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ANIMAL GENETIC RESOURCES: DEVELOPING THE RESEARCH OF ALLELE POOL OF RUSSIAN CATTLE BREEDS — MINIREVIEW

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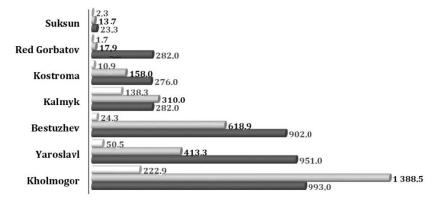
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Abstract

In modern biological science, the study and conservation of biodiversity is considered an important field of research (L.F. Groeneveld et al., 2010). In the twentieth century, a limited number of breeds were used in animal husbandry worldwide, leading to a significant decrease in the number of local breeds, which until recently, had been actively involved in agricultural production (B. Rischkowsky et al., 2007). This review describes the current state of knowledge of research on the cattle gene pool, with special attention paid to Russian genetic resources. The evolution of methods used for studying genetic diversity is briefly described. The results of studies of the allele pool of cattle breeds based on polymorphisms of mitochondrial DNA and microsatellites are summarized (M.-H. Li et al., 2009; J. Kantanen et al., 2009; P. V. Gorelov et al., 2011; T. Yu. Kiseleva et al., 2014; A. A. Traspov et al., 2011; R. Sharma 2015). The advantages of using single nucleotides polymorphisms (SNP) at the genome-wide level to study the population structure and genetic relationships between breeds are discussed (R. Fries, G. Durstewitz, 2001; R. Martinez-Arias et al., 2001; C. Xing et al., 2005). Data on the divergence of breeds based on whole-genome SNP analysis are presented (J. E. Decker et al., 2009; L. A. Kuehn et al., 2011; E. J. Mctavish et al., 2013; J. E. Decker et al., 2014; J. E. Decker et al., 2016; T. Iso-Touru et al., 2016). The allele pool of modern populations of Russian cattle breeds is characterized (N. A. Zinovieva et al., 2016; A. Yurchenko et al., 2018; A. A. Sermyagin et al., 2018). In comparative studies of Eurasian taurine breeds, high genetic divergence of Yakut cattle was detected. This review describes the maintenance of significant parts of authentic genetic components in several Russian breeds (Kholmogor, Yaroslavl, Red Gorbatov), bolstering their status as valuable national genetic resources and confirming the need for more indepth studies and the preservation of these breeds. Notably, the use of powerful tools such as multiple SNP analysis does not always allow unambiguous interpretation of results from the point of view of the demographic history of Russian breeds due to the significant changes in the allele pool of modern populations of both Russian breeds and their presumed ancestor breeds. The informative power of molecular genetic analysis of breed evolution can be substantially enhanced by studying historical DNA samples, such as bone material from cranial and osteological collections (O. I. Boronetska et al., 2017). To date, methods have been developed to obtain DNA suitable for a wide range of molecular genetic studies of both mitochondrial and nuclear DNA, including individual gene and complete genome analysis (D. E. McHugh et al., 2000; A. Beja-Pereira et al., 2006; M. Gargani et al., 2015). Studying historical samples will provide new data on the allele pool evolution in Russian breeds and clarify the origin of modern populations. The results of such studies will be used to develop programs for breed conservation, as well as to establish organic production systems based on local genetic resources.

The study and conservation of biodiversity are increasingly important parts of modern biological science [1]. Agricultural genetic resources are the biological capital essential to develop production systems in the future [2]. In the XX century, animal husbandry development around the world used a limited number of breeds, leading to a significant decrease in the number of local breeds, which until recently, were actively involved in agricultural production [3]. Thus, over the past half-century, the total number of six Russian local dairy cattle breeds (Kholmogor, Yaroslavl, Bestuzhev, Kostromsky, Red Gorbatov, and Suksun) has decreased by more than 10-fold—from 3.4 million heads in 1960 to 312.6 thousand heads in 2015; the number of Yaroslavl, Kostroma and Bestuzhev animals decreased by 19-37-fold. The current population of Red Gorbatov cattle is approximately 0.6% of that in the middle of the last century (Fig.).



Changes in the number of the Russian local cattle breeds (thousand heads): \Box – year 2015, \blacksquare – year 1991, \blacksquare – year 1960 [4-6].

