Ukrainian Journal of Ecology

Ukrainian Journal of Ecology, 2019, 9(1), 251-261

ORIGINAL ARTICLE *UDC 636.4.082.25:575.22*

Assessing genomic taurine/zebuine admixture in the southern meat cattle based on microsatellite markers

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Received: 12.02.2019. Accepted: 20.03.2019

Hybridization between wild and domestic bovine species occurs worldwide either spontaneously or by organized crossing. The Southern Meat (SM) cattle is a composite developed by crossing Cuban zebu (*Bos indicus*) with different cattle breeds (*Bos taurus*) – local Red Steppe, Hereford, Charolais, Santa Gertrudis, Dairy Shorthorn. The main aim of this work was to study the genetic structure of the Southern Meat breed (SM) cattle and to assess the taurine/zebuine admixture in the SM population using microsatellites. A set of 192 heifers representing the SM cattle (the 'Askaniiske' State Pilot Farm, Kherson region, Ukraine) was included in the study during 2013-2014. Based on the origin of the individuals studied, all heifers were attributed to two groups according to the different degree of Zebu blood: the LZ group (≤ 3/8 percent Zebu blood; *n*=100) and the UZ group (>3/8 percent Zebu blood; *n*=92). Ten bovine autosomal polymorphic microsatellite loci (*BM1818, BM1824, BM2113, ETH3, ETH10, INRA023, TGLA53, TGLA122, TGLA227* and *SPS115*) were genotyped to estimate various parameters of genetic diversity. The total number of genotype estimates ranged substantially over loci from 18 (locus *BM1824*) to 37 (locus *INRA023*), giving a mean number of 27.9 ± 1.96 genotypes per locus. Overall, one hundred and four alleles were observed across the 10 microsatellite markers examined, with allelic diversity (the average number of observed alleles per locus) of 10.4 ± 0.76. Significant difference (*P*<0.05-0.001) was found between the LZ and UZ groups with regard to distribution of allele frequencies across all loci. The values of *Ae*, *Ho*, *He* and *Fis* in two SM cattle groups did not differ significantly (a non-parametric paired Wilcoxon's test; for all cases *P*>0.05). At each locus some alleles were identified that were present at higher frequencies in the LZ group and absent or present at relatively lower frequencies in the UZ group, or vice versa. Evidence for an association between specific alleles at every locus with *B.indicus/B.taurus* breed was assessed by using a Logistic Regression model. Significant relationship was discovered only for two loci, *TGLA227* (χ^2=22.30; *P*<0.001) and *ETH10* (χ^2=27.70; *P*<0.001). It can be assumed that the *TGLA227* (77 bp) and *ETH10* (209-211 bp) alleles among the SM cattle examined individuals were inherited from a *B.indicus* ancestor. On the other hand, the *TGLA227* (89 bp) and *ETH10* (217-219 bp) alleles which prevails among individuals in the LZ group were inherited from a *B.taurus* ancestor. Thus, the SM cattle presented with high level of taurine/zebuine admixture, which is consistent with the breeding history.

Keywords: *Bos indicus*; *Bos taurus*; hybridization; southern meat cattle; taurine/zebuine admixture; microsatellite markers

Introduction

Hybridization between species may occur if closely related species share an overlapping habitat or through human intervention during captive breeding. Uncontrolled hybridization, as it occurs in nature, may have had a significant impact on the formation of domestic breeds, but can also affect the genetic integrity of domestic and wild species. Monitoring the species composition of these animals may become essential for the future preservation of genetic diversity (Nijman et al., 2003).

Ongoing hybridization that results in admixture of parental genes from 2 different species and introgression (i.e., transfer of genes from one species to another by repeated backcrossing), can cause the native population to be replaced by one genetically and phenotypically resembling the nonnative form in some traits (Huxel, 1999).

Hybridization between wild and domesticated forms has been documented: in canids between coyotes (*Canis latrans*) and domestic dogs (*Canis familiaris*) in the USA (Adams et al., 2000); in felids between domestic cats (*Felis silvestris catus*) and African wildcats (*Felis silvestris lybica*) (Le Roux et al., 2015) or European wildcats (Nussberger et al., 2013); in suids between wild boars (*Sus scrofa*) and domestic pigs (*Sus scrofa domestica*) in Bulgaria (Nikolov et al., 2017), in Belgium and Luxembourg (Frantz et al., 2013); in birds between wild common quails (*Coturnix coturnix*) and domesticated Japanese quails (*Coturnix japonica*) in France (Charaza et al., 2010). Hybridization and high degree of genetic introgression has been observed between wild and domesticated reindeer populations (*Rangifer tarandus*) (Kharzinova et al., 2016).

