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Research Article

Analysis of the genetic diversity of Ayrshire cattle in Russia. Message 2. Genome analysis based on data on the distribution of ROH patterns in Ayrshire cows

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ABSTRACT

BACKGROUND: The analysis of ROH distribution is an important focus of genetic resource conservation programs of cattle. Characterization of ROH-islands allows to identify genetic factors affecting productivity traits of dairy cattle.

AIM: was to analyze intra-breed genetic diversity and population structure of Ayrshire cattle, based on data on distribution of homozygosity patterns, as well as to identify loci associated with selection intensity and utility traits.

MATERIALS AND METHODS: ROH distribution data were obtained using whole genome genotyping on Illumina BovineSNP50 (50K) DNA chips (Illumina Inc., USA). The object of the study was the DNA of Ayrshire cows (600 cows), which belonged to farms with different levels of selection and breeding work.

RESULT: The results of our studies showed a generally similar level of inbredness of the analyzed Ayrshire cattle herds. The homogeneity of the population is confirmed by a large number of animals (72.83%) with F_{ROH} values between 0.10 and 0.20. Cluster analysis revealed consolidated groups of individuals, due to their ancestral origins. The discovered ROH-patterns included 268 genes, 32 of which were involved in regulation of the synthesis of protein and fat milk components. The results obtained may be used in breeding programs for Ayrshire cattle in Russia.

CONCLUSIONS: The Russian population of Ayrshire cattle is distinguished by unique qualities in protein and fat milk composition and genome architecture, while maintaining genetic diversity and insignificant traces of Ayrshire cattle gene pool.

Keywords: homozygous regions; gene; genomic inbreeding; milk production.

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Научная статья

Анализ генетического разнообразия айрширского скота России. Сообщение 2. Анализ генома на основе данных распределения ROH-паттернов коров айрширской породы

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АННОТАЦИЯ

Актуальность. Анализ распределения ROH — важное направление в программах сохранения генетических ресурсов крупного рогатого скота. Характеристика ROH-островков позволяет выявить генетические факторы, оказывающие влияние на продуктивные качества молочного скота.

Цель — анализ внутрипородного генетического разнообразия и структуры популяции на основе данных распределения паттернов гомозиготности и идентификация локусов, ассоциированных с интенсивностью отбора по хозяйственно-полезным признакам у коров айрширской породы.

Материалы и методы. Данные о распределении ROH были получены на основании полногеномного генотипирования на ДНК-чипах Illumina BovineSNP50 (50K) (Illumina Inc., США). Объектом исследования была ДНК коров айрширской породы (600 голов), которые принадлежали хозяйствам с различным уровнем селекционно-племенной работы.

Результаты. Результаты наших исследований показали в целом схожий уровень инбредности анализируемых стад айрширского скота. Однородность популяции подтверждается большим числом животных (72,83 %) со значениями F_{ROH} в интервале от 0,10 до 0,20. Кластерный анализ выявил консолидированные группы особей, что обусловлено происхождением их предков. Обнаруженные ROH-паттерны включали 268 генов, 32 из которых вовлечены в регуляцию синтеза белково-жировых компонентов молока.

Выводы. Полученные результаты могут быть использованы в программах селекции айрширского скота, разводимого в России.

Ключевые слова: гомозиготные районы; ген; геномный инбридинг; молочная продуктивность.