With the increasing demand for livestock products throughout the world as well as in Russia, we expect production systems to continue to use a few major breeds, which will result in further reductions in biodiversity.

Along with the decrease in the number of local breeds, crossbreeding within the small amount of purebred livestock puts local breeds at risk of extinction [3]. From a genetic point of view, crossbreeding leads to the disappearance of a number of unique alleles, especially rare ones, which can result in the loss of valuable traits and properties of breeds, including the composition of raw materials, disease resistance, the ability to adapt to the local and climatic conditions of specific regions, etc. In this regard, it is important to assess the current state of the allele pool of breeds and to identify populations and individuals that carry authentic breed-specific alleles and unique allelic combinations to develop programs to maintain the genetic authenticity of breeds.

This review describes the current state of knowledge in cattle gene pool research, with special attention paid to Russian local genetic resources. The possibilities of using historical samples to study the evolution of breeds are discussed.

Diverse types of DNA markers have been used to reconstruct the demographic history of domestic animal breeds [7]. In the 1960s, the main tools for characterizing genetic diversity, population structure and genealogical relationships between breeds were blood groups and milk protein polymorphisms [8, 9]. The detection of mtDNA polymorphisms and highly polymorphic microsatellites has since presented new opportunities for more powerful genetic studies [10]. Studies of polymorphisms of D-loop mtDNA have shown the presence of two independent centres of the domestication of taurine and indicine cattle [11-13]. which were subsequently confirmed by microsatellite analysis [14, 15]. Microsatellites were used to verify the hybrid origin of Middle Eastern cattle breeds [15, 16], demonstrate the various historical origins of Mediterranean and North European cattle populations [17], elucidate the classification of Eurasian cattle breeds [18], and determine the origin of some local cattle breeds [19, 20]. Mitochondrial DNA polymorphisms and microsatellites have been successfully used to study diversity, establish genetic relationships, and characterize the population structure of a number of Russian cattle breeds at the global [21] and regional levels [22-24]. The results obtained by M.-H. Li and J. Kantanen [18] confirmed the expansion of highly productive breeds, such as Danish Red, Angeln, Holstein-Friesian and Ayrshire, to Northern and Eastern Europe, including Russia. The authors pointed to the composite origin of the Yaroslavl, Istoben and Kholmogor cattle breeds, which, in their opinion, was a consequence of crossbreeding and may reflect the presence of multiple migration events from neighbouring regions of Europe, Asia and the Middle East. In all of the abovementioned breeds, a significant component of European Black Pied lowland cattle was found. However, it should be noted that this conclusion contradicts the opinion of a number of authors who claim that Kholmogor, Yaroslavl and Istoben cattle were developed with a slight influence of Holstein-Friesian cattle [25, 26]. In comparative studies of paternal (Y-chromosomal microsatellite haplotypes) and material (mtDNA haplotypes) variability, J. Kantanen et al. [21] showed the accelerated loss of Y-chromosomal variation in locally derived cattle breeds, including Russian breeds (Kholmogor, Yaroslavl, Istoben, Suksun, and Red Gorbatov), due to the intensive culling of breeding bulls and the paternal forms of cross-breeding. Based on mtDNA analysis, the similarity of Finnish and Northern Russian cattle breeds was shown. The allele pool diversity and the genetic structure of Sychev and Simmental breeds were characterized [22, 24] with linkage disequilibrium data of 29 microsatellite loci in six Russian cattle populations [23].

Another method for simultaneously analysing polymorphisms in many loci, which has been widely used in research of agricultural animal gene pools, is the analysis of polymorphisms in DNA fragments flanked by inverted repeats of microsatellite loci, or Inter Simple Sequence Repeats (ISSR) markers. ISSR markers enable the evaluation of the similarities and differences in the gene pools of species and breeds (intra-breed groups) and the assessment of genetic patterns and purebred and genealogical relationships [27, 28]. Studies of Russian and commercial cattle breeds have identified a large number of ISSR loci which can be used to distinguish *Bos taurus* and *Bos indicus*—that describe the "standard" of breeds, their genetic profile, and breed-specific patterns [29, 30]. Polymorphism analysis of mtDNA, microsatellites and ISSR markers has expanded our understanding of the origin and evolution of breeds; however, due to the insufficient power of these types of DNA markers, the results have not always been clearly interpreted.