Hybridization between wild and domestic bovine species occurs worldwide either spontaneously or by organized crossing (Nijman et al., 2002). Within the group of the Bovini several hybrids have been described: a cross of banteng (*Bos javanicus*) and zebu (*Bos indicus*) (Nijman et al., 2002; Hartati et al., 2015); a cross of yak (*Poephagus grunniens*) and taurine cattle (Tumennasan et al., 1997; Luo et al., 2014); the North-American beefalo, a cross of taurine cattle (*Bos taurus*) and the American bison (*Bison bison*) (Polziehn et al., 1995; Halber et al., 2005). In Africa, introgression of Indian zebu bulls (*Bos indicus*) in taurine herds occurs and has improved the tolerance of the cattle (*Bos taurus*) to hot and dry environments (Bradley et al., 1994). Bongso et al. (1988) described a spontaneous hybridization of wild gaur (*Bos gaurus*) and zebu (*Bos indicus*).

The Southern Meat cattle is a composite developed by crossing Cuban zebu (*Bos indicus*) with different cattle breeds (*Bos taurus*) – local Red Steppe, Hereford, Charolais, Santa Gertrudis, Dairy Shorthorn. The Southern Meat breed is the fourth in representation among Ukrainian breeding achievements of meat production. The body shape similar to zebu, coat mainly red. External features include the strong constitution, light bones, balanced body shape, well-shaped muscles of the hip and shoulder, long thorax, especially in the rump part. The head is light with large jowl, topline straight, tough limbs, skin smooth and flexible. The breed is well adapted to hot climate and extreme conditions of the steppes. It is resistant to diseases. The growth intensity is high as well as the meat yield and good quality of beef. The roughage is used effectively. Body weight of cows is 580-620 kg and weight of bulls is 900-1100 kg (Pilarczyk et al., 2015; Suprun et al., 2016).

The use of molecular markers has increased the ability to identify species, subspecies and populations and different molecular markers (e.g. microsatellite DNA loci) also have been used to detect, quantify and to determine the age of hybridization and introgression events in wild (Rodriguez et al., 2008) and captive-reared animals (Nijman et al., 2003; Lecis et al., 2006; Kharzinova et al., 2016).

Several DNA markers are now available to analyse the genetic background of hybrid Bovini. Mitochondrial DNA (D-loop) markers and cytochrome-b typing reveal introgression via the maternal lineage (Verkaar et al, 2003; Nijman et al., 2003). The species origin of the nuclear genome can be inferred from species-specific microsatellite alleles (Frisch et al., 1997; MacHugh et al., 1997), AFLP patterns (Buntjer et al., 2002) or mutations in satellite DNA.

Nijman et al. (1999) has shown that amplified fragment length polymorphisms (AFLP) correlated with introgression of zebu (*Bos indicus*) in African cattle populations. While, a cattle-specific mtDNA control region fragment and cattle-specific alleles at three autosomal microsatellite loci (*ILSTS013, ILSTS050* and *SPS115*) has been used by Qi et al. (2010) for a diagnostic approach to assess the impact of cattle introgression on domestic yak populations. Moreover, a panel of 54,609 SNPs (50k) was used to genetically characterize Indonesian Peranakan Ongole cattle by comparison with *B. taurus, B. indicus, B. javanicus* and composite *B. taurus* × *B. indicus* breeds (Hartati et al., 2015).

The main aim of this work was to study the genetic structure of the Southern Meat breed (SM) cattle and to assess the taurine/zebuine admixture in the SM population using microsatellites.

Materials and methods

A set of 192 heifers representing the SM cattle (the 'Askaniiske' State Pilot Farm, Kherson region, Ukraine) was included in the study during 2013-2014. The animals were unrelated and randomly selected from herd.

Based on the origin of the individuals studied, all heifers were attributed to two groups according to the different degree of Zebu blood: the LZ group (≤ 3/8 percent Zebu blood; *n*=100) and the UZ group (>3/8 percent Zebu blood; *n*=92).

Total genomic DNA was extracted from tissue samples using Nexttec column (Nexttec Biotechnology GmbH, Germany) following the manufacturer's instructions. The DNA concentration was estimated by measuring the absorbance at 260 nm and the DNA quality was checked by separation on agarose gels.

Ten bovine autosomal polymorphic microsatellite loci (*BM1818, BM1824, BM2113, ETH3, ETH10, INRA023, TGLA53, TGLA122, TGLA227* and *SPS115*) were genotyped to estimate various parameters of genetic diversity.

