1]. Over the several millennia of domestication of goats, significant morphological changes have occurred, which, to some degree, have affected all organs and tissues. In particular, their exterior was transformed (the legs became shorter and wider), the neck became shorter, and the body became somewhat longer and deeper mainly due to the development of the rear part.

Domestic goats are mostly smaller than wild goats, while their live weight and growth vary greatly depending on the productivity and breeding area. Domestic goats do not have such strong horns as wild relatives; moreover, almost half of the modern breeds are hornless. Domestic goats have lost the protective coloration and powerful mane characteristic of wild species. Significant changes also affected the skin and hair. The wool fibers of domestic coarse-haired goats although similar in morphological composition to the wool of their wild relatives, differ significantly in the diameter of the down and over hair. Moreover, transitional hairs appeared in the coat of domestic goats. The fleece of angora goats consists mainly of transitional hair, has a white color andluster, and contains a significant amount of grease, which does not look anything like the hairline of wild goats. A recent large-scale study identified 13 genes associated with coat color in domestic goats, among which the ASIP gene duplication wasassociated with light coloration (4).

Dairy goats significantly surpass their wild relatives in mammary gland size, milk production, and lactation duration. Furthermore, domestic goats surpass their wild relatives in wool shearing (2-5 times), down production (10-15 times), and milk yield (10-20 times) (5).

The greatest genetic changes during domestication occurred due to natural selection and random genetic drift, which led to the fixation of genes in small populations (6). Directional selection for certain traits of domesticated goats has brought geographical differences, which are confirmed by several modern studies (7-10).

The impetus for the breeding of dairy goats in Europe (especially in its northern regions) and their subsequent spread throughout the world were two significant historical events. The first, which occurred approximately 3,000 years after the domestication of the goat, was a mutation in the human lactase gene (11), which made it possible to assimilate milk sugar in adulthood (12, 13). The second event was the defeat of the Umayyad army at Poitiers (central France) in 732 AD(14). One of the trophies left by the hastily retreating Umayyad forces was their goats, which were used to make milk and cheese. Instantly, this region of France became the main center for breeding dairy goats (15).

Wool goat breeding is inferior in time to dairy farming. Specialized wool breeds of goats were formed in Asia Minor and North Africa only in the second millennium BC. Wool goats came to Europe in the middle of the 16th century. Subsequently, they began to spread throughout the world, such as South Africa, North America, and Central Asia (5).

The domestic goat has become so widespread due to its unique biological features. This species is primarily distinguished by its unpretentiousness and high resistance to unfavorable living conditions, adaptability to pastures that are scarce and inaccessible to other types of farm animals. At the same time, the products obtained from goats have a number of distinctive economically valuable features in comparison with other types of farm animals. These features include the finest goat down, hypoallergenic goat milk, and dietary goat meat due to its low-fat content.

Currently, goat breeding is one of the most dynamically developing branches of animal husbandry. Over the last 25 years, the global goat population has doubledfrom 589 million in 1991 to 1,100 million in 2017. According to the Food and Agriculture Organization,there are 373 goat breeds in the world that are bred in 170 countries.The breed diversity of goats justifies the interest of researchers in the study of their genetic structure, intraspecific distribution of genetic variability, and the degree of differentiation of breeds and populations. Here, one of the informative methods is the analysis of microsatellites or short tandem repeats (STR) (16). A number of authors have shown the relevance of STR for population-ecological studies of goats of various types of productivity in countries, such as Korea (17), Iran (18), the Netherlands (19), the Canary Islands (20), China(21), Brazil (22), and Thailand (23).

Russian scientists have conducted a series of studies on the development of a multilocus panel for the analysis of microsatellites to control the reliability of the origin and characteristics of the genetic diversity of some goat breeds (24, 25). In recent years, the milk-meat-wool or combined goat breeds, which are represented mainly by local breeds, bred mostly in the foothill and mountain regions of the North Caucasus, Altai, Tyva, and Khakassia andhave gained popularity in Russia.