The development of new high-throughput genotyping technologies has led to the widespread use of DNA markers based on single nucleotide polymorphisms (SNPs) in the study of animal genomes. Currently, SNPs are the preferred markers for genomic evaluation, establishing the relationship between individuals, determining the degree of inbreeding and hybridization, highresolution genetic mapping and more complete characterization of genetic resources [31, 32]. The main advantages of SNPs compared to microsatellites are their wide distribution in the genome and clear mutation mechanism, with a low level of homoplasy and lower mutation degree. The technical advantages of SNP analysis are the absence of special requirements for DNA quality (SNP analysis is mainly carried out by obtaining short amplicons of less than 100 bp), the lower degree of incorrect genotyping, the possibility of automating the process using high-throughput genotyping technologies, and the standardization of data [33-35]. SNPs provide wider genome coverage compared to STR and can be used to study both neutral and selection-affected genes [36, 37]. Despite the variety of SNP analysis methods [37], whole-genome analysis performed on the BeadArrayTM platform (Illumina, Inc., San-Diego, CA, USA) is becoming increasingly widespread, allowing the simultaneous analysis of several tens to several hundred thousand SNPs [38]. The development and market introduction of commercial DNA chips that allow simultaneous analysis of tens and even hundreds of thousands of SNPs has led to the dominance of SNP markers in animal genome analysis [39].

SNP analysis at the whole-genome level performed using Bovine SNP50 BeadChip (Illumina, Inc., USA) has been successfully applied to elucidate the historical origin and characterize the current structure of cattle populations worldwide [40-45]. In a large-scale study by Decker J.E. et al. [40], a phylogenetic network of 48 cattle breeds (n = 372) was constructed, which provided an accurate description of the genetic relationships between breeds and improved our understanding of the history of domestication and development of breeds. McTavish E.J. et al. [38] showed that North American breeds, as well as many related breeds in southern Europe, are of hybrid origin, exhibiting both taurine and indicine genomic components. Using a wide range of analytical methods, Decker J.E. et al. [43] were able to clearly distribute 134 breeds of domestic cattle (n = 1543) among three groups: Asian indicine, Eurasian taurine, and African taurine. The African taurine group contains a large proportion of the African tour ancestors, leading to its divergence from the Eurasian taurine group. The influence of species other than Bos taurus taurus and Bos taurus indicus on the development of Asian breeds of cattle was shown. A significant contribution of European Shorthorns in the origin of European breeds was found. The introgression of African taurine in Iberian and Italian cattle breeds was revealed [43].

Studies of Russian local cattle breeds at the whole-genome level have been less extensive. A total of 35874 polymorphic SNPs were used to estimate the genetic diversity and population structure of modern populations of five cattle breeds, including Bestuzhev, Kholmogor, Kostromsky, Red Gorbatov and Yaroslavl [46]. Analysis of the obtained SNP genotypes differentiated the Russian breeds from each other and from the Holstein breed, which was used for comparison. All the studied Russian breeds had a complex origin, and the analysis revealed the presence of genomic components from the other Russian breeds and, in several cases, the admixture of Holsteins. The study of 274 individuals from 18 domestic breeds in comparison with 135 world breeds [47] showed their distribution into four clusters, reflecting their ancestral relationships with other breeds. It was shown that some breeds (for example, Kholmogor, Yakut, and Yaroslavl) have specific genomic components, which makes them a priority target for further in-depth research. A detailed study of the population structure and relationships of nine Russian cattle breeds (Bestuzhev, Black-and-White, Kalmyk, Kholmogor, Kostromsky, Red Gorbatov, Suksun, Yakut, and Yaroslavl) with 36 other Eurasian *taurine* breeds was carried out by Sermyagin A.A. et al. [48]. Multi-Dimension Scaling (MDS)-analysis confirmed the taurine origin of all the studied local breeds. According to the neighbour-net and admixture results, all the breeds could be divided into three groups. The Yakut and Kalmyk cattle formed a separate group due to their Turan-Mongolian origin. The Blackand-White, Kostroma and Suksun breeds had a significant proportion of ancestral components of transboundary European breeds, Holsteins, Brown Swiss and Danish Red, respectively. The Kholmogor, Yaroslavl, Red Gorbatov and Bestuzhev breeds were characterized by the lowest share of introgression of transboundary breeds, which makes them the most important national genetic resource.

