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Study of *LGB* Gene Polymorphisms of Small Ruminants Reared in Eastern Europe

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ABSTRACT

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The objectives of the current research were: (*i*) to determine the allele and genotype frequencies of the *LGB* gene in the sheep and goat breeds reared in Eastern Europe; (*ii*) to implement a comparative study in order to evaluate the milk production potential and efficiency of the main sheep and goat dairy breeds reared in Romania; (*iii*) to test the genetic basis and feasibility of introducing the molecular-marker assisted selection for this trait into future breeding schemes designed for small ruminants. Totally 731 purebred unrelated sheep (Turcana: 111, Racka: 98, Tsigai: 79, Karakul of Botosani: 60, Transylvanian Merino: 77) and goats (Carpatina: 82, Banat's White: 73, Saanen: 74, French Alpine: 77) were sampled and genotyped for the earlier detected alleles. The frequencies of *A* (0.44–0.53) and *B* (0.42–0.51) alleles of *LGB* gene were generally equal, while the *C* allele incidence was significantly lower for all sheep breeds studied. A relatively low or missing incidence of the *C* allele and no *BC* genotype were detected in the studied sheep breeds. All studied sheep breeds were in Hardy–Weinberg equilibrium. Gene homozygosity was lower than gene heterozygosity, with the effective allele numbers ranging from 2.00 (Transylvanian Merino) to 2.23 (Tsigai). Two alleles (*A* and *B*) and two genotypes (*AA* and *AB*) were detected in the four goat breeds studied. Allele *A* was the most frequent allele found in all breeds (0.57–0.68), while *AB* genotype had the highest frequency. Gene homozygosity was higher than gene heterozygosity, while the effective allele numbers varied between 1.76 (Banat's White) and 1.96 (Carpatina). The frequency of alleles and genotypes was similar to that reported in other Eastern sheep and goat breeds, however polymorphism has not been studied yet among these breeds in such a high number in Romania. An association study between single nucleotide polymorphisms and milk production traits should follow.

Keywords: β-LG; sheep; goats; milk production; Hungary

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In Eastern and Southern Europe, majority of sheep and goat flocks are being reared in mountainous and disadvantageous areas, called Less Favoured Areas (LFAs) as defined in the Council Directive 75/268/EEC, having an important economic, social and ecological role, and also contributing to the conservation of the environment (Sossidou et al. 2013). Most of the sheep and goats reared are being regarded as indigenous (Gavojdian et al. 2013). In Romania 9.87 million sheep and 1.48 million goats are being reared, over 95% of them under extensive low-input production systems, and the breed structure is dominated by indigenous, unimproved breeds (Turcana and Tsigai for sheep, and Carpatina for goats). There are a limited number of studies describing the polymorphisms and associations with milk production of *LGB* gene in Romanian sheep and goat native breeds (Kusza et al. 2015; Georgescu et al. 2016).

The main milk proteins in sheep and goat milk are identical (Park et al. 2007), being separated in caseins (α_{s1}-CN, β-CN, α_{s2}-CN, and κ-CN encoded respectively by *CSN1S1, CSN2, CSN1S2,* and *CSN3* genes) and whey proteins (α-LA and β-LG encoded respectively by *LAA* and *LBG* genes).

The studies conducted over the last decade have revealed high polymorphism in dairy ruminants at *LGB* locus. In sheep and goats, the *LGB* is characterized by a generally significantly lower genetic variation, in comparison to bovine species. Two genetic variants (*A* and *B*) have been described for the *LGB* locus in goats up-to-date (GenBank accession No. Z33881.1). In sheep, *LGB* polymorphism was investigated in several breeds worldwide and a number of three alleles (*A, B,* and *C*) were reported, based on different amino acid changes. The alleles *A* and *B* (Tyr→His) differ at the amino acid position 20 (Moioli et al. 1998) and the genetic variant *C*, discovered by Erhardt 1989, differs from variant *A* by an amino acid exchange at position 148 (Arg→Gln) (GenBank accession No. X12817). The most common genetic variants detected in all studied sheep breeds are *A* and *B,* while the variant *C* is regarded as rare, being found with a low frequency in breeds such as Merinoland, Lacha, Carranzana, Spanish Merino, Serra da Estrela (Selvaggi et al. 2015).