At the beginning of 2019, only 15% of 2.2 million goats wererepresented by downy, wool, and dairy bred animals, while 85% of the goat population werelocal aboriginal breeds of the combined productivity (24). The most interesting of them for genetic research are the populations of Karachai and Dagestan goats. Their distribution is due to their exceptional unpretentiousness and unique adaptive abilities, which make it possible to adapt to the extremely natural and climatic conditions of the mountainous and foothill zones of the Caucasus. Karachai and Dagestan goats can eat about 550 species out of more than 700 species of plants of the North Caucasus mountains. These goats are very activein search of food, and they can walk 15-18 km daily.

Sharing a common area with their wild relatives-the West Caucasian (*Carpa caucasica*) and Dagestan (*Capra cylindrocornis*) tur, which form the so-called hybrid zones, make the North Caucasian goats unique (26).Despite the high applied significance of goat breeding, there is a littleSTR-based genetic research of Russian goat breeds comparing them with foreign breeds; moreover, there has been no comparative study with wild forms, which determined the relevance and objective of our study.

2. Materials and Methods

To study the allele pool and determine the interbreed differentiation of breeds of goats of Russian and foreign selection of different areas of productivity based on the STR-loci in traditional breeding regions, tissue and blood samples were taken from the animals of different breeds (Table 1). The sample included 297 samples of biomaterial (skin, blood) of seven breeds of goats, including Karachai (KRCH-K, n=73, mountain zone; KRCH-Z, n=33, foothill zone), Dagestan Downy (DAGD, n=30), Dagestan Wool (DAGW, n=30), Soviet Wool (SOVW, n=30), Saanen (SAAN, n=34), and Murciano-Granadina (MURS, n=37).

Table 1. Characteristics of the allele and genetic diversity of the goats of various breeds of Russia

Indicators	Breeds						
	KRCH	OREN	SOVW	DAGW	DAGD	SAAN	MURS
N_A	9.154±0.750	6.538±0.637	6.769±0.545	7.385±0.747	7.538±0.713	5.923±0.525	6.538±0.584
N_I	5.385±0.500	4.846±0.451	5.308±0.398	5.000±0.641	5.615±0.417	4.077±0.415	4.538±0.418
N_E	5.002±0.551	3.402±0.384	4.039±0.299	4.635±0.658	5.028±0.498	3.385±0.291	3.321±0.351
A_R	7.713±0.592	6.425±0.621	6.673±0.534	7.353±0.743	7.538±0.713	5.665±0.489	6.250±0.544
H_O	0.736±0.057	0.667±0.053	0.701±0.042	0.662±0.055	0.732±0.045	0.674±0.049	0.628±0.051
H_E	0.741±0.053	0.645±0.049	0.734±0.022	0.725±0.040	0.774±0.025	0.673±0.033	0.658±0.037
F_{IS}	0.012[-0.032;0.056]	-0.042[-0.13; 0.046]	0.053[-0.02; 0.126]	0.09[-0.01; 0.19]	0.05[-0.053; 0.153]	0.003[-0.081; 0.087]	0.044[-0.057; 0.145]

Note: N_A - average number of alleles per locus, N_I - average number of informative alleles per locus, N_E - average number of effective alleles per locus, A_R - allelic diversity; H_O - observed heterozygosity, H_E - expected heterozygosity, F_{IS} - inbreeding coefficient

The research material was also the STR-based wild goat genomic variability database of the object of scientific infrastructure (OSI), BioTechZh, Federal State Budgetary Scientific Institution "L.K. Ernst Federal Research Center for Animal Husbandry", represented by three species of mountain goats (n=52), such as Siberian Capricorn (Capra sibirica) of Altai (CSIB-S, n=6), Tajikistan (CSIB-T, n=4), Kyrgyzstan (CSIB-K, n=6), and the Himalayas (CSIB-H, n=4); Bezoar goat (Capa aegagrus) of Turkey (CAEG, n=3) and Pakistan (CAEG-S, n=3); West Caucasian tur (*Capra caucasica*): western Caucasian (Kuban, CCAU-K, n=10), central Caucasian (CCAU-M, n=8), and eastern Caucasian (Dagestan, CCAU-D, n=8).DNA was isolated using a DNA-Extran reagent kit (CJSC "Syntol", Russia) according to the manufacturer's protocol.

The quantitative and qualitative assessment of the resulting DNA specimens was carried out using a NanoDrop 8000 microspectrophotometer (ThermoFisher, USA). The concentration of genomic DNA specimens was determined by measuring the absorbance at 260 nm, and the purity of DNA was assessed by the absorbance ratios at 260 and 280 nm.

