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FRAGMENTS OF ENDOGENOUS RETROVIRUSES AS "ANCHORS" TO SCAN OF GENOMES OF CATTLE, SHEEP AND HORSE

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ABSTRACT

The comparative analysis of the multilocus spectra obtained on the basis of use as primers in polymerase chain reaction of fragments of long terminal repeats (LTR) of endogenous retroviruses – SIRE-1, PawS5, BARE-1, BERV-K1 and BERV β-3 – in a number of breeds of cattle, sheep and horses was carried out. We compared the obtained multilocus spectra with homologous sequences from the reference genomes of cattle, sheep, horses, represented in GenBank, and miRNAs databases. It was discovered that the complexity of the resulting multilocus spectra could be related to the frequency of homologous sites to primers in the genomes of the studied species, the functional significance of the genomic elements that are associated with them and the comparative "oldness" of endogenous retroviruses. The most significant interbreed differences in cattle and sheep were detected in the spectra of PawS5 and BERV β-3 primers, in horses – in SIRE-1 and PawS5 spectra.

INTRODUCTION

Genetic resource management requires the development of easy to interpret and low-cost generations of molecular genetic markers that could identify multilocus genotypes of farm animals, evaluate the features of gene pools of various groups of animals, and plan and predict their consolidation and variability. In order to identify genomic targets for artificial selection associated with the desired development of productivity traits in beef and dairy cattle, genomic maps of mononucleotide polymorphism distribution (Single Nucleotide Polymorphisms — SNP) have been developed. However, the associations between SNP and productivity traits were breed-specific and characterized by ahigh intrabreed variability (Zhao *et al.,* 2015). To increase the efficiency of genomic domain revealing, polymorphism of which could be used to solve the problems of genomic selection, a new generation of markers were being employed in addition to SNPs, which were based on the analysis of polymorphisms of the copy number of short DNA segment of at least 1 kb in size (Copy Number Variability — CNV; Scherer *et al.,* 2007) and their genomic distribution (Xu *et al.,* 2014, 2016; Bickhart *et al.,* 2016). It was found that using these two approaches (SNP and CNV) for multilocus genotyping of cattle genomes also did not lead to consistent results (Xu *et al.,* 2014).

Solving the problems of multilocus genotyping or genome scanning has significantly changed with the emergence of complete genome sequencing. However, the results of this approach had made it possible to identify a far greater intrabreed and intraspecies variation of nucleotide sequences than it was previously assumed. For example, a direct comparison of genome sequencing results of 62 bulls from three breeds of dairy cattle (Holsteins, Montbéliards, Normandes) allowed to confirm a high level of polymorphism in different genomic regions (Boussaha *et al.,* 2015). It was known, that a large part of farm mammal genomes is almost half-composed of dispersed repeats closely associated with the spread of endogenous retroviruses (Tellam and Worley, 2009). In this regard, in search of a new generation of molecular genetic markers, we had previously performed comparisons of multilocus spectra in different farm species using in polymerase chain reaction (PCR) as primers the fragments of long terminal repeats of five endogenous retroviruses (Inter-Retrotransposon Amplyfied Polymorphism — IRAP-markers) identified in plants and animals (Elkina *et al.,* 2015; Glazko *et al.,* 2015).

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A comparative analysis of polymorphism of genomic DNA fragments of different lengths derived from multilocus spectra of IRAP-markers in breeds of cattle, sheep and horses was performed in this study.

MATERIALS AND METHODS

The analysis included the multilocus spectra of IRAP-markers in cattle (173 animals), such as holsteinized Black-and-White breed (Moscow and Moscow Region), Yakut (Sakha Republic), zebu-like cattle (Moscow Region); sheep (119 animals), such as Edilbay breed (Volgograd Region), Kalmyk (Kalmykia Republic); horses (155 animals) — Altai breed (Altai Republic), Karachay breed (Stavropol region), and Trotters (Moscow Region).