Как цитировать

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ЭКО•ВЕКТОР

BACKGROUND

Assessing genetic diversity and population structure is important when developing strategies for improving dairy cattle, namely, maintaining and increasing their productive potential [1]. Herd performance is improved through classical selection tools, such as selection of the best animals and parental pairs. In this case, an important aspect is inbreeding, whose rational use enables to consolidate the best qualities of ancestors in subsequent generations and increases the profitability of herds in a shorter time. However, an increase in spontaneous inbreeding can lead to inbreeding depression, which negatively affects both productive qualities and animals' fertility [2]. Inbreeding influences genetic variability by reducing the proportion of heterozygosity and increasing the number of homozygous genotypes [3]. Traditionally, assessments of the inbreeding level in herds are based on pedigree information. The introduction of genetic technologies into dairy cattle breeding programs has made it accessible and possible to obtain more accurate data, even in the absence of a pedigree [4]. A tool for analyzing genomic inbreeding is runs of homozygosity (ROH) patterns, which are continuous homozygous regions of DNA passed on to offspring from parents with a common ancestor. Characterizing the length of ROH islands enables the assessment of the inbreeding level. Thus, long ROH patterns are typical for inbred individuals, whereas the presence of short regions in the genome indicates the presence of "ancient" or "spontaneous" inbreeding [5, 6]. An increase in the frequency of ROH patterns characterizes the populations subjected to artificial selection. Selection of the best individuals with high productivity is accompanied by a decrease in the diversity of haplotypes and an increase in homozygosity around the target genomic loci. As a result, ROH frequency is increased in genome regions that include selection "targets", which generally allows ROH to be used for identifying groups of genes associated with selection intensity for economically useful traits in dairy cattle [7, 8].

The population of Ayrshire cattle in Russia is small and ranks seventh among 25 dairy cattle breeds. At the same time, it's population size in recent years remains relatively stable, and due to the valuable milk properties against the background of increasing milk yields, this breed ranks second in milk productivity after Holsteins. The breeding area of Ayrshire cattle includes most of Russia, except for the Ural and Far Eastern Federal Districts [9]. Increasing the competitiveness of Ayrshire cattle is possible with the introduction of both individual and population-based genetic assessment into breeding programs. This will allow not only to establish the origin and breeding history, but also to significantly improve the breeding efficiency by reducing the negative consequences of inbreeding and identifying the genome loci that define the unique Ayrshire breed traits in Russia.

This study aimed to analyze intrabreed genetic diversity and population structure based on ROH distribution data and to identify loci associated with the intensity of selection for economically useful traits in Ayrshire cattle.

MATERIALS AND METHODS

For the study, six groups of Ayrshire cattle were formed, which belonged to farms with different levels of selection and breeding work (Table 1).

The study analyzed DNA samples from cows. Whole-genome genotypes were obtained using Illumina BovineSNP50 BeadChip array (50K) DNA chip (Illumina Inc., USA). SNP markers located on sex chromosomes were removed to exclude the influence of sex on the assessment. After quality control, 40498 SNPs remained for the analysis. PLINK 1.9 software was used for, 1) calculation of the observed (H_o) and expected (H_e) heterozygosity and fixation index (F_{is}); 2) assessment of the genomic architecture based on principal component analysis (PCA), followed by visualization in RStudio using the ggplot2 package; 3) a search for homozygous regions (ROH) on individual chromosomes, followed by visualization utilizing the

Table 1. The studied groups of Ayrshire cows

Таблица 1. Исследуемые группы коров айрширской породы

Group No.	Number of animals in the sample and heads	Category of the breeding farm	Region of the Russian Federation
1	98	Stud farm	
2	60	Stud farm	
3	178	Stud farm	Leningrad region
4	159	Pedigree breeding unit	
5	76	Pedigree breeding unit	
6	29	Stud farm	Moscow region

detectRuns library in RStudio with the following parameters: window size of 15 SNPs, window overlap threshold of 0.1, and minimum number of SNPs in the region of 15. The inbreeding index graph, calculated from ROH, was visualized in GraphPad Prism 12.0. For putative ROH islands, overlapping homozygous regions were detected with frequencies of 50%. The minimum size of the homozygous region was set at 500,000 bp. Localization of homozygous regions and gene annotation were performed using the cow genome assembly ARS-UCD1.2 (https://www.ensembl.org/Bos_taurus/Info/Index?db=core, access date 05/12/2023) in the Ensembl genome database (https://www.ensembl.org/index.html, access date 05/12/2023).