The studies were conducted on 16 microsatellite loci, including INRA006, ILSTS087, INRA063, CSRD247, FCB20, ILSTS019, ILSTS011, MAF065, INRA005, ILSTS008, SRCRSP003, SRCRSP008, SRCRSP023, MCM527, INSP0523, and SRCRSP023 using three multiplex panels for 8, 6, and 2 loci developed by OSI BioTechZh, Federal State Budgetary Scientific Institution "L.K. Ernst Federal Research Center for Animal Husbandry" (Figure 1).

Capillary electrophoresis was performed on ABI 3130xl genetic analyzer (Applied Biosystems, USA) with subsequent determination of the allele lengths of microsatellites on GeneMapper (version 4.0.; Applied Biosystems). For the population genetic characteristics of each breed, the GenAlEx 6.5 software (27) was used to determine the average number of alleles (N_A), the average number of informative alleles (N_I), the effective number of alleles (N_E) per locus (28), allelic

diversity calculated with the ratification procedure (A_R) (29), as well as the observed (H_O) and expected (H_E) heterozygosity and inbreeding coefficient (F_{IS}) (30) in thediveRsity R package, followed by visualization in the pophelper package (31). The degree of genetic differentiation of the studied goat breeds was assessed on the basis of pairwise D_{Jost} values (32). The Jost's D matrix was employed to construct a phylogenetic tree using the Neighbor-Net algorithm in SplitsTree 4.14.5 (33). Principal Component Analysis was performed using the adegenet R package (34) with visualization in the gglot2 R package (35). The source files were formed in the R software environment (version 3.5.0) (36). The assessment of the genetic structure of the studied goat breeds was carried out in STRUCTURE (version 2.3.4) following the method byPritchard, Stephens (37), with subsequent visualization in pophelper (31). The phylogenetic tree was built based on M. Nei genetic affinity (38) in Populations (version 1.2.30).
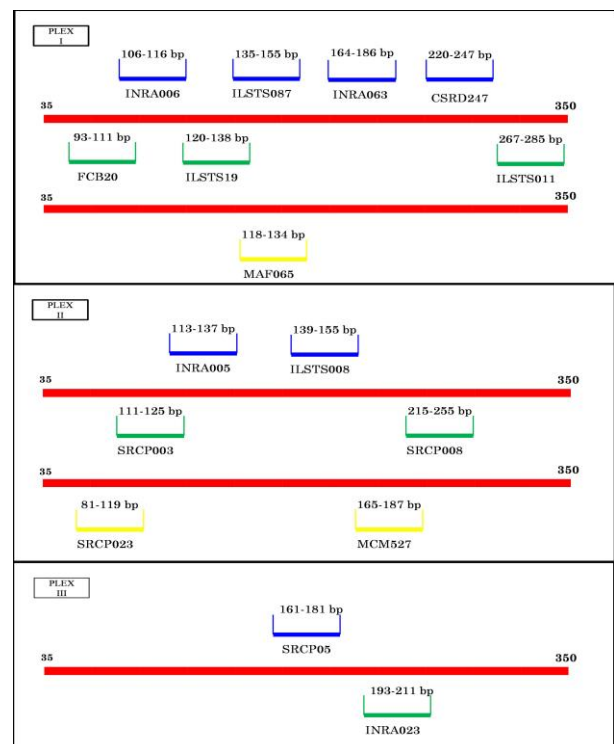

Figure 1. Scheme of the multiplex panel developed by OSI, BioTechZh, Federal State Budgetary Scientific Institution "L.K. Ernst Federal Research Center for Animal Husbandry" and used for goat STR research

3. Results

Analysis of the allelic diversity of goats being bred in Russia found Karachai goats to be the most genetically diverse. Furthermore, they had the highest value of the average number of alleles per locus and allelic diversity (N_A=9.154±0.750 and A_R=7.713±0.592, respectively). Relatively high levels of these parameters werealso determined in the Dagestan Downy and Dagestan Wool breeds (7.385±0.747 and 7.538±0.713; 7.353±0.743 and 7.538±0.713, respectively).The minimum value of allelic diversity was in Saanen goats (Table 1). In addition, the Karachai and Dagestan Down goats had the largest number of effective alleles per locus (N_E-5.0), followed by the Soviet Wool and Dagestan Wool (4.0-4.6), as well asthe Orenburg, Saanen, and Murciano-Granadina (3.3-3.4).