Genomic DNA was isolated from peripheral blood cells of the tested animals using a commercial reagent kit DNA-Extran-1 (Syntol, Russia). IRAP-PCR was performed using a modified procedure by Zietkiewicz E. and coauthors (Zietkiewicz *et al.*, 1994). Oligonucleotide sequences (Syntol, Russia) homologous to terminal inverted fragments of mobile elements were used as primers: LTR SIRE-1 (GCAGTTATGCAAGTGGGATGAGCA, LTR SIRE-1 primer), R173 family (AACGAGGGGTTCGAGGCC, PawS5 primer), BARE-1 (CCAACTAGAGGCTTGCTAGGGAC, BARE-1 primer), bovine endogenous retroviruses BERV K-1 and BERV β-3 (TATCAGGCCTCTCCGCATG, BERV k-1 primer; GGACCTTCTCCTTCAAGGC, BERV β-3 primer). PCR was performed in a total volume of 20 μL using a commercial reagent kit for RT-PCR (Syntol, Russia). Amplification conditions: initial denaturation (t = 94 °C, 2 min.); denaturation (t = 94 °C, 30 sec.), annealing (t = 55 °C, 30 sec.), elongation (t = 72°C, 2 min.) - 30 cycles; final elongation (t = 72 °C, 10 min). PCR was performed on a Tertsyk thermocycler (DNA Technology, Russia). The amplification products were separated on horizontal 1.5 % agarose gels. Gels were stained with ethidium bromide. DNA fragment sizes were determined with the help of a molecular weight marker of 100 bp + 1.5 Kb + 3 Kb (12 fragments of 100 to 3,000 bp) M27 (SibEnzyme, Russia). Each fragment in the obtained DNA spectra was regarded as a distinct locus. The presence/absence of a fragment of a particular length in the spectra was assessed as locus genotype. Phylogenetic calculations were performed in TFPGA open access software. PIC (Polymorphic Information Content) score calculation was carried out using the formula for biallelic loci based on the Hardy-Weinberg principle, for which PIC = 2f(1 – f), where f is the frequency of one of the two alleles.

Using BLASTn program algorithms optimized for highly similar sequences, a search was performed in the reference genomes of cattle, sheep, and horses represented in the GenBank sequences for regions homologous to the DNA fragments which were used in the PCR as primers (resource http://www.ncbi.nlm.nih.gov). To assess the presence of homology between selected primers and microRNAs, the microRNA database at http://www.mirbase.org/ was used.

RESULTS AND DISCUSSION

Genotyping was performed on the PCR spectra obtained with the use as primers of the fragments LTR different endogenous retroviruses: in total on 64 loci of cattle breeds – primers LTR SIRE-1 (14 loci), PawS 5 (14 loci), BARE-1 (11 loci), BERV k-1 (18 loci), BERV β-3 (7 loci); on 75 loci in sheep genomes – primers LTR SIRE-1 (16 loci), PawS 5 (17 loci), BARE-1 (16 loci), BERV k-1 (14 loci), BERV β-3 (12 loci) and on 54 loci in horse genomes – primers LTR SIRE-1 (10 loci), PawS 5 (19 loci), BERV k-1 (14 loci), BERV β-3 (11 loci).

The spectra of genomic DNA fragments (amplicons) of the studied animals were divided into three groups according to their lengths which were calculated based on a molecular weight marker: "light" (100 to 900 base pairs [bp]), "medium" (900 to 1,900 bp) and "heavy" (1,900 to 3,000 bp) (see Figure 1). It is assumed, that these groups represent a relatively close (light fragments, distance from 100 to 900 bp) position of regions homologous to the location of the long terminal repeat (LTR) fragments of endogenous retroviruses in the alternative DNA strands, while a distant location of such sequences results in the formation of heavy fragments (from 1,900 to a maximum length of approximately 3,000 bp that is potentially amplifiable under the amplification conditions used), and a group of medium-sized DNA fragments with intermediate length values.