Microsatellites were amplified in two multiplex reactions. Electrophoresis was carried out using an ABI 3130xl Genetic Analyzer (Applied Biosystems, USA). Allele sizes of each microsatellite marker were determined using GeneMapper ver. 4.0 (Applied Biosystems).

For each group (LZ and UZ) we calculated the total number of genotypes (TNG), number of singleton genotypes (NGS) and number of unique genotypes (NGU), i.e., variants that were encountered in a single sample set for each microsatellite locus.

The two-way ANOVA (for qualitative traits) was used for the evaluation of differences in the NGS and NGU frequency between the SM cattle groups and across the microsatellite loci.

GenAlEx v.6.5 software (Peakall and Smouse, 2012) was used to estimate basic population genetic descriptive statistics for each marker in the two SM cattle groups: the allelic frequencies, total number of alleles (*TNA*), effective number of alleles (*Ae*), number of private alleles, most frequent alleles with frequencies higher than 0.2 (MFA), observed (*Ho*) and expected heterozygosity (*He*), fixation indices (*Fis*).

Significant differences of all genetic descriptive statistics in the two SM cattle groups were obtained through a non-parametric paired Wilcoxon's test using the PAST software (Hammer et al., 2001).

Deviations from Hardy-Weinberg equilibrium (HWE) were performed for each locus using the Pearson's chi-square goodness-of-fit test using the GenAlEx v.6.5 software.

Significant differences of genotype and allelic frequencies in two SM cattle groups were determined from the contingency tables 2×k (where k is the total number of genotypes or the total number of alleles) in terms of chi-square (χ^2) and the Monte Carlo significance test procedure (with 100000 random permutations) was used in the PAST software (Hammer et al., 2001).

Results

The total number of genotypes, the number of singleton genotypes and the number of unique genotypes per locus in the two SM cattle groups (LZ and UZ) are given in Table 1. First, we show that the TNG estimates ranged substantially over loci from 18 (locus *BM1824*) to 37 (locus *INRA023*), giving a mean number of 27.9 ± 1.96 genotypes per locus. Significant differences over loci were also found in the NGS frequency ($F_{9;399}$=2.23; P=0.019). A two-way ANOVA revealed significant main effect for the SM cattle group in the NGU frequency ($F_{1;538}$=4.39; P=0.037). Additionally, there was a significant interaction between microsatellite markers and the SM cattle groups ($F_{9;538}$=2.57; P=0.007).

Table 1. The total number of genotypes (TNG), number of singleton genotypes (NGS) and number of unique genotypes (NGU), i.e., variants that were encountered in a single sample set at the 10 microsatellite loci in the two SM cattle groups.

Locus	n	TNG	NGS		NGU		χ^2 (P_{MC})
			LZ	UZ	LZ	UZ	
TGLA227	146	34	44105	13/27	7	14	50.64 (<0.01)
BM2113	191	28	43282	45536	4	10	86.65 (<0.001)
TGLA53	109	25	42248	44075	5	10	41.78 (<0.001)
ETH10	192	25	44774	45170	2	3	47.83 (<0.001)
SPS115	192	19	42826	42064	4	2	28.89 (<0.001)
TGLA122	192	31	45597	46569	4	7	91.42 (<0.001)
INRA023	192	37	44013	16/32	5	17	88.83 (<0.001)
BM1818	189	32	46204	43922	12	6	94.12 (<0.001)
ETH3	168	30	13/22	44105	10	8	55.39 (<0.001)
BM1824	192	18	42095	43802	6	3	72.33 (<0.001)

n represents sample size; χ^2 (P_{MC}) is chi-square test and the Monte Carlo significance test procedure (with 100,000 random permutations).

Secondly, the unique genotypes were more abundant in the LZ group for loci *BM1818, ETH3* and *BM1824* than in the UZ group. On the other hand, for loci *TGLA227, BM2113, TGLA53* and *INRA023* the unique genotypes were more relatively plentiful in the UZ group than in the LZ group (Table 1).

Significant difference (P_{MC}<0.01-0.001) was found between the LZ and UZ groups with regard to the distribution of genotypes across all microsatellite markers (Table 1).

Overall, one hundred and four alleles were observed across the 10 microsatellite markers examined, with allelic diversity (the average number of observed alleles per locus) of 10.4 ± 0.76. When analyzing the two SM cattle groups separately, the number alleles per locus ranged from seven (locus *BM1824*) to 12 (locus *TGLA53*) with a mean of 9.1 ± 0.53 for the LZ group, and from seven (loci *BM1824* and *SPS115*) to 14 (locus *TGLA227*) with a mean of 9.4 ± 0.69 for the UZ group (Table 2).