None of the studied breeds had a significant deviation of the observed heterozygosity from the expected values.Analysis of the spatial arrangement of the studied goat breeds shows a clear distinction according to the first component of the populations and breeds of the North Caucasus goats (Karachai, Dagestan Downy, and Dagestan Wool) from Orenburg, Saanen, and Murciano-Granadina, while the Soviet Wool breed occupied an intermediate position (Figure 2). Saanen goats differ from other studied breeds in terms of the second component.
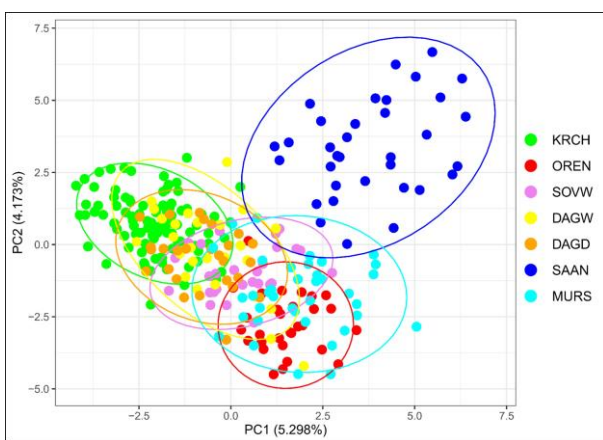
Figure 2. Results of the analysis of the main components of the studied Russian breeds of goats
Note: the interpretation of abbreviations for goat breeds is given in Materials and Methods
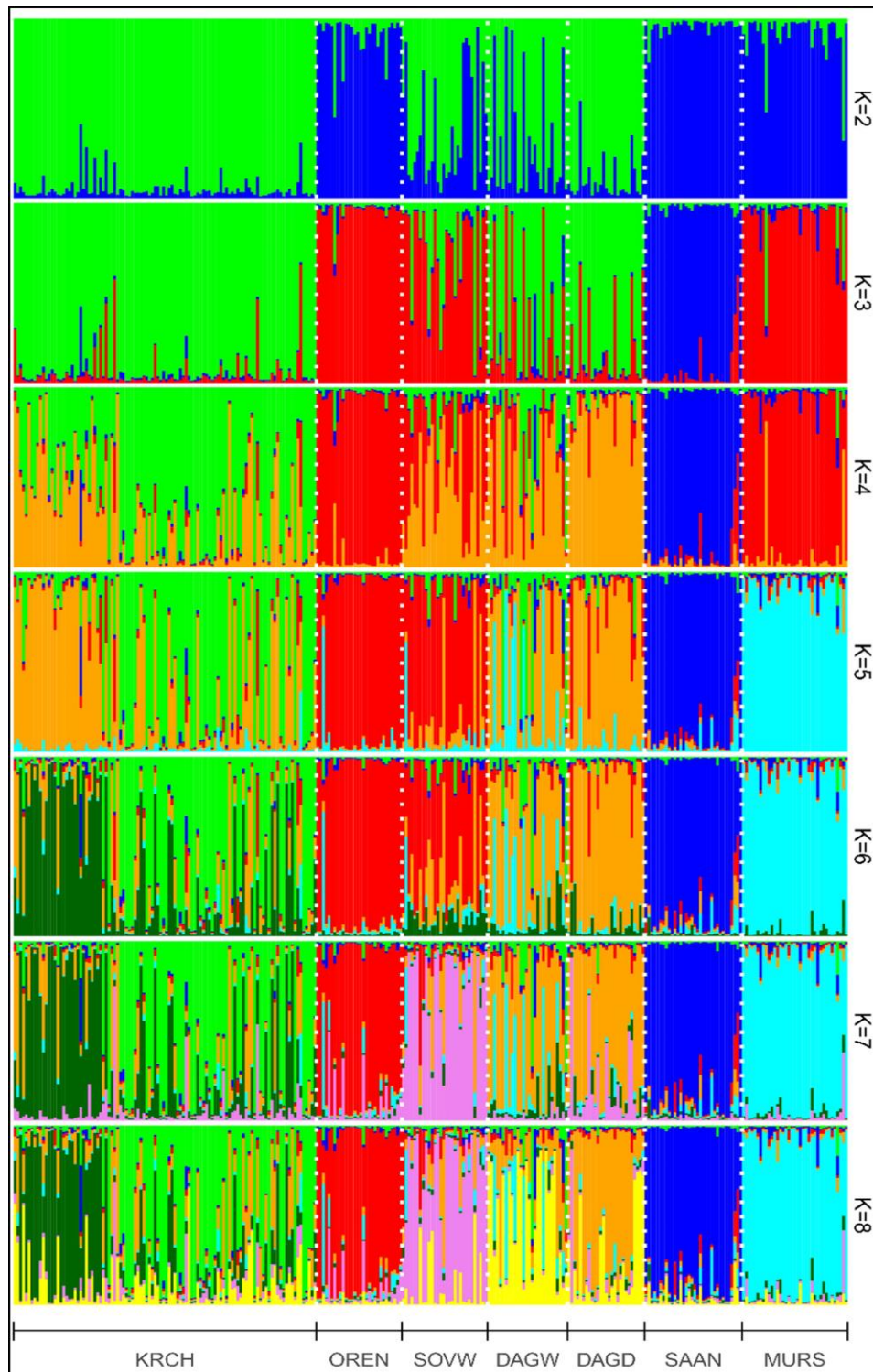
Data on the genetic structure of the studied breeds of goats bred in Russia are presented in figure 3. If *k*=2, there is a clear division of the studied breeds into two groups, one of which is represented by the Karachai goats, and the second is indicated by the Orenburg, Saanen, and Murciano-Granadina. The Dagestan Wool, Dagestan Downy, and Soviet Wool breeds show their mixed origin with a noticeably higher proportion of genetic components specific to Karachai goats. If *k*=3, the Karachai and Saanen goats form two clusters, while the third is formed by the Murciano-Granadina. The Dagestan Wool, Dagestan Downy, and Soviet Wool breeds show their mixed origin, while the Dagestan Wool and Dagestan Downy breeds have a greater share of the genetic components of the Karachai goats, and the Soviet Wool has more from the Orenburg breed.