RESULTS

Analysis of genetic diversity based on heterozygosity indicators (H_o and H_e) and fixation index (F_{is}), revealed that group 4 was characterized by a slight heterozygote deficiency, as evidenced by low positive F_{is} values (0.009 ± 0.009) and minimal H_o values (0.323 ± 0.003). For the remaining samples, the F_{is} had negative values, and the level of observed heterozygosity was higher than the expected level (H_o min 0.350 ± 0.001, max 0.359 ± 0.002; H_e min 0.339 ± 0.000, max 0.346 ± 0.001; Table 2).

According to the inbreeding indicator (F_{ROH}), the analyzed cattle groups were relatively homogeneous, except for group 4. On average the F_{ROH} values ranged from 0.10 to 0.20 in 72.83% of individuals, from 0.06 to 0.10 in 26.67%, and >0.30 in 0.50% (3 heads) (Fig. 1).

Analysis of the genetic diversity based on PCA (Fig. 2) revealed that individuals of all groups formed one common cluster. However, consolidation of some individuals in group 3 was noted. In addition to the formation of a cluster that included several cows from groups 1 and 5, a convergence of individuals from groups 1–3 was noted, which resulted in a segment equidistant from the other clusters. The presence of separate groups may be related to the origin of the male parents of the cows under study (Fig. 2*c,* 2*d*).

Table 2. Genetic diversity of analyzed populations of Ayrshire cattle
Таблица 2. Генетическое разнообразие анализируемых популяций айрширского скота

Group No.	*n*	H_o (*SD*)	H_e (*SD*)	F_{is} (*SD*)
1	98	0.358 ± 0.001	0.339 ± 0.000	–0.055 ± 0.004
2	60	0.359 ± 0.002	0.346 ± 0.001	–0.036 ± 0.005
3	178	0.350 ± 0.001	0.343 ± 0.001	–0.021 ± 0.002
4	159	0.323 ± 0.003	0.326 ± 0.001	0.009 ± 0.009
5	76	0.355 ± 0.001	0.343 ± 0.001	–0.037 ± 0.003
6	29	0.354 ± 0.002	0.340 ± 0.000	–0.041 ± 0.004

Note. *n*, number of animals in the sample, heads; H_o, registered heterozygosity; H_e, expected heterozygosity; F_{is}, inbreeding coefficient

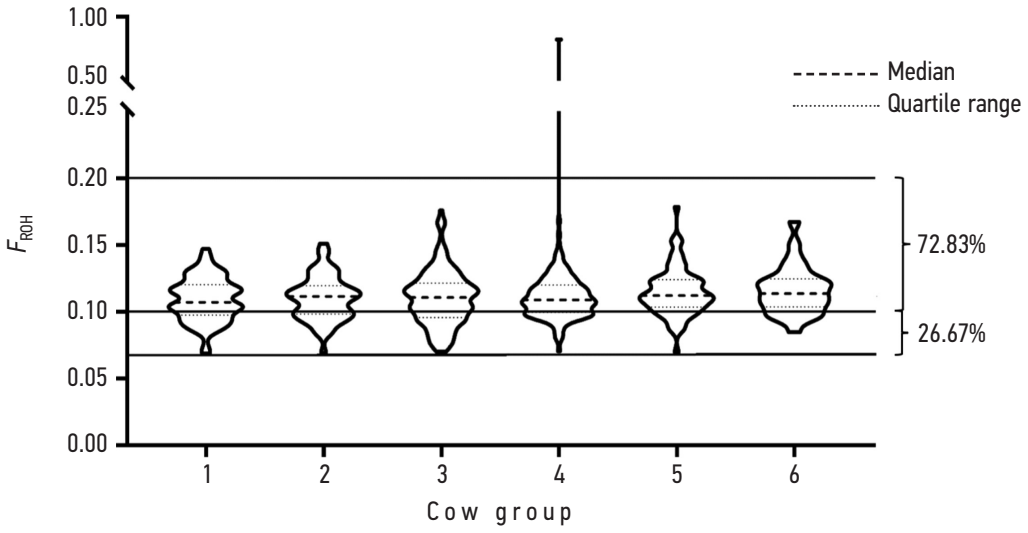

Fig. 1. Inbreeding Index (F_{ROH}) for analyzed samples of Ayrshire cows
Рис. 1. Индекс инбридинга (F_{ROH}) для анализируемых выборок айрширских коров