Table 2. The total number of alleles (TNA), group-private and most frequent alleles (with frequencies higher than 0.2) at the 10 microsatellite loci in the two SM cattle groups.

Locus	TNA		Private alleles, bp		MFA, bp		χ^2 (P_{MC})
	LZ	UZ	LZ	UZ	LZ	UZ	
TGLA227	11	14	103	79, 85, 99, 101	77, 89	77	40.14 (<0.001)
BM2113	9	9	131	127	125	135	80.68 (<0.001)
TGLA53	12	11	168, 184	154	156, 164	156, 162	46.99 (<0.001)
ETH10	8	8	225	223	209, 211, 217	209, 217	35.27 (<0.001)
SPS115	8	7	244	-	248, 250	248, 250	16.88 (<0.05)
TGLA122	8	9	-	141	143, 151	149	81.38 (<0.001)
INRA023	9	10	-	196	202, 214	214	75.59 (<0.001)
BM1818	8	8	272	274	264, 268	262, 266	101.17 (<0.001)
ETH3	11	11	101, 131	109, 113	117, 121	115, 117	38.32 (<0.001)
BM1824	7	7	184	190	180	180, 182	86.65 (<0.001)

MFA – the most frequent alleles. χ^2 (P_{MC}) is chi-square test and the Monte Carlo significance test procedure (with 100000 random permutations). Group-specific alleles are indicated in bold.

A total of 23 group-private alleles were found in the SM cattle, 10 were identified in the LZ group, while 13 were detected in the UZ group (Table 2). Significant difference (P_{MC}<0.05-0.001) was also found between the LZ and UZ groups with regard to distribution of allele frequencies across all loci (Table 2). The *TGLA227* (77 bp), *TGLA53* (156 bp), *ETH10* (209 and 217 bp), *SPS115* (248 and 250 bp), *INRA023* (214 bp), *ETH3* (117 bp) and *BM1824* (180 bp) alleles of the microsatellite markers were predominant in the LZ group as well as in heifers of the UZ group. On the other hand, 17 group-specified alleles (with frequencies higher than 0.2) were found for the nine microsatellite loci (except at the *SPS115* locus) in the SM cattle, 10 were only detected in the LZ group, while 7 were only observed in the UZ group (Table 2).