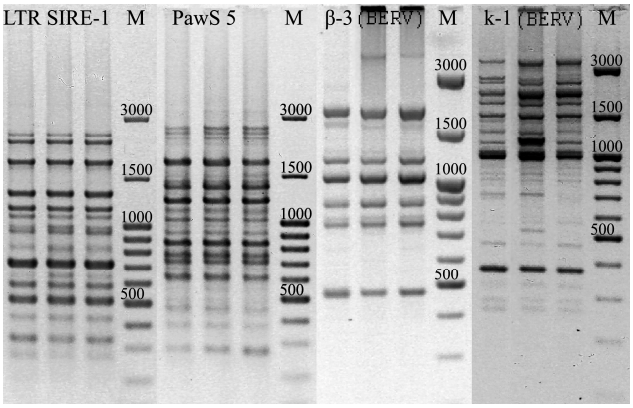

Figure 1 Spectra of Holstein (Black-and-White) cattle genomic DNA fragments flanked by inverted repeats of LTR SIRE-1, PawS 5, BERV β-3, BERV k-1 (M-marker of molecular weights of 3,000, 1,500, 1,000, 500 bp)

The data obtained as a result indicate the complex organisation of spectra of amplification products derived when using the different LTR types as primers in PCR (see Figure 2-6).

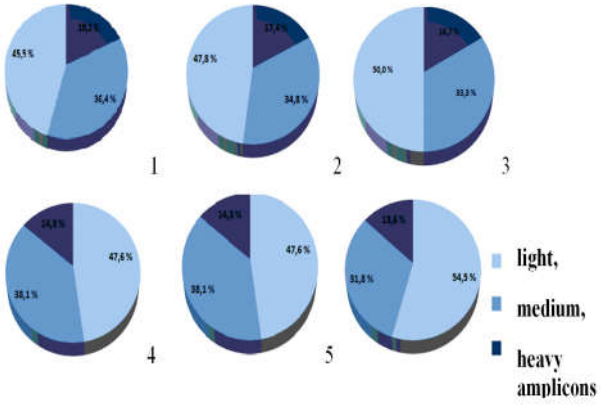

Figure 2 Contribution (in %) of heavy, medium and light amplicons to the spectra of genomic DNA amplification products obtained when using in PCR fragment of SIRE-1 sequence as a primer: 1 - Black-and-White cattle, 2 - Yakut breed, 3 - Zebu-like cattle; 4 - Edilbay sheep (Suyunduk type), 5 - Edilbay sheep (Birilik type), 6 - Kalmyk sheep.

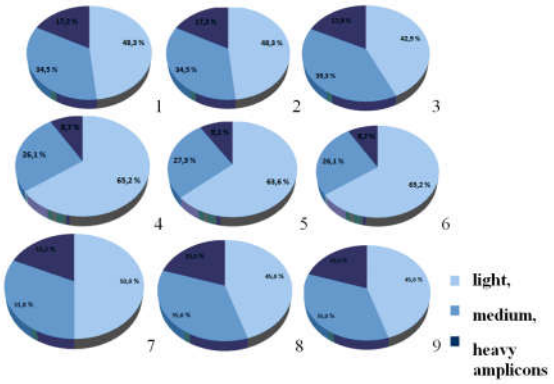

Figure 3 Contribution (in %) of heavy, medium and light amplicons to the spectra of genomic DNA amplification products obtained when using in PCR fragment of PawS5 sequence as a primer: 1 - Black-and-White cattle, 2 - Yakut breed, 3 - Zebu-like cattle; 4 - Edilbay sheep (Suyunduk type), 5 - Edilbay sheep (Birilik type), 6 - Kalmyk sheep; 7 – Trotters, 8 - Karachay horses, 9 - Altai horses.