If *k*=8, each of the studied breeds shows its unique genetic structure, while the Karachai breed has two clusters corresponding to the studied populationsfrom the foothill and mountain breeding zones.Analysis of the genetic affinity between the studied breeds of goats bred in Russia showed the greatest affinity of the Karachai goats to the Dagestan Wool and Dagestan Downy breeds and the greatest distance from the Saanen and Murciano-Granadina breeds (Table 2). The DJost-based Neighbor-Net dendrogram (Figure 4) shows it in the formation of a common branch by these breeds. The Orenburg and Soviet Wool breeds form a common branch, while the Orenburg Breed is characterized by greater genetic divergence.

Comparative analysis of the STR variability of domestic and wild species, as well as the structure of the D_{Jost} phylogenetic tree (Figure 5), shows the formation of three clusters, the firstof which is formed by the subspecies of the Caucasian tur, followed by the second and third that are formed by Siberian ibexand domestic breeds, respectively. The root of the last cluster localizes the groups of Bezoar goats, the ancestor of domestic sheep, while the Bezoar goats of Turkey are located directly on the ribs of the grid, and the group of Bezoar goats of Pakistan forms a separate

branch within the cluster. The involvement of Bezoar goats as an ancestral form of domestic goats is also

confirmed by the results of the genetic structure (Figure 6).
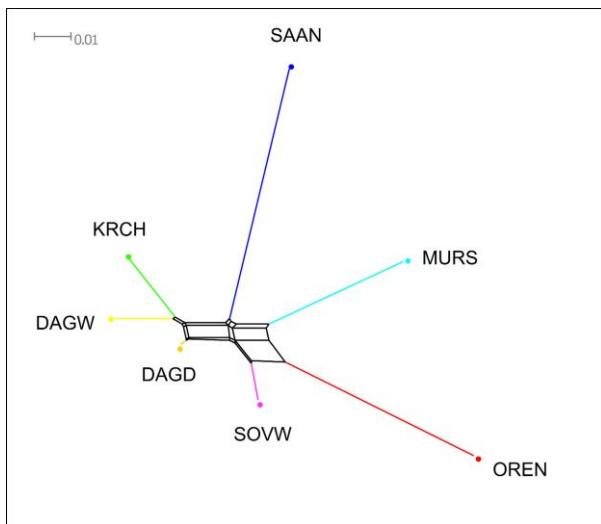