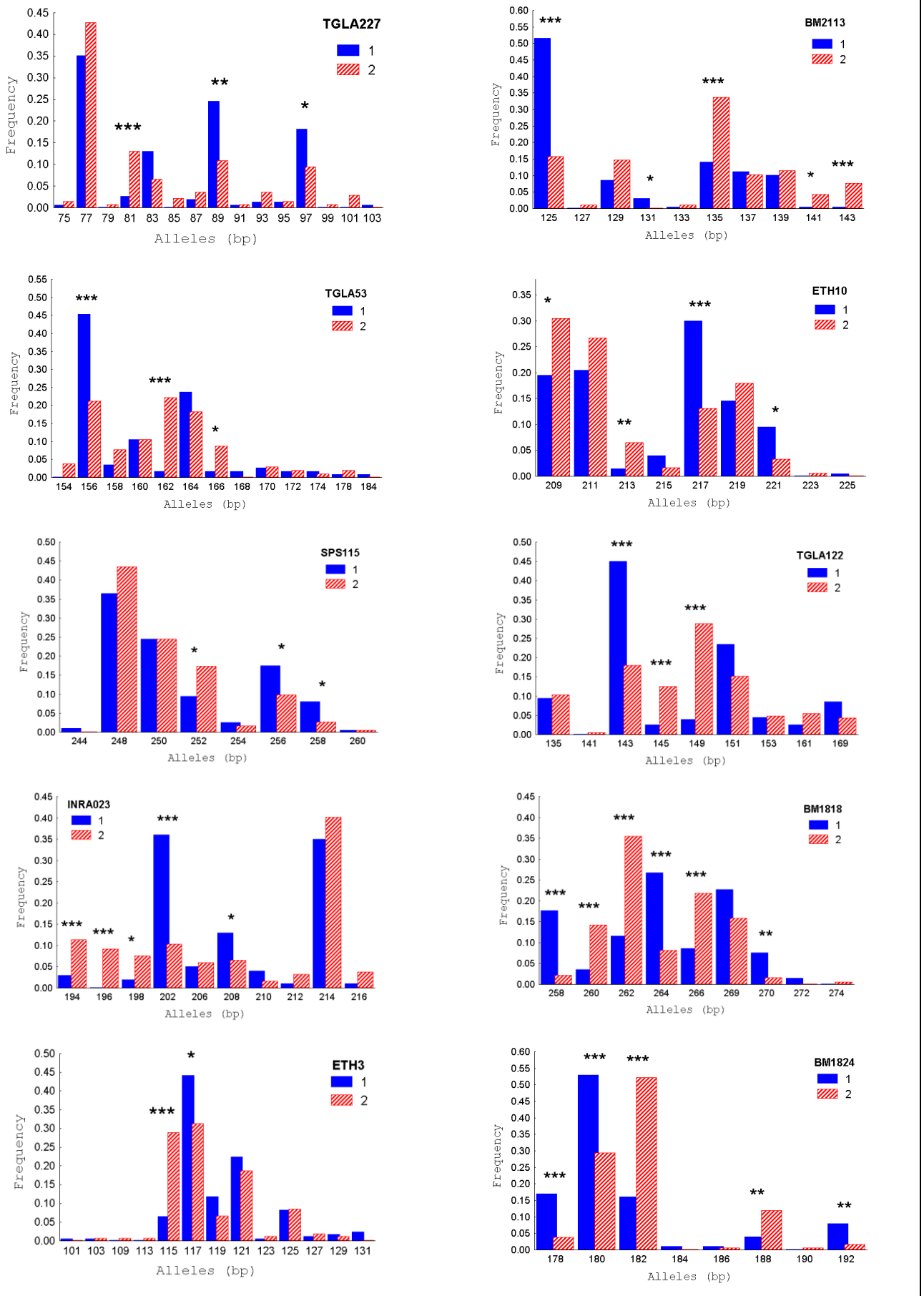

Figure 1. Allelic frequency distribution across the 10 microsatellite markers in the LZ (1) and UZ (2) groups. Frequency of alleles marked with *, ** and *** was significantly different between groups (* P<0.05; ** P<0.01; *** P<0.001).

Allele frequency profiles for each of the microsatellite marker in the two SM cattle groups and alleles with the statistically significant differences in frequencies between the comparing groups are shown in Figure 1.

A high disparity in microsatellite allelic distribution between the LZ and UZ groups was observed. At each locus some alleles were identified that were present at higher frequencies in the LZ group and absent or present at relatively lower frequencies in the UZ group, or vice versa.

The effective number of alleles (*Ae*), the observed (*Ho*) and expected heterozygosity (*He*), and fixation indices (*Fis*) across the 10 microsatellite markers in the two SM cattle groups are shown in Table 3.

Average effective numbers of alleles were 3.90 ± 0.26 and 4.61 ± 0.34 per locus in different cattle groups. In the LZ group the markers with the highest *Ho* values were *BM1818*, followed by *ETH10*, and in the UZ group the markers with the highest *Ho* values were *BM2113* and *TGLA122*. The expected heterozigosities across the LZ and UZ groups varied from 0.656 (locus *BM1824*) to 0.818 (locus *BM1818*) and from 0.626 (locus *BM1824*) to 0.845 (locus *TGLA53*), respectively.

Of the 10 microsatellite markers, the fixation indices of *TGLA227, TGLA53, ETH3* and *BM1824* loci were positive and significantly different from 0 ($P<0.05$) in the LZ group as well as in heifers of the UZ group. The average *Fis* values were 0.114 ± 0.070 and 0.096 ± 0.051 in the two SM cattle groups, respectively.

Table 3. The effective allele numbers (*Ae*), heterozygosity (*Ho* – observed, *He* – expected) and within-population inbreeding estimates (*Fis*) at the 10 microsatellite loci in the two SM cattle groups.

Locus	Ae		Ho		He		Fis	
	LZ	UZ	LZ	UZ	LZ	UZ	LZ	UZ
TGLA227	4.25	4.36	0.649	0.609	0.765	0.771	0.151#	0.210#
BM2113	3.16	5.22	0.717	0.859	0.684	0.808	-0.049	-0.062
TGLA53	3.2	6.46	0.351	0.481	0.688	0.845	0.490#	0.431#
ETH10	4.95	4.58	0.81	0.793	0.798	0.782	-0.015	-0.015
SPS115	4.17	3.45	0.72	0.717	0.76	0.71	0.053#	-0.01
TGLA122	3.59	5.82	0.73	0.859	0.721	0.828	-0.012	-0.037
INRA023	3.64	4.75	0.74	0.772	0.725	0.79	-0.02	0.023
BM1818	5.43	4.38	0.867	0.769	0.816	0.772	-0.063	0.003
ETH3	3.7	4.37	0.329	0.566	0.729	0.771	0.548#	0.266#
BM1824	2.91	2.67	0.62	0.533	0.656	0.626	0.055#	0.149
Mean	3.9	4.61	0.653	0.696	0.734	0.77	0.114	0.096
SE	± 0.26	± 0.34	± 0.057	± 0.044	± 0.016	± 0.020	± 0.070	± 0.051