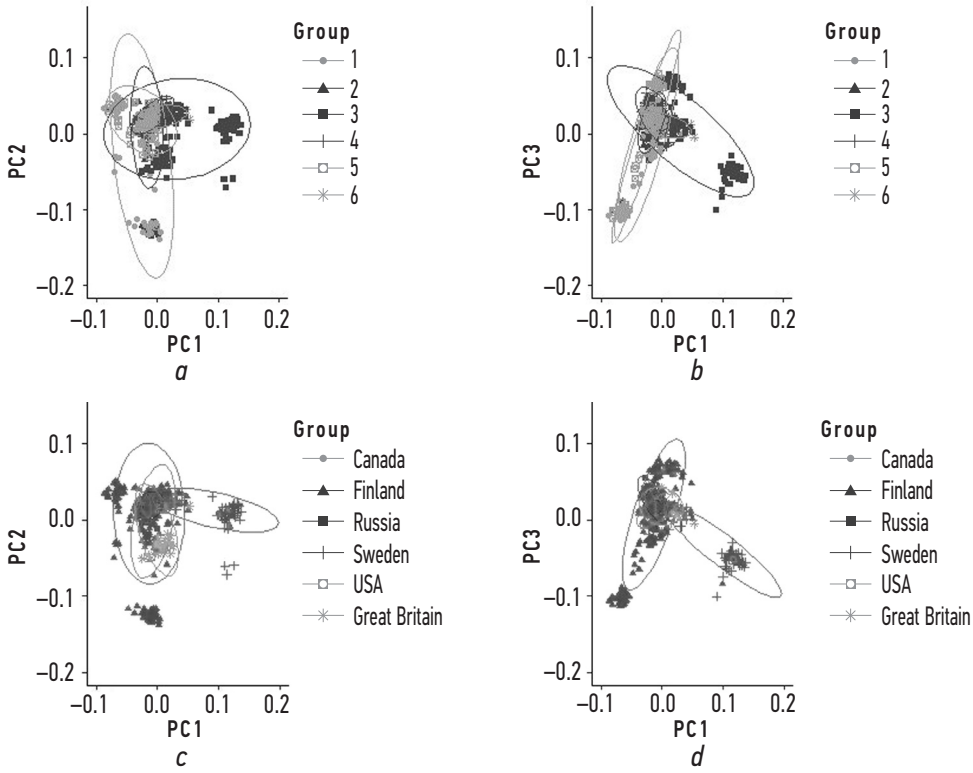

Fig. 2. Principal Component Analysis (PCA) based on genome-wide SNP genotypes of studied Ayrshire cows (*a*, *b*) and their fathers (*c*, *d*)
Рис. 2. Анализ главных компонент (PCA) на основании полногеномных SNP-генотипов айрширских коров (*a*, *b*) и их отцов (*c*, *d*)

Table 3. The length and number of ROHs in the analyzed Ayrshire cattle
Таблица 3. Протяженность и количество ROH в выборке айрширских коров

Group No.	*n*	Number of homozygous regions	Total length of homozygous areas (Kb)	Average length of the region (Kb)	F_{ROH} (Kb)
1	98	155.62 ± 1.318	327642.7 ± 4943.9	2106.1 ± 27.53	0.109 ± 0.002
2	60	157.17 ± 1.493	330732.1 ± 6368.6	2103.1 ± 34.05	0.110 ± 0.002
3	178	152.08 ± 0.938	331207.9 ± 4550.6	2170.4 ± 28.95	0.110 ± 0.002
4	159	163.35 ± 3.275	363417.9 ± 19795.1	2411.9 ± 249.47	0.121 ± 0.007
5	76	159.58 ± 1.592	343778.9 ± 6110.1	2158.2 ± 35.58	0.115 ± 0.002
6	29	162.28 ± 2.175	348305.6 ± 10061.5	2147.7 ± 56.89	0.116 ± 0.003

Note. *n*, number of animals in the sample, heads.