In Europe, sheep and goats production systems vary greatly among countries and regions. In most Mediterranean and Balkan countries, the production of dairy sheep is predominant while in Northern and Central Europe, meat represents the main product (Todaro et al. 2015). The substantial diversity among sheep and goat breeds, production environments, and management systems requires systematic and comprehensive breed evaluations, in order to allow producers to identify genotypes that are best suited for their production systems and meet current market demands (Leeds et al. 2012). Currently, 85.7 million sheep and 12.3 million goats are being reared in the European Union (http://ec.europa.eu/eurostat/data/database).

The objectives of the current research were: (*i*) to determine the allele and genotype frequencies of the *LGB* gene in the sheep and goat breeds reared in Eastern Europe; (*ii*) to implement a comparative study in order to evaluate the milk production potential and efficiency of the main sheep and goat dairy breeds reared in Romania; (*iii*) to test the genetic basis and feasibility of introducing the molecular-marker assisted selection for this trait into future breeding schemes designed for small ruminants.

MATERIAL AND METHODS

Animal sampling. Totally 731 purebred unrelated sheep and goats were sampled for the implementation of the current study. In sheep, the following breeds were included: Turcana (111 individuals, from 14 commercial farms), Racka (98 individuals, from 6 commercial farms), Tsigai (79 individuals, from 5 commercial farms), Karakul of Botosani (60 individuals, from 4 genetically unrelated lines), and Transylvanian Merino (77 individuals, from 3 farms). Wool follicles were collected only from multiparous ewes, ages ranging between 3 and 4 years.

In goats, the following breeds were sampled and included in the current study: Carpatina (82 individuals, from 7 commercial farms), Banat's White (73 individuals from 3 commercial farms), Saanen (74 individuals, from 12 genetically unrelated lines), and French Alpine (77 individuals, from 12 genetically unrelated lines). Hair follicles were collected only from multiparous does, ages ranging between 2 and 3 years.

Three sheep breeds (Racka, Karakul of Botosani, and Transylvanian Merino) and one goat breed (Banat's White) from the animals involved in the study are endangered breeds currently be-

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ing included in a genetic conservation program (heritage breeds).

Ethics statement. The research activities were performed in accordance with the European Union's Directive for animal experimentation (Directive 2010/63/EU).

DNA extraction. Hair and wool follicles samples were kept individually registered in nylon bags and stored at –20°C until the laboratory analysis. Genomic DNA was extracted from hair follicles using standard protocol (FAO/IAEA 2004) and then quantified by using a Nanodrop ND-1000 spectrophotometer (Thermo Fisher Scientific, USA). Genomic DNA was also evaluated visually by standard agarose gel electrophoresis (1% agarose (w/v) in TBE). After extraction, all DNA samples were diluted for 100 ng and stored at –20°C until the further analysis.

Genotyping. PCR amplification was carried out in a 25-μl reaction mixture containing 100 ng DNA. Ovine *LGB A* and *B* alleles at position 1617 ($T < C$) at exon 2 (GenBank accession No. X12817) were determined, as previously reported by Feligini et al. (1998); *LGB C* allele was characterized from *LGB A* at position 4626, as described by Anton et al. (1999). The polymorphic site at position 4601 ($G < A$) was detected from exon 7 to the 3' flanking region of the caprine *LGB* gene (Genbank accession No. Z33881.1) as described Pena et al. (2000).

Data analysis. Gene homozygosity (H_o), gene heterozygosity (H_e), effective allele number (N_e), polymorphic information content (PIC), genotype and allele frequencies of *LGB* were calculated by Popgene software, Version 1.33. (Yeh and Yong 1999). Deviations from Hardy–Weinberg equilibrium (HWE) were tested for all investigated breeds using the chi-square test.

Milk production data collection. All commercial farms had their flocks included in the official performance recording system, with ancestry of the animals known for at least two generations.