Loci shoving significant deviation from Hardy-Weinberg equilibrium. *SE* – standard error.

The values of *Ae, Ho*, *He* and *Fis* in two SM cattle groups did not differ significantly (a non-parametric paired Wilcoxon's test; for all cases $P>0.05$). Table 4 lists the high-frequency alleles in the different breeds of zebu (Asian, African and South American origin) and beef cattle (European origin) across the 10 microsatellite markers used. A literature review was carried out across publications (research papers and PhD theses) on the genetic diversity of the zebu and beef cattle breeds based on the microsatellite loci from our list.

Evidence for an association between specific alleles at every locus with *B. indicus/B. taurus* breed was assessed by using a Logistic Regression model. Significant relationship was discovered only for two loci, *TGLA227* ($\chi^2=22.30$; $P<0.001$) and *ETH10* ($\chi^2=27.70$; $P<0.001$).

Locus *TGLA227*: Short alleles (77 and 79 bp) were found more often among *B.indicus* breeds, while long alleles (89 and 91 bp) were common in the *B.taurus* breeds (Table 4, Figure 2A). Thus, it can be assumed that the *TGLA227* (77 bp) allele among the SM cattle examined individuals was inherited from a *B.indicus* ancestor (Figure 1).

On the other hand, the *TGLA227* (89 bp) allele which prevails among individuals in the LZ group was inherited from a *B.taurus* ancestor (Table 2).

Locus *ETH10*: Short alleles (209 and 211 bp) were found more often among *B.indicus* breeds, while long alleles (217 and 219 bp) were common in *B.taurus* breeds (Table 4, Figure 2B). This suggests that the *ETH10* (209-211 bp) alleles in the SM cattle examined individuals were inherited from a *B.indicus* ancestor and the *ETH10* (217-219 bp) alleles which dominate among individuals in the LZ group were inherited from a *B.taurus* ancestor (Figure 1, Table 2).

Discussion

Two hundred and seventy-nine genotypes were detected from the 10 microsatellite markers surveyed in the SM cattle population, yielding a mean value of 27.9 genotypes per locus. In a Sicilian cattle population studied by Cosenza et al. (2015), *TGLA53* locus has shown the highest total number of genotypes (*TNG*=89), while the lowest *TNG* was 15 in *BM1824*, and the average was 47.18, i.e. at least than double the population of the SM cattle. In the Ongole Grade cattle (the Indonesian native beef cattle, *B.indicus*), all the microsatellite loci (*TGLA227, ETH225, BM1824, INRA005* and *MM12*) showed a genotype variation except for the *TGLA227* locus in which all samples were uniformly (Saturano, 2018).

For the Nellore cattle (Brazil, *B.indicus*) ninety-four alleles were detected from the 10 loci surveyed, yielding a mean value of 9.4 alleles per locus. The *TGLA227* locus had one allele with a much higher frequency than the other alleles (75 bp) and the *ETH10* locus had two alleles with high frequencies (207-209 bp).

Table 4. A list of the high-frequency alleles in different zebu and the beef cattle (Ch – Charolais, Her – Hereford, Sim – Simmental) breeds across the 10 microsatellite markers.