**Figure 3.** Genetic structure of the studied Russian breeds of goats
Note: the interpretation of abbreviations for goat breeds is given in Materials and Methods

Table 2. Genetic distances among the studied Russian breeds of goats

| F	KRCH	OREN	SOVW	DAGW	DAGD	SAAN	MURS
KRCH	*	0.111	0.053	0.038	0.032	0.108	0.093
OREN	0.199	*	0.078	0.113	0.090	0.150	0.110
SOVW	0.113	0.089	*	0.061	0.034	0.095	0.073
DAGW	0.072	0.184	0.116	*	0.027	0.099	0.079
DAGD	0.074	0.152	0.050	0.041	*	0.090	0.071
SAAN	0.232	0.258	0.184	0.194	0.21	*	0.121
MURS	0.241	0.183	0.134	0.136	0.149	0.201	*

Figure 4. NeighborNet DJost phylogenetic dendrogram of interbreeding genetic differentiation of goat breeds
Note: the interpretation of abbreviations for goat breeds is given in Materials and Methods
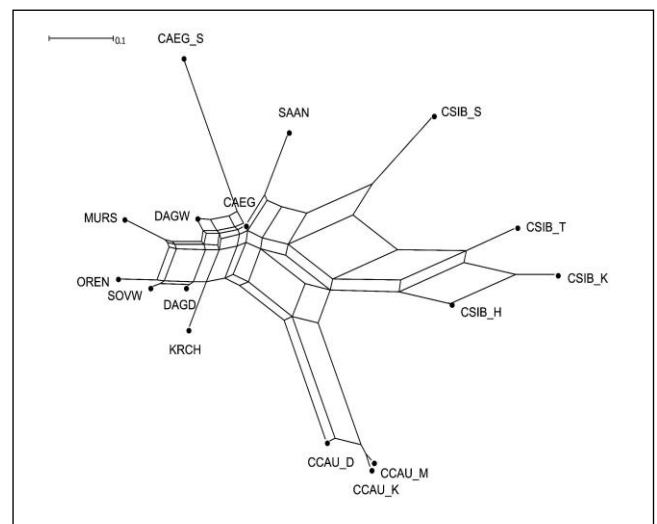
Figure 5. DJost phylogenetic dendrogram of genetic differentiation of domestic and wild goat breeds
Note: the interpretation of abbreviations for domestic and wild goat species is given in Materials and Methods