Analysis of the length and number of ROH patterns in the studied sample of Ayrshire cattle revealed some features (Table 3). Groups 4 and 6 were characterized by several homozygous regions and high F_{ROH} values; however, the average length of homozygous regions was slightly lower in group 6 (2147.7 ± 56.89) than in group 4 (2411.9 ± 249.47). For groups 2 and 3, with equal F_{ROH} values (0.110 ± 0.002), the number and average length of ROH patterns were different. Group 3 exhibited a smaller number of homozygous regions (152.08 ± 0.938) with high values of their average length (2170.39 ± 28.95), while group 2 with higher number of ROH patterns (157.17 ± 1.493) exhibited lower average length (2103.1 ± 34.05).

The distribution of the length and number of homozygous regions along chromosomes for the entire population analyzed is presented in Table 4. On BTA1 (Bos taurus autosome), the largest number of ROH patterns (11.51 ± 0.124) was detected with maximum values of the total length of homozygous regions (25843.7 ± 614.7) and F_{ROH} (0.086 ± 0.002). A smaller number of ROH islands in the studied cows was noted on BTA18, 19, and 23–29 (min 2.575 ± 0.056; max 3.885 ± 0.070).

The distribution of homozygous regions along various chromosomes in the studied population of Ayrshire cattle showed that homozygous loci with an occurrence frequency of ⩾50% are located on BTA1, 2, 6, 8, 13, 14, 16, 17, 21, 22, 24, and 26. A total of 268 genes

were identified based on the detected ROH islands (Table 5).

For all analyzed animals, genes involved in the regulation of lactation and synthesis of protein–fat components of milk were annotated (Table 6). A total of 32 genes were identified on 10 autosomes. The larger number of genes was detected on BTA6 and 16 (5 and 7 genes, respectively).

Table 4. The length and number of ROHs by chromosomes in the analyzed Ayrshire cattle

Таблица 4. Протяженность и количество ROH по хромосомам в выборке айрширских коров

BTA	Number of homozygous regions	Total length of homozygous regions (Kb)	Average length of the region (Kb)	F_{ROH} (Kb)
1	11.51 ± 0.124	25843.7 ± 614.7	2388.1 ± 113.8	0.086 ± 0.002
2	8.710 ± 0.120	18908.8 ± 500.6	2333.8 ± 130.2	0.063 ± 0.002
3	7.810 ± 0.110	16699.3 ± 436.2	2446.9 ± 226.5	0.056 ± 0.001
4	7.130 ± 0.104	15490.1 ± 433.5	2479.9 ± 226.7	0.051 ± 0.001
5	6.288 ± 0.105	16626.1 ± 487.7	2786.6 ± 108.8	0.055 ± 0.002
6	9.211 ± 0.110	19055.2 ± 450.3	2231.4 ± 121.9	0.064 ± 0.002
7	7.770 ± 0.111	16133.7 ± 411.3	2210.8 ± 91.94	0.054 ± 0.001
8	7.593 ± 0.101	15342.9 ± 399.4	2156.3 ± 106.5	0.051 ± 0.001
9	6.153 ± 0.097	13911.2 ± 443.6	2443.4 ± 121.2	0.046 ± 0.001
10	6.317 ± 0.098	12694.5 ± 381.1	2101.9 ± 89.67	0.042 ± 0.001
11	6.193 ± 0.101	13307.1 ± 431.9	2512.9 ± 194.8	0.044 ± 0.001
12	4.671 ± 0.081	10444.6 ± 320.8	2279.8 ± 75.88	0.035 ± 0.001
13	5.185 ± 0.086	11217.1 ± 324.5	2333.4 ± 111.7	0.037 ± 0.001
14	5.578 ± 0.084	12762.2 ± 343.6	2382.8 ± 84.21	0.043 ± 0.001
15	5.467 ± 0.093	12416.9 ± 348.7	2490.5 ± 124.6	0.041 ± 0.001
16	5.333 ± 0.091	11271.8 ± 322.6	2184.5 ± 87.56	0.036 ± 0.001
17	5.350 ± 0.087	10997.5 ± 312.9	2247.3 ± 144.9	0.037 ± 0.001
18	3.827 ± 0.079	7352.5 ± 261.6	2068.1 ± 145.1	0.025 ± 0.001
19	3.837 ± 0.077	8007.5 ± 278.9	2261.0 ± 117.3	0.027 ± 0.001
20	4.537 ± 0.083	9677.7 ± 303.3	2255.4 ± 99.46	0.032 ± 0.001
21	4.358 ± 0.079	8548.8 ± 271.3	2060.2 ± 87.09	0.028 ± 0.001
22	3.885 ± 0.070	10163.1 ± 302.4	2683.9 ± 91.03	0.034 ± 0.001
23	2.998 ± 0.067	5827.3 ± 207.3	2020.8 ± 106.8	0.019 ± 0.001
24	3.463 ± 0.073	7226.4 ± 258.5	2206.2 ± 130.5	0.024 ± 0.001
25	2.583 ± 0.064	5680.9 ± 209.9	2312.0 ± 126.7	0.019 ± 0.015
26	3.092 ± 0.063	8093.3 ± 264.2	2679.7 ± 118.7	0.027 ± 0.001
27	3.005 ± 0.062	5696.9 ± 207.6	1977.4 ± 106.5	0.019 ± 0.001
28	2.575 ± 0.056	5432.9 ± 197.9	2096.9 ± 81.50	0.018 ± 0.001
29	3.378 ± 0.074	6668.7 ± 232.4	1921.2 ± 64.84	0.022 ± 0.001