Milk production data were available for the sheep breeds Turcana, Racka, and Tsigai, and for the goat breeds Carpatina, Banat's White, Saanen, and French Alpine. Reference year for the lactation for all ewes and does included in the research was 2016.

From the farm records and the official performance recording data, the following individual production traits were analysed in order to evaluate each breed's milk producing potential: milk yield per lactation (kg), milk fat content (%), and milk protein content (%). Standard lactation length for sheep was considered 180 days, for goats 280 days.

In order to assess the effect of the breed on the above-mentioned milk production traits, the STATISTICA software was used (Hill and Lewicki 2007). The Main Effect ANOVA analysis of variance was applied. Given that data were recorded in different farms, the model included this as a correction factor. The model used for statistical analysis is presented below:

$$y_{ijk} = \mu + pc_i + g_j + e_{ijk}$$

where:

y_{ijk} = milk production trait
μ = overall mean
pc_i = fixed effect of the farm
g_j = fixed effect of the breed
e_{ijk} = residual effect

When significant effects of the genotype were observed, the comparison among populations was tested by performing contrast analysis, using Tukey's test.

RESULTS AND DISCUSSION

Genotypes for ovine BLG. At the *LGB* locus, three alleles (*A*, *B*, *C*) and five genotypes (*AA*, *AB*, *BB*, *AC*, *CC*) were detected (Table 1).

The frequencies of *A*, *B* alleles of *LGB* gene were generally equal, while the *C* allele incidence was significantly lower for all the sheep breeds studied. Results revealed that the *LGB A* allele was slightly more frequent than the *B* allele in the Racka and Karakul of Botosani breeds. Current results are in accordance with other published data, with previous reports suggesting that *LGB A* has a higher frequency, compared to the *B* allele in sheep breeds such as the Iranian Karakul, Finnish Landrace, Russian Karakul, Ghezel, Hungarian Racka (Amigo 2000; Mohammadi 2006; Kusza 2015). The *LGB B* allele was found to be more frequent than *A* in the Turcana breed, similar to previous data for the Romanov and Chios (Macha and Novackova 1974) sheep breeds. However, Georgescu et al. (2016) found a significant higher frequency of the *B* allele, compared to the *A* allele in Romanian Merino breed. A relatively low or missing incidence of the *C* allele was found in the herein studied sheep breeds, as previously reported for the Merino, Merinoland, Kivircik, Gokceada, and Sakiz breeds by Erhardt (1989) and Elmaci et al. (2006). Amigo et al. (2000) reported in their works that the *LGB A* could be the original form of ovine *LGB*.

The most frequent genotype in all the studied sheep breeds was *AB,* similar to results found in Pag, Iranian breeds, and crosses derived from Finn, Romanov, and Booroola rams (Cubrik-Curik et al. 2002; Elyasi et al. 2010). Even though, with a lower frequency, the *BB* genotypes were detected in all the studied sheep breeds, conversely to results found for Russian sheep breeds (Mohammadi et al. 2006). The *BC* genotype was not detected in any of the studied sheep breeds. All studied sheep breeds were found to be in Hardy–Weinberg equilibrium ($P > 0.05$).

As shown in Table 2, gene homozygosity (H_o) was lower than gene heterozygosity (H_e) for both the studied ovine SNPs, with the effective allele numbers ranging from 2.00 (in Transylvanian Merino) to 2.23 (in Tsigai). The value of PIC was the lowest in Merino and the highest in Tsigai.

Table 1. Frequency of *BLG* genotype and alleles of Turcana, Racka, Tsigai, Karakul of Botosani, and Transylvanian Merino sheep