On the other hand, it should be noted that the study of modern populations of local Russian cattle breeds - even with a powerful tool such as wholegenome SNP-analysis — does not always allow an unambiguous interpretation of the demographic history of breeds. This is because the allele pool of modern populations of both Russian breeds and their presumed ancestors has undergone significant changes during centuries-old development. On the one hand, this is due to the influence of the changing environmental conditions, and on the other hand, is due to the alteration in breeding goals. Intensive breeding for a limited number of traits, which has been practiced in recent decades, had undoubtedly led to the population-wide distribution of alleles positively associated with selected traits and the elimination of other alleles that are neutral or negatively associated with the selected traits. Another difficulty in the identification of authentic genetic components in modern populations of domestic livestock is the active use of crossbreeding with highly productive transboundary breeds, which has been practiced in recent decades. Thus, intensive use of Red Holstein cattle to improve the Bestuzhev cattle breed [49], Black-and-White Holstein cattle to improve the Kholmogor [54, 55] and Tagil breeds [56, 57], Brown Swiss to improve the Kostromsky breed [54-56], and others, has been observed. The Russian Black-and-White breed has been almost completely replaced by Holsteins; pedigree analysis of more than 500 AI bulls in Russia [57] showed the presence of only a few animals with 50% or more blood from the Black-and-White breed. Another difficulty in interpreting molecular genetic results is that some of the initial breeds involved in the origin of Russian cattle breeds have ceased to exist. This extinction happened, for example, with Tyrolean cattle, which were widespread in Europe in the XIX century [58]. It is assumed that Tyrolean cattle, whose massive export to Russia occurred in 1848 [59], significantly impacted the formation of the Bestuzhev and Red Gorbatov allele pools [60].

Results from molecular genetic analyses of the demographic origins of breeds can be improved by including historical DNA samples from animals that existed at least 100 years ago. DNA for this analysis can be derived from skull samples, which are stored in craniological collections [61]. Craniological methods were the main method for studying the origins of domestic animals before the discovery of biological markers. Craniological methods were first used in 1865 by the Swiss scientist and professor of comparative anatomy L. Rutimever (1825-1898) [cited according 62]. L. Rutimeyer's development of this method led to a series of similar kinds of work in different cattle breeds. In Russia, the comparative anatomical method has been used to examine cattle by K. Linderman (1873 and 1874), A. von-Middendorf (1884), P. Kuleshov (1888), E. Liskun (1910), Filipchenko (1915 and 1916), V. Ustyantsev (1915), and A. Browner (1919) [cited according 62]. The craniological method was most developed by the academician E.F. Liskun. He developed a detailed method of craniological research [63] that was widely used for more than 50 years to study farm animals from different breeds. E.F. Liskun started the unique craniological and osteological collection of domestic animals from different parts of Europe and Asia, which has no counterpart in our country or abroad. In 1947, the collection was donated to the Timiryazev Moscow Agricultural Academy. The collection contains more than 700 skulls of animals, including 350 skulls of 41 cattle breeds [64]. Considering that the exhibits of the collection are dated from the end of XIX and beginning of the XX century, they may be used as reference profiles for cattle breeds in molecular genetic analyses and to trace the evolution of more than 100 years of history.

To date, methods have been developed to obtain DNA (both mitochondrial and nuclear DNA) that is suitable for a wide range of molecular genetic studies, including individual gene and complete genome analyses [65-67]. The first molecular genetic study using 10 microsatellite loci (TGLA227, BM2113, ETH10, SPS115, TGLA122, INRA23, TGLA126, BM1818, ETH225, and BM1824) revealed noticeable genetic differences between modern and historical samples of the Yaroslavl and Kholmogor cattle breeds. The development of research involving an additional number of historical samples and expanding the range of DNA markers used will enable the collection of new data on the allele pool evolution of Russian local cattle breeds over the last century.

Thus, the results of research conducted on the gene pools of Russian cattle breeds show the maintenance of the authentic genomic components in most breeds, which makes them the most important national genetic resources and a reserve of variability, which is necessary to sustain agricultural production systems in the future. Comparing modern and historical samples at the genomic level using a set of DNA markers will be useful for developing conservation programs for breeds, as well as for creating organic production systems based on the use of local genetic resources.

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