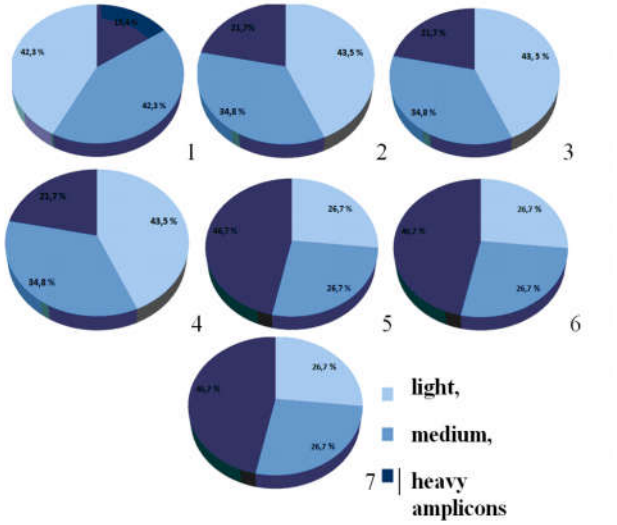

Figure 4 Contribution (in %) of heavy, medium and light amplicons to the spectra of genomic DNA amplification products obtained when using in PCR fragment of BARE-1sequence as a primer: 1 - Zebu-like cattle; 2 - Edilbay sheep (Suyunduk type), 3 - Edilbay sheep (Birilik type), 4 - Kalmyk sheep; 5 – Trotters, 6 - Karachay horses, 7 - Altai horses.

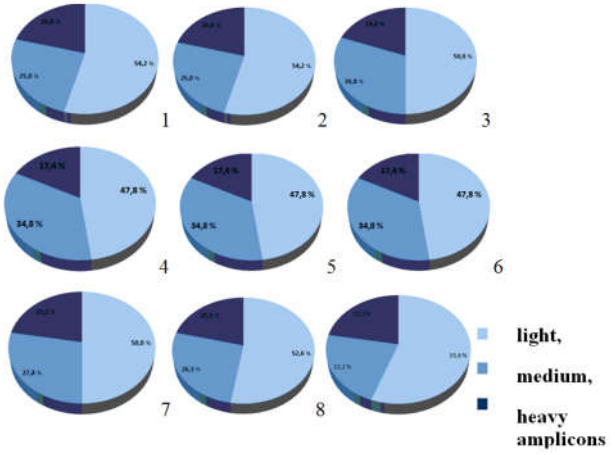

Figure 5 Contribution (in %) of heavy, medium and light amplicons to the spectra of genomic DNA amplification products obtained when using in PCR fragment of BERV k-1 sequence as a primer: 1 - Black-and-White cattle, 2 - Yakut breed, 3 - Zebu-like cattle; 4 - Edilbay sheep (Suyunduk type), 5 - Edilbay sheep (Birilik type), 6 - Kalmyk sheep; 7 – Trotters, 8 - Karachay horses, 9 - Altai horses.

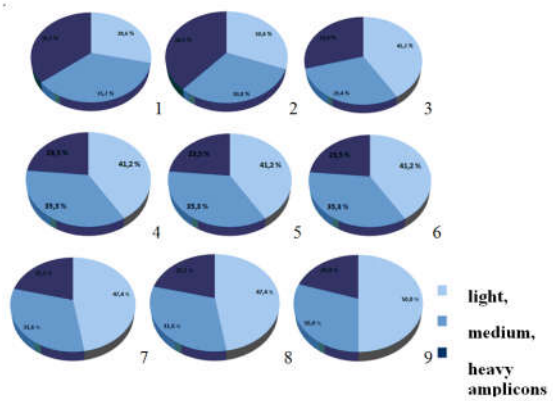

Figure 6 Contribution (in %) of heavy, medium and light amplicons to the spectra of genomic DNA amplification products obtained when using in PCR fragment of BERV β-3 sequence as a primer: 1 - Black-and-White cattle, 2 - Yakut breed, 3 - Zebu-like cattle; 4 - Edilbay sheep (Suyunduk type), 5 - Edilbay sheep (Birilik type), 6 - Kalmyk sheep; 7 – Trotters, 8 - Karachay horses, 9 - Altai horses.