Table 5. Quantitative characterisation of the identified genes in the studied ROH regions

Таблица 5. Количественная характеристика идентифицированных генов на основе исследуемых ROH-районов

BTA	Region	Genes (*n*)
1	1.264.369–2.415.018	13
1	75.588.102–79.324.497	12
1	146.790.949–149.279.017	12
2	71.023.597–75.885.774	17
6	35.211.888–38.042.011	20
6	77.186.116–79.126.321	1
6	81.042.351–82.605.943	1
8	36.191.988–37.451.828	2
8	57.592.438–59.245.157	3
8	61.014.570–62.015.685	12
13	53.091.922–54.106.367	28
14	23.946.436–26.836.013	19
16	42.625.201–46.192.353	27
17	35.586.493–36.118.075	1
17	57.172.637–58.734.028	10
21	7.694.470–8.927.671	3
22	48.063.014–49.273.889	40
24	30.265.281–33.000.605	12
26	21.832.456–23.689.229	35

Note. *n*, number of genes.

DISCUSSION

Genetic variability and inbreeding levels should be monitored and analyzed to ensure diversity of genetic resources of Russian dairy cattle [38]. Analysis of genetic diversity showed that the inbreeding coefficient in Ayrshire cattle in Russia had positive and negative values. Based on the results of the study, heterozygote deficiency can be assumed in group 4, as indicated by positive F_{is} values (Table 2). In other studied groups, the inbreeding coefficient was negative, which indicates the absence of a deficiency of heterozygous genotypes and, in turn, confirms the presence of genetic diversity. Previous studies using semen samples from bulls used for breeding in the Russian Federation have reported positive F_{is} values, indicating a higher degree of genomic inbreeding, which is generally acceptable for bulls [39]. In this study, genetic differences between groups are not only caused by group size, but also by differences in the breeding strategy used on the farms. High inbreeding coefficient values indicate a decrease in group heterozygosity. However, we did not find a deficiency of heterozygotes in any of the studied herds, except for herd 4; thus, we can state the absence of inbreeding depression and the presence of effective selection aimed at maintaining heterozygosity, which indicates that the selection of parental pairs was targeted.

According to Visser et al. [38], the inbreeding rate in the South African Ayrshire cattle is 0.053 on average, with most individuals having F_{ROH} values ranging from 0.04 to 0.05. However, in our study, the average F_{ROH} value for all 6 groups of Ayrshire cattle was higher and amounted to 0.114, and for most cows (72.83%), these values ranged from 0.10 to 0.20 (Fig. 1, Table 3).