If k=2, the group of Bezoar goats of Turkey forms a common cluster with domestic goats. If k=3, the largest share of the genetic components of Bezoar goats is preserved in domestic breeds of goats, including Dagestan Wool, Dagestan Downy, and Soviet Wool. Analysis of the genetic structure of domestic goat breeds at k=3-9 suggests the participation of two ancestral populations in their formation. Based on one of them, the modern allele pool of Karachai goats was formed, while the second served as the basis for other domestic breeds.
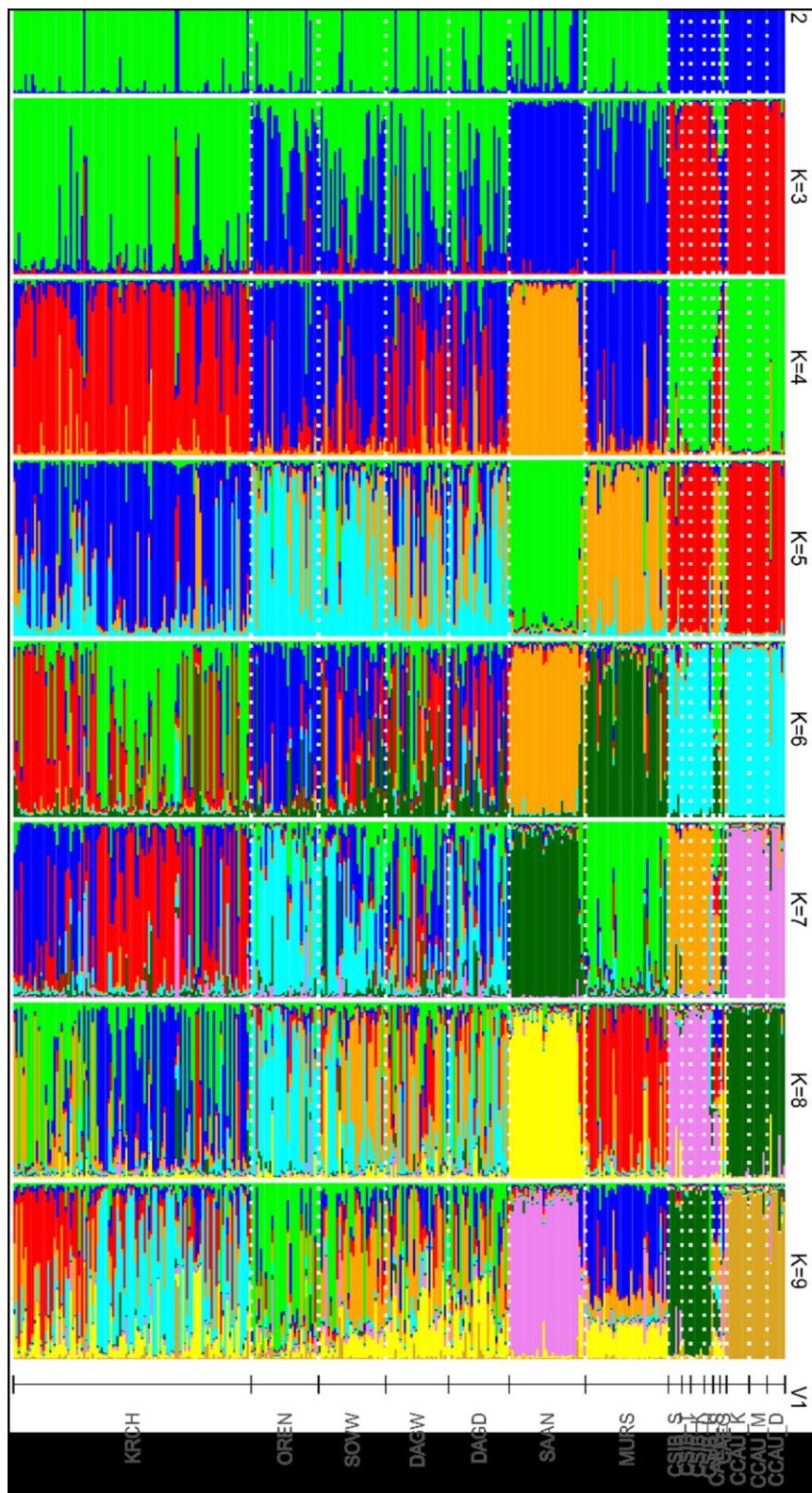
Figure 6. Genetic structure of domestic and wild goat species
Note: the interpretation of abbreviations for domestic and wild goat species is given in Materials and Methods

4. Discussion

The traditional regions for breeding goats of the combined productivity are the republics of the North Caucasus, Tyva, and Altai Mountains. The exceptional ability of indigenous goat breeds to use hard-to-reach forage resources makes them attractive for creating geographically oriented livestock production systems. The development of a breeding improvement strategy for such breeds should be based not only on the phenotypic assessment of animals but also on the genetic characteristics of each breed and population. Microsatellite DNA loci due to their availability, low cost, and sufficient information content remain one of the most common markers for phylogenetic, taxonomic studies, and application in programs for the rational use of genetic resources of farm animals.

The STR markers used in the study revealed the average number of alleles per locus in the combined, wool, and downy breeds of Russian goats ranging from 6.5 to 9.1, while in the dairy goats of foreign selection, this corresponding number was from 5.9 to 6.5. Vahidi, Tarang (10) reported the high allelic diversity of seven native wool and meat-milk-down breeds of goats of Iran and identified an average of 10.7 alleles per locus. Astudy onnine dairy breeds of Canary Islands goats using 27 microsatellite markers revealed anaverage value of 5.9 (20), and for the Alpine and Saanen goats, the values were from 5.8 to 7.0 (22, 24). Apparently, dairy goats undergo higher selection pressure and a much lower influx of new genes. The greater genetic diversity of native breeds provides them with better adaptability and resistance to specific breeding conditions.