Thus, for the investigated cattle breeds, it was discovered that light DNA fragments were the major contributors (nearly half of the spectrum) to the spectra of LTR SIRE-1, PawS 5, BARE-1, BERV k-1 primers, especially in the ERV K-1 primer spectra (over 50 %), and only in the BERV β-3 primer spectra almost a third of the spectrum was represented by heavy fragments. No significant interbreed differences were found for this feature. In sheep as well as in the cattle, light DNA fragments made the major contribution (almost half of the spectrum) to the spectra of LTR SIRE-1, BARE-1, BERV K-1 primers. The spectra of the PawS 5 primer were uniquely enriched with light fragments (over 60 %). The BERV β-3 primer spectra in sheep differed from those in cattle; in them the heavy fragments were less common, and the light fragments occupied more than 40 % of the spectra. In horses, the primary contribution (almost half of the spectrum) to the spectra of PawS 5, BERV K-1, BERV β-3 primers was made by light DNA fragments, while the spectra of the BARE-1 primer were uniquely enriched with heavy fragments (over 47 %).

Thus, the following interspecies differences in the representation of DNA fragments of different lengths were identified in the spectra of amplification products. In cattle, the spectra of the ERV K-1 primer consisted mainly (over 50 %) of light fragments, and only the spectra of the BERV β-3 primer were represented almost up to a third by heavy fragments. In sheep, the spectra of the PawS 5 primer were uniquely enriched with light fragments (over 60 %). The BERV β-3 primer spectra in sheep differed from those in cattle; in them the heavy fragments were less common, and the light fragments occupied more than 40 % of the spectra. In horses, the spectra of the BARE-1 primer were uniquely enriched with heavy fragments (over 47 %).

Polymorphism characteristics (the proportion of polymorphic loci — P, in %; Polymorphic Information Content — PIC) of the amplification product spectra obtained with different primers were presented in the Table. The polymorphism characteristics presented in the Table indicated that the highest values of PIC in holsteinized Black-and-White and Yakut cattle (*Bos taurus*) were found in the spectra of the PawS 5, BARE-1 and BERV k-1 primers, and in the Yakut cattle also in the spectrum of the BERV β-3 primer.

Table Polymorphism characteristics (P, PIC) of IRAP-PCR marker spectra in cattle, sheep, and horses

Primers	LTR SIRE-1		PawS 5		BARE-1		BERV k-1		BERV β-3	
Species and breeds	PIC	P, %	PIC	P, %	PIC	P, %	PIC	P, %	PIC	P, %
Black-and-White cattle	0.088	21	0.117	36	0.141	82	0.147	33	0	0
Yakut breed	0.060	14	0.231	50	0.178	55	0.165	39	0.206	43
Zebu-like cattle	0.000	0	0.035	7	0.009	9	0.151	39	0	0
Kalmyk sheep	0.112	31	0.159	47	0.154	25	0.099	21	0.037	17
Edilbay sheep	0.081	19	0.113	35	0.157	38	0.152	36	0.111	25
Altai horses	0.192	67	0.169	40	-	-	0.029	14	0.203	64
Karachay horses	0.145	33	0.048	11	-	-	0.057	21	0.138	36
Trotters	0.027	6	0.035	10	-	-	0.087	29	0.154	45

In other words, the highest polymorphism was observed in those spectra where the main contribution came from light DNA fragments, and only in the Yakut cattle was it found in the spectrum with the largest contribution from the heavy fragments (see Figure 2-6).

Zebu-like cattle (*Bos indicus*) differed in the spectra of all the primers except for the BERV k-1 primer. According to the Table, when assessing the differentiation of animal groups of the *Bos taurus* breeds, the most compelling results were obtained for the polymorphism of the spectra of the BERV β-3 primer, and also for the spectra of the PawS 5 and BARE-1 primers between *Bos taurus* and *Bos indicus*. In sheep as well as in cattle, the most pronounced interbreed differences in polymorphism were found in the spectra of the BERV β-3 primer, despite the fact that in sheep, unlike in cattle, heavy fragments of DNA were less common.

In terms of the polymorphism characteristics, spectra in horses differed from those identified in cattle and sheep, especially by a low level of polymorphism of the BERV k-1 primer. The highest level of polymorphism among different breeds of horses was observed in the spectra of the BERV β-3 primer, in the Altai horses — also in the spectra of the LTR SIRE-1 and PawS 5 primers, and in the spectrum of the LTR SIRE-1 primer in Karachay horses.