The results of the PCA revealed (Fig. 2) the homogeneity of the Russian Ayrshire cattle. However, some animals were grouped into separate clusters, which is probably related to the origin of their male parents, which are part of the population of Swedish and Finnish Ayrshire cattle (Fig. 2). Similar results were obtained in a study of Holstein cows from 13 farms in the Leningrad region, where the genetic homogeneity of herds was also revealed [40].

Based on data on F_{ROH}, number and average length of ROH along chromosomes, a conclusion can be drawn about the level of inbreeding. The increase in the length of homozygous regions can be attributed to both the introduction

Таблица 6. Аннотированные гены-кандидаты, ассоциированные с признаками молочной продуктивности и находящиеся под селекционным давлением

Table 6. Annotated candidate genes associated with milk productivity traits, that are under selection pressure

Region	BTA	Gene	Functional role	References
75,588,102–79,324,497	1	*IL1RAP*	Lipid metabolism in white adipose tissue in humans	[10]
146,790,949–149,279,017	1	*DOP1B*	It participates in the formation of milk fat in milk	[11]
		HLCS	Fatty acid synthesis and amino acid catabolism in humans	[12, 13]
71,023,597–75,885,774	2	*DBI*	Oxidation of fatty acids in the mitochondria and biosynthesis and accumulation of lipids in the muscles	[14]
35,211,888–38,042,011	6	*FAM13A*	Proliferation of adipocyte progenitors in cattle	[15]
		HERC3, HERC5, HERC6	Synthesis and secretion of β-casein	[16, 17]
		ABCG2	It participates in the formation of milk fat and protein in milk	[18]
53,091,922–54,106,367	13	*NPBWR2*	Lipid metabolism in humans	[19]
		ABHD16B	Lipid biosynthesis	[20, 21]
		ZGPAT	Protein synthesis and secretion in mammary gland tissue	[22]
23,946,436–26,836,013	14	*CYP7A1, RAB2A*	Lipid metabolism	[23]
42,625,201–46,192,353	16	*CLSTN1*	Fatty acid synthesis	[24]
		CA6, ENO1	It participates in the formation of milk fat in milk	[25]
		PARK7, TNFRSF9, UTS2, CAMTA1	Fat deposition in muscle tissue	[26]
57,172,637–58,734,028	17	*SPRING1*	Lipid metabolism	[27]
48,063,014–49,273,889	22	*NT5DC2*	It participates in the formation of milk fat and protein in milk	[28]
		TNNC1, GLYCTK	Fat deposition in muscle tissue	[29, 30]
		PARP3	Lipogenesis	[31]
30,265,281–33,000,605	24	*ZNF521*	Fat deposition in muscle tissue	[32]
		OSBPL1A	Phospholipid binding	[33]
21,832,456–23,689,229	26	*LZTS2*	It participates in the formation of milk fat in milk	[34]
		NPM3	In humans, it promotes the transition of fatty acids from white to brown adipose tissue	[35]
		ARMH3	Transport of proteins and lipids	[36]
		ELOVL3	Lipid metabolism	[37]

of genomic selection in cattle breeding programs and recent inbreeding [41]. For all chromosomes in the studied cows F_{ROH} values ranged from 0.018 to 0.086 (Table 4), which is somewhat consistent with data obtained from Finnish Ayrshire cattle, where F_{ROH} ranged from 0.00 to 0.05 [42]. This is most likely due to the use of Finnish stud bulls in Ayrshire breeding programs in Russia.

Homozygous regions resulting from inbreeding have a chaotic distribution throughout the genome [43]. However, the selection pressure in these regions can be determined by the frequency of the occurrence of ROH islands [44]. Our work identified several homozygous regions with an occurrence frequency of >50% on BTA1, 6, 8, and 17 (Table 5). Similar results were obtained in a study conducted on major dairy cattle breeds in the USA, where a higher number of ROH patterns were identified on BTA4–6 and BTA8 [45]. The accumulation of ROH patterns on these BTAs may be caused by the intense selection for milk productivity [46].