	Genotype	*n*	Frequency of genotype	Allele	Frequency of allele	χ^2
Turcana	*AA*	17	15.32	*A*	0.44	38.19**
	AB	58	52.25	*B*	0.51	
	BB	28	25.23	*C*	0.05	
	AC	5	4.50			
	BC	0	0.00			
	CC	3	2.70			
Racka	*AA*	28	28.57	*A*	0.49	40.08**
	AB	38	38.78	*B*	0.47	
	BB	27	27.55	*C*	0.04	
	AC	3	3.06			
	BC	0	0.00			
	CC	2	2.04			
Tsigai	*AA*	15	18.99	*A*	0.47	19.05**
	AB	40	50.63	*B*	0.47	
	BB	17	21.52	*C*	0.06	
	AC	5	6.33			
	BC	0	0.00			
	CC	1	1.27			
Karakul	*AA*	16	27.59	*A*	0.53	11.84*
	AB	27	46.55	*B*	0.42	
	BB	11	18.97	*C*	0.04	
	AC	3	5.17			
	BC	0	0.00			
	CC	1	1.72			
Merino	*AA*	23	29.87	*A*	0.5	3.12**
	AB	31	40.26	*B*	0.5	
	BB	23	29.87	*C*	0.0	
	AC	0	0.00			
	BC	0	0.00			
	CC	0	0.00			

statistically significant at *$P < 0.05$, **$P < 0.001$

Table 2. Polymorphism information of ovine and caprine *BLG* gene in Romanian sheep and goat indigenous breeds

SNP	Breed	H_o	H_e	N_e	PIC
T1617C	Turcana	0.45	0.55	2.19	0.85
	Racka	0.46	0.54	2.14	0.82
	Tsigai	0.44	0.56	2.23	0.87
	Karakul	0.46	0.54	2.15	0.83
	Merino	0.50	0.50	2.00	0.69
G4601A	Banat's White	0.57	0.44	1.76	0.62
	Carpatina	0.51	0.49	1.96	0.68
	Saanen	0.51	0.49	1.95	0.68
	French Alpine	0.52	0.48	1.90	0.67

SNP = single nucleotide polymorphism, H_o = gene homozygosity, H_e = gene heterozygosity, N_e = effective allele number, PIC = polymorphic information content

Previous reports by Kawecka and Radko (2011) have not found statistical differences between the *LGB* genotype and milk production traits in Polish Merino. Although, other studies have reported contrasting results (Mroczkowski et al. 2004) for the same sheep breed. Ramos et al. (2009) reported significant associations between the *AB* genotype of *LGB* with high percentages of fat and lactose in different sheep breeds.

Genotypes for caprine BLG. Two alleles (*A* and *B*) and two genotypes (*AA* and *AB*) were detected in the four studied goat breeds. Allele *A* was the most frequently found allele in all the breeds (Table 3), while the heterozygous *AB* genotype had the highest frequency in all the studied goat breeds. El-Hanafy et al. (2015) found that the *AB* genotype has the highest frequency for Barki and Habsi goat breeds (0.80 and 0.41, respectively), the lowest (0.1) for Damascus goats, and intermediate (0.51) for the Damascus × Barki crossbred goats. In the case of other studied native Saudi goats (Ardi and Harri), the homozygous *BB* genotypes were the most frequent (0.52 and 0.55, respectively) (El-Hanafy et al. 2015). However, in the current study the *BB* genotype was absent, while it had the lowest frequency and ranged from 0.05 to 0.1 in the two previous studied goat breeds and their crossbred as reported by El-Hanafy et al. (2015). In Turkish goat breeds (Hair and Saanen), the *BB* genotype was the second most frequent, while in Turkish Honamli goats it was the least frequent genotype (Korkmaz et al. 2012).

Gene H_o was higher than gene H_e for both SNPs of *BLG*, while the effective allele numbers varied between 1.76 (in Banat's White) and 1.96 (in Carpatina). The value of PIC was at the medium level (Table 2).

Milk production traits. A comparison between the three main Romanian indigenous dairy sheep breeds for their milk yield and milk chemical composition under European temperate conditions were considered necessary for the sheep industry. This comparative study was the first attempt to provide information on the production efficiency in Turcana, Racka, and Tsigai breeds bred under temperate climate conditions of Eastern Europe.