Overall, the lowest differences in polymorphism characteristics between species were detected in cattle and sheep in the spectra of the LTR SIRE-1 and BERV k-1 primers, in horses - in the spectra of the BERV k-1 primer, while the largest differences were found in cattle and sheep in the spectra of the BERV β-3 primer, and in horses - in the spectra of the LTR SIRE-1 and PawS 5 primers.

The obtained data indicate that the genomic regions in the investigated groups of animals homologous to DNA fragments of endogenous retroviral LTR, first characterized in plants and animals and used as primers in PCR, are largely characterized by a high level of variability in their positioning in the alternative DNA strands.

We had previously evaluated the polymorphism of DNA fragments flanked by LTR of soy SIRE-1 transposone (P/N: AF053008), in the Lebedinsky cattle breed.

It was found that in the spectrum of the amplification products obtained using this primer in a polymerase chain reaction, 14 DNA fragments were revealed, 11 of which had no individual variation and were also observed in the spectra of the amplification products in animals from anther breed — Holstein. Only three distinct DNA fragments were characterized by pronounced polymorphism (Glazko and Glazko, 2011).

In order to evaluate the possibility of localising DNA regions homologous to the soy transposone LTR in the genome of cattle, a corresponding search was performed in the GenBank sequence database using the BLASTn program. We had found that regions with partial homology (>80%) were presented in sequences of 20 of 29 autosomes of cattle, as well as in X and Y chromosomes.

In our earlier studies (Glazko *et al.,* 2006; 2009), we carried out genotyping of some varieties and regenerants of rice and wheat using fragments of DNA flanked by inverted repeated fragments of retrotransposone-like elements of the same R173 family, in particular, PawS5. It was found that the DNA fragments flanked by inverted repeats of these sequences varied significantly between varieties of rice, wheat and even between regenerants, which have a common varietal origin. Then we carried out a corresponding search of regions of PawS5 homology in Genbank, particularly in cattle, using the BLASTn program. We found a large number of regions with partial homology to sequences of the flanks of these retrotransposones, which were usually localized in the region of the P450 polygenic family, and genes associated with immune system function and transcription regulation factors. Regions of homology to these flanks of the R173 family members were somewhat more extensive in taxonomic representation than the soy retrotransposone flank, and are also found in prokaryotes.

Species-specific genomic sequences found in Genbank and available for homology search were comparatively depleted of repeated DNA sequences which allowed to evaluate the regions of homology mainly in gene and intergenic regions. Using the BLASTn program, we performed a homology search in the reference genomes of cattle, sheep and horses to the sequences which we used as primers. The following data was obtained. For the SIRE-1 primer sequence, 170 homologous regions (> 80 %) were identified in the genome of cattle, 170 regions in sheep, and 196 regions in horses. For the PawS5 primer, 150 homologous regions were identified in the genome of cattle, 310 regions in sheep, and 155 regions in horses. For the BARE-1 primer, 160 homologous regions were identified in the genome of cattle, 159 regions in sheep, and 158 regions in horses. For the BERV k-1 primer, 171 homologous regions were identified in the genome of cattle, 165 regions in sheep,

and 200 regions in horses. For the BERV β-3 primer, 187 homologus regions were revealed in cattle, 197 regions in sheep, and 200 regions in horses. In general, the primer sequences do not differed significantly from each other in the number of homologous regions in the reference genomes of the investigated species, except for the sheep genome and the PawS5 primer sequence. It appears that it is specifically related to high frequency of the PawS5 sequence in the genomes of sheep that results in the unique contribution of light DNA fragments (greater than 60 %) in the spectra of the amplification products, indicating a relatively high frequency of homologous sequence presence in alternative DNA strands at a short distance from one another (100 to 900 bp).

It is interesting to note that the same search for regions of homology in the reference genomes of soybean (*Glycine max* (L.) Merr.) and wheat (common wheat) allowed to identify nearly the same number of homology regions as in farm mammals, and while such regions were mostly found in the nuclear genome of soybean, in wheat they mostly occurred in chloroplast and mitochondrial DNA, though at a much lower frequency.