The analysis of genetic distances showed that F_{ST} between the breeds bred in the North Caucasus was within 0.05, which indicates an insignificant interbreed differentiation between them according to the classification proposed by Hartl, Clark (30). The values amongthe Orenburg (Orenburg region), Soviet Wool (Tyva), dairy breeds of foreign selection, Saanen and Murciano-Granadina, and the breeds of the North Caucasus, were 0.07-0.150, which indicateda moderate genetic difference.

The obtained data are consistent with the results of studies by other scientists who demonstrated the great genetic distance of the most common dairy breeds (Saanen, Alpine, and Toggenburg) from the wool and milk-meat-wool goats grown in their breeding countries, such as Russia (24), China (21), Thailand (23), and Brazil (22). Phylogenetic analysis based on genetic distances between domestic goats and their wild relatives confirmed the origin of domestic goats from Bezoar goats. A large-scale study of the genome of Bezoars and representative breeds of domestic goats made it possible to find deeper confirmation of this fact, as well as identify genomic changes that probably occurred during the domestication of goats and the formation of breeds. Domestic goats had genes identified that control their coat color, behavior, immune response, and productivity traits (4).

Large areas of mountain pastures in the republics of the North Caucasus, Tyva, Altai Mountains, as well as the possibility of producing eco-friendly products determine the interest in breeding native dairy/meat/wool or combined goats. This, in turn, justifies the expediency of studying their genetic characteristics, both between the breeds of Russian and foreign selection, as well as wild relatives.

The obtained data on the 16 loci STR-based genetic differentiation of goats bred in Russia indicate that the genetic differences amongthem are mainly determined by their type of productivity and the breeding area. The used microsatellite loci were sufficiently informative markers to demonstrate the genetic isolation amongthe populations of the Caucasian tur, Siberian ibex, and breeds of domestic goats, and at the same time, confirm the origin of domestic goats from bezoar ones.

To obtain new information on the genetic diversity and differentiation of domestic goats, as well as their wild relatives, it is advisable to expand the sample of domestic and foreign breeds and conduct full-genome studies with the use of a DNA chip. The accumulation

of data on the genomic profile of goat breeds based on a variety of SNPs will make it possible to more accurately search for loci formed under selection pressure, and subsequently, use the obtaineddata to improve the productive traits of different goat breeds.

5. Conclusion

In our studies,it was observed that the allele pool performed an interbreed differentiation of domestic goats bred in Russia and demonstrated their genetic relationship with wild species.Goats bred in the North Caucasus were characterized by the greatest genetic diversity. Karachai, Dagestan Wool, and Dagestan Downy breeds had 7,353-7,713 alleles per locus, while Saanen and Murciano-Granadina breeds had 5,665 and 6,250alleles per locus, respectively. Furthermore, Karachai, Dagestan Wool, and Dagestan Downy goats show the greatest genetic affinity, followed by the Orenburg and Soviet Wool breeds, while the dairy goats of foreign breeding show the lowest affinity.The phylogenetic analysis found that the subspecies of the Caucasian tur, Siberian ibex, and domestic goat breeds form their separate clusters. At the same time, the close location of the branch of the Bezoar goat to the cluster of domestic goats confirms its participation as an ancestor.

Foot Note

1. Occupies modern territories of Lebanon, Israel, Syria, Iraq, southeast Turkey, southwest Iran, and northwest Jordan. The Fertile Crescent is considered the first of the centers where agriculture and cattle breeding originated during the Neolithic Revolution

Authors' Contribution

Experimental design was conducted by: M. I. S, S. V. B, A. V. D.
Statistical analysis was conducted by: A-. M. M. A, S. N. P, N. A. Z.
Data collection was conducted by: T. V. M, Iu. A .S, V. R. Kh.

Ethics

All the procedures were approved by the Ethics Committee at the Russian State Agrarian University, Moscow, Russia, under the project number of (No. 19-76-20006 and No. 19-76-20061).

Conflict of Interest

The authors declare that they have no conflict of interest.

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