Milk yield was significantly ($P < 0.001$) affected by the breed factor (Table 4), with the least perform-

Table 3. Frequency of *BLG* genotype and alleles of Banat's White, Carpatina, Saanen, and French Alpine goat

	Genotype	*n*	Frequency of genotype	Allele	Frequency of allele	χ^2
Banat's White	*AA*	27	36.99	*A*	0.68	15.05**
	AB	46	63.01	*B*	0.32	
	BB	0	0			
Carpatina	*AA*	11	13.41	*A*	0.57	47.10**
	AB	71	86.59	*B*	0.43	
	BB	0	0			
Saanen	*AA*	12	23.38	*A*	0.62	37.77**
	AB	62	76.62	*B*	0.38	
	BB	0	0			
French Alpine	*AA*	18	16.22	*A*	0.58	29.12**
	AB	59	83.78	*B*	0.42	
	BB	0	0			

statistically significant at $^{**}P < 0.001$

Table 4. Milk production and milk fat and protein content in Turcana, Racka, and Tsigai sheep breeds

Breed	Milk yield per lactation (kg)	Fat content (%)	Protein content (%)
Turcana	76.8 ± 2.99	7.38 ± 0.33	5.91 ± 0.24
Racka	54.4 ± 3.47	8.57 ± 0.45	5.94 ± 0.43
Tsigai	86.3 ± 4.15	6.11 ± 0.21	5.08 ± 0.18
Differences between sheep breeds			
Turcana × Racka	**	*	ns
Turcana × Tsigai	*	*	**
Racka × Tsigai	***	**	**

statistically significant at *$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$, ns = not significant

ing breed being the Racka ewes, which produced on average 54.4 ± 3.47 kg of milk per lactation, with the highest yielding breed being the Tsigai, with an average milk production of 86.3 ± 4.15 kg. Current results are in accordance with previous milk production estimates for each of the three breeds studied (Gavojdian et al. 2013).

Milk fat content ranged between 6.11 ± 0.21% to 8.57 ± 0.45% in the studied breeds, having the lowest values for the higher producing Tsigai, and the highest value for the Racka breed. Although for the protein content the discrepancies were less significant, ranging between 5.94 ± 0.43% and 5.08 ± 0.18%, the pattern was similar and significant. Current results are in accordance with previous studies which have shown that milk yield in sheep and goats is strongly and negatively correlated with milk fat and protein content (Balthazar et al. 2017).

Comparative production data for milk related traits in Carpatina, Banat's White, Saanen, and French Alpine goat breeds are shown in Table 5. The breed factor influenced significantly ($P < 0.001$) milk production in all four genotypes taken into study. Milk production ranged from 348.2 ± 1.61 kg per lactation in Carpatina to 1028.5 ± 1.92 kg in French Alpine goats. The specialized Saanen and French Alpine breeds produced three times more if compared to the unimproved Romanian indigenous Carpatina. Results for the milk production as well as the milk chemical composition are in accordance with previous estimates for each of the breeds taken into study (Palhiere et al. 2014).

Given the high number of animals sampled and genotyped from all the five sheep breeds and four goat breeds, as a next step, we would like to characterize all known alleles of ovine and caprine milk protein genes in the studied breeds, sequence the whole promoter region of *LGB,* and determine genetic variability within breeds. Hereby we took the first steps towards allergy-free dairy products

Table 5. Milk production and milk fat and protein content in Carpatina, Banat's White, Saanen, and French Alpine goat breeds

Breed	Milk yield per lactation (kg)	Fat content (%)	Protein content (%)
Carpatina	348.2 ± 1.61	3.92 ± 0.45	3.85 ± 0.18
Banat's White	561.4 ± 1.43	3.74 ± 0.31	3.67 ± 0.64
Saanen	923.0 ± 2.28	3.79 ± 0.17	3.59 ± 0.41
French Alpine	1028.5 ± 1.92	3.80 ± 0.27	3.63 ± 0.21
Differences between goat breeds			
Carpatina × Banat's White	***	*	*
Carpatina × Saanen	***	*	**
Carpatina × French Alpine	***	*	*
Banat's White × Saanen	***	ns	*
Banat's White × French Alpine	***	ns	*
Saanen × French Alpine	**	ns	*

statistically significant at *$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$, ns = not significant

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based on genotyped animals from the most frequent sheep and goat breeds reared in Romania, in order to evaluate the genetic basis and feasibility of introducing the molecular marker assisted selection in the small ruminants sector in Eastern European native breeds.

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