In this study, the genes identified by ROH analysis are thought to be associated with milk productivity in Ayrshire cattle (Table 6). Homozygous regions on various BTAs included genes whose transcription products in early studies were associated with lipid metabolism (BTA1: *IL1RAP*, BTA13: *NPBWR2*, BTA13: *ABHD16B*, BTA14: *CYP7A1*, *RAB2A*, BTA17: *SPRING1*, and BTA26: *ELOVL3*) [10, 19–21, 23, 27, 37]. Protein-coding genes *DOP1B* and *ABCG2, ZGPAT, CA6* and *ENO1, NT5DC2*, and *LZTS2* may be related to milk fat and protein formation in Ayrshire cows' milk. Their functions have been previously described in studies on Holstein cows [11, 18], yaks [22, 25], Asian buffaloes [28], and Gir breed (*Bos indicus*) [34]. Proteins encoded by *HERC3*, *HERC5,* and *HERC6*, which were studied in the works of Pedrosa et al. [16] and Do et al. are responsible for the synthesis and secretion of β-casein [17]. Regions on BTA1, 2, 16, and 26 include genes whose functions are associated with synthesis and oxidation of fatty acids (*HLCS*, *DBI*, and *CLSTN1*) [12–14, 24]. In the work of Liang et al. [15], *FAM13A*, located on BTA6, is associated with proliferation of adipocyte progenitors. Abou-Rjeileh U., et al. (2023) linked *PARP3* gene transcription products to lipogenesis [31]. The *OSBPL1A* gene found on BTA24 encodes a protein that is responsible for phospholipid binding in cattle bred in China. The homozygous region on BTA26 included ARMH3, which, according to the findings of Jayawardana et al. [36], is involved in the protein and lipid transport pathway in New Zealand dairy cattle. This chromosome also contains *NPM3*, the transcription products of which have adipokine characteristics, thereby regulating the transition of fatty acids from white to brown adipose tissue in humans. On BTA16, a group of proteins encoded by *PARK7*, *TNFRSF9*, *UTS2*, and *CAMTA1* was identified in all groups of Ayrshire cattle. Their functional role is associated with the deposition of fat in muscle tissue in Nerole cattle [26]. This functional role is also performed by genes on BTA22 and BTA24 (*TNNC1, GLYCTK,* and *ZNF521*) [29, 32]. It is likely that the presence of genes that function as indicators of milk productivity in homozygous regions is associated with intensive selection of Ayrshire cattle in Russia. In the future, these genes could serve as markers of milk productivity.

CONCLUSION

The results of our study showed a generally similar level of inbreeding in the analyzed herds of Ayrshire cattle. Population homogeneity was confirmed by the fact that most animals (72.83%) had F_{ROH} values ranging from 0.10 to 0.20, with an average F_{ROH} of 0.114. Cluster analysis revealed consolidated groups of individuals, the presence of which was determined by the origin of their paternal ancestors. The discovered ROH patterns included 268 genes, 32 of which are involved in the regulation of the synthesis of protein–fat components of milk. ROH accumulation at these loci provides evidence of selection pressure aimed to improve milk quality characteristics in Ayrshire cattle. The results obtained can be used in breeding programs for Ayrshire cattle bred in Russia.

ADDITIONAL INFORMATION

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Authors' contribution. Thereby, all authors made a substantial contribution to the conception of the study, acquisition, analysis, interpretation of data for the work, drafting and revising the article, final approval of the version to be published and agree to be accountable for all aspects of the study. Contribution of each author: M.V. Pozovnikova — research concept; A.E. Ryabova, M.V. Pozovnikova — curatorship, writing of the text of the article, editing; A.I. Azovtseva — formal analysis, writing and editing of the text of the article; M.V. Pozovnikova, Yu.S. Shcherbakov — research methodology; Yu.S. Shcherbakov, A.E. Ryabova — software; Yu.S. Shcherbakov, O.V. Tulinova — validation; E.A. Romanova, O.V. Tulinova — conducting research, writing and editing the text of the article.

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