Also, a search for homology of sequences that were used as primers was performed in the microRNA database (http://www.mirbase.org/) (Kozomara and Griffiths-Jones, 2014). It was discovered that SIRE1 had a high degree of homology (> 60 %) to bdi-MIR7752 of cereal grasses (Bertolini *et al.*, 2013), stu-MIR8003 of potatoes (Zhang *et al.,* 2013), miR-2431 of *Bos taurus* (Glazov *et al.,* 2009) and gsa-mir-1993 of flatworms (Fromm *et al.,* 2013). The PawS5 sequence had homology to hsa-mir-1304, which is expressed in embryogenesis in humans (Morin *et al.,* 2008), the BERV β-3 sequence had homology to hsa-miR-5682, the expression of which is associated with metastatic prostate cancer (Watahiki *et al.,* 2011). Only two primers, BARE-1 and BERV k-1, had no regions of homology detected in the microRNA database.

It could be expected that the relatively low level of polymorphism in cattle and sheep in the spectra of the LTR SIRE-1 primers may be due to the involvement of the homologous regions of this sequence in the processes related to microRNA, which leads to them being relatively highly conserved. However, this appears to be the case only for cattle and sheep, since in horses the polymorphism characteristics are the highest for the spectra of the LTR SIRE-1 and PawS primers (see Table).

The similarity in polymorphism in BERV-1 primer spectra and its structure in different breeds of cattle and sheep, and an equally low level of polymorphism of the spectra of this primer in different breeds of horses indicated a relatively low variation of the distribution of regions homologous to it in the genomes of the studied animals, in contrast to the distribution of sequences homologous to the BERV β-3 primer (see Table). At the same time, data from the literature suggest that BERV β-3 endogenous retrovirus is older than BERV k-1, which could explain the relatively higher variation in the spectra of the BERV β-3 primer, due to its longer evolution in the genomes of bovidae (Garcia-Etxebarria and Jugo, 2013).

According to data as of 2014 (Garcia-Etxebarria *et al.,* 2014) the genomes of cattle contain approximately 18 families of endogenous retroviruses of Class I (Epsilonretrovirus, Gammaretrovirus), 6 of Class II (Alpha-, Beta-, Delta- and Lentiretrovirusis), and so far none of Class III (Spumavirus). Several families have been described which are similar in sequence to those identified in the genome of sheep, i.e. BERV γ4, γ7 and γ9 Class I and one BERV β3 family of Class I. Compared to others, BERV β3 is conserved and its sequence is similar to the human HERV-K family. The same paper highlights the fact that the members of the identified families of endogenous retroviruses may have different occurrences in the genomes of cattle belonging to different breeds, e.g. be present in the genomes of Limousin and Simmental cattle, while absent in the genomes of Herefords, which reflects the high polymorphism of these sequences.

It was established that the same families of retroviruses are represented in the genomes of zebu-like cattle and yaks (Garcia-Etxebarria and Jugo, 2013). A high degree of homology had been identified between the endogenous bovine retrovirus ERV β and ovine ERV β1 (Torresi *et al.,* 2015).

CONCLUSION

Our data suggests that polymorphism of multilocus spectra derived when using sequences of endogenous retroviral terminal repeats as PCR primers may be associated with the frequency of homologous regions in the genomes of the species studied (as in case of the PawS5 primer in sheep), functional significance of the genomic elements associated with them (SIRE-1 sequence homology to microRNA), or with the comparatively ancient origin of endogenous retroviruses (as in the case of differences in the spectra of BERV β-3 and BERV k-1 primers). In other words, the use of fragments of endogenous retroviruses (IRAP markers) for multilocus genotyping to identify the gene pool differences between the groups of animals requires prior clarification of their distribution in the genomes of the species studied, due to their mobility and high variability. Meanwhile, our data demonstrate that the spectra of PawS 5 and BERV β-3 primers can be used to identify interbreed differences in cattle and sheep, and the spectra of SIRE-1 and PawS 5 primers can be used to identify such differences in horses.

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