Breed	Locus									
	TGLA227	**BM2113**	**TGLA53**	**ETH10**	**SPS115**	**TGLA122**	**INRA023**	**BM1818**	**ETH3**	**BM1824**
Zebu[a]	79, 81	131, 143	159, 167	210, 212, 214	247, 255	137, 149	215		113, 115	183
Zebu[b]	77	129, 135, 141		209, 213	246, 248	143, 153	214			180, 182
Zebu[c]	77	123, 131	158	209	239, 241, 243	141, 143	208		111	180
Zebu[d]	77, 81	141	160, 168	209, 213	246, 248, 250	137, 151	214		115, 117	180, 182
Zebu[e]	77	129, 139, 141	160, 168	209, 211, 213	246, 248	137, 151	214		115, 117	180, 182
Zebu[f]	77, 79		157	209, 211, 213	246	153	214		115	
Zebu[g]	75	129, 141	160	207, 209		137	214, 216		115, 117	178, 180, 182
Zebu[h]	77, 87	135, 137, 141		209, 2013	246	133, 141	198, 214			180
Zebu[h]	77, 79	135, 139		209	248	143	198, 214			180, 182, 192
Zebu[h]	77, 79	129, 135, 139		217	248, 256	143	208, 214			180, 182, 192
Ch[i]	89	131		217	248	151	206	262	117	182
Ch[j]	83, 89, 91	131, 135		217	248	143, 151	202, 206		117, 125	280, 282, 288
Ch[k]		131, 133	151, 153, 157	209, 211, 215			203, 205, 207, 209			178, 180, 182, 184
Her[l]	91, 93, 95	133, 139	160, 162	219, 221, 223	248	143, 153	206, 216		117, 119	180, 182, 184
Her[j]	89, 91	135, 139		217, 219	248, 260	143	214		117, 119	182
Her[m]	94			218, 220, 222						
Sim[n]	80	128	164	214	242	150	208, 212, 214		112, 114, 124	182, 188
Sim[l]	81	131		217	248	151	214	268	117	188
Sim[o]	81	131, 139	168	217	248, 256	143, 151	214		117, 127	180, 188

a) Kesvulu et al., 2009; b) Bicalho et al., 2006; c) Escobar et al., 2009; d) Novoa, Usaquen, 2010; e) Gomez et al., 2013; f) Egito et al., 2007; g) Cervini et al., 2006; h) Hussein, 2008; i) Putnova et al., 2011; j) Kundrat, 2007; k) Sifuentes-Rincon et al., 2007; l) Janik et al., 2002; m) Yoon et al., 2005; n) Stevanović et al., 2009; o) Choroszy et al., 2006.

The mean observed heterozygosity value was 0.564 (from 0.323 to 0.847) and the mean expected heterozygosity value was 0.679 (from 0.422 to 0.855). A total, eight loci recorded positive inbreeding coefficients indicating presence of inbreeding with respect to these loci and the overall mean inbreeding coefficient (*Fis*) for this zebu population was 0.164 (Cervini et al., 2006).
Egito et al. (2007) showed that among the Brazilian zebuine breeds (Gyr, Guzerat and Nellore) the mean allele number was very similar – 8.4-8.8 alleles per locus, while the two domesticated taurine breeds (Holstein and Jersey) were less diverse with a smaller average number of alleles slightly above 8.0.
The mean observed heterozigozity values ranged from 0.636 to 0.654 and from 0.632 to 0.685 for the zebuine and taurine breeds, respectively. In all breeds observed heterozygosity values were nominally smaller than the expected ones. Highest values of *Fis* were seen for Jersey (0.121) followed closely by the three zebuine breeds Gyr (0.120), Guzerat (0.113) and Nellore (0.096).
In the Punganur cattle (India, *B. indicus*), a total of 66 alleles were produced by eleven markers with a mean of 6.0 alleles per locus, the overall mean observed and expected heterozygosities were 0.684 and 0.666, respectively, and the overall mean coefficient of inbreeding (*Fis*) was -0.001 and it ranged from -0.225 to 0.512 (Kesvulu et al., 2009).

Escobar et al. (2009), identified the genetic variability of the zebu (*B.indicus*) herd with the Brahman (Red and White) and Gyr breeds in Colombia, detecting that one hundred and fifty seven alleles were detected from the 11 loci surveyed, yielding a mean value of 14.3 alleles per locus. The overall mean observed heterozygocity was 0.706, and the mean expected heterozygocity was 0.777.

In other Colombian Brahman (*B. indicus*) population (Novoa, Usaquen, 2010) the number of alleles per locus (*TNA*) fluctuated between 5 and 12 with an average of 7.9, and the inbreeding coefficient (*Fis*) was positive, low for the whole population (0.067), and significantly different from zero, suggesting a deficit of heterozygotes in the sample. The overall mean expected and observed heterozygosity values were 0.637 and 0.667, respectively.

Eleven microsatellites were used to evaluate the genetic variation from three populations of Charolais cattle (*B. taurus*) located in northeast Mexico (Sifuentes-Rincon et al., 2007). Twelve alleles per loci was the average. Allele number per locus ranged from 7 alleles in *ETH10* locus, to 18 alleles in *TGLA53*. The allele diversity was similar among the ranches. Expected heterozygocity was higher than the observed for all loci in the three ranches. The overall mean heterozygocity was 0.500. Observed heterozygosity ranged from 0.388 to 0.780, from 0.235 to 0.816, and from 0.230 to 0.732 for ranches 1, 2, and 3, respectively.

MacHugh et al. (1998) reported a value of heterozygosity for Charolais of 0.525, and Maudet et al. (2002) found a heterozygosity of 0.640 in Charolais in France. These heterozygocity values are similar than those estimated by Sifuentes-Rincon et al. (2007), suggesting the genetic diversity of Charolais in Mexico is comparable to that reported in Europe.

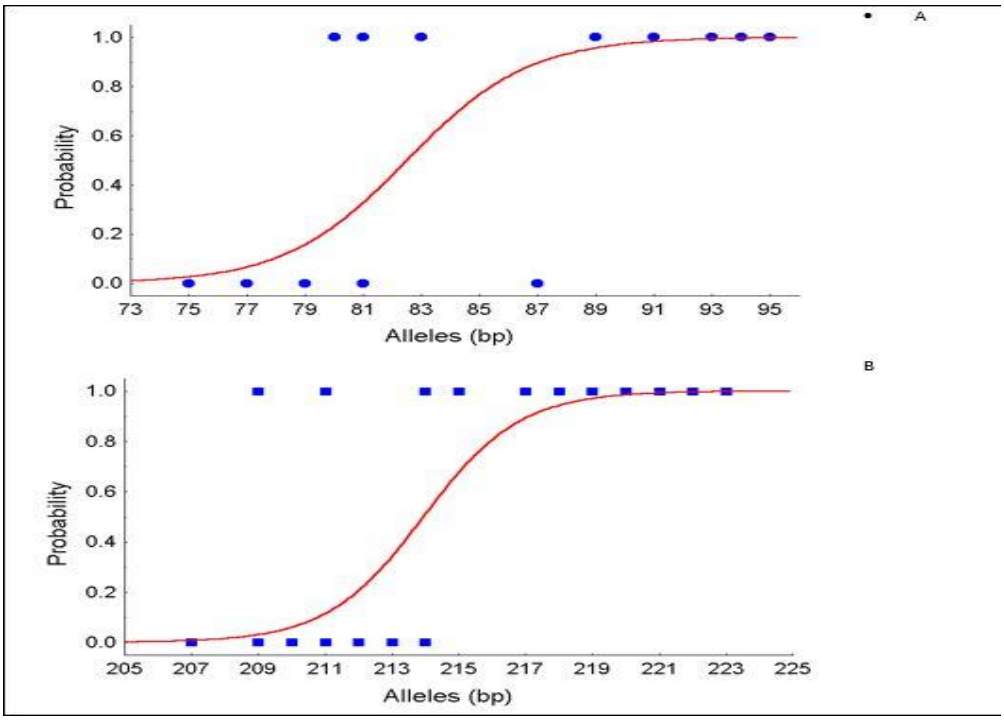

Figure 2. Logistic Regression results: A – locus *TGLA22*; B – locus *ETH10*. Model displays the probability of outcome (0 – *B.indicus*, 1 – *B.taurus*) versus significant predictor variable (allele length).

In the Serbian population of Simmental cattle (*B. taurus*) a total of 92 alleles were detected and the mean number of alleles (*TNA*) per locus was 8.4 (Stevanović et al., 2009). The most polymorphic microsatellite were *TGLA53* (14 alleles), *TGLA227* (11 alleles) and *INRA023* (11 alleles) loci. In addition, *Ho* values ranged from 0.452 to 0.774, with overall mean value of 0.662, whilst *He* values varied from 0.557 to 0.893, with an average of 0.753. Overall, microsatellite DNA markers analysed in the Serbian population of Simmental cattle appeared more polymorphic than in other breeds of Simmental cattle (from Poland, Slovakia, Czech Republic) (Janik et al., 2001; Choroszy et al., 2006; Czerneková et al., 2006).

The mean *TNA* per locus observed in Serbian population of Simmental cattle (8.3) is higher than 7.27 found in Simmental cattle from Poland (Choroszy et al., 2006). Moreover, the total number of alleles we observed in Serbian population of Simmental cattle (92) is higher than Janik et al. (2001) and Choroszy et al. (2006) found in Simmental cattle from Poland for the same set of microsatellite loci (79 and 80, respectively).

Putnova et al. (2011) reported that in the Czech beef cattle (*B.taurus*) populations the mean number of allele per each locus ranged from 4 to 11 with a mean of 7.4 for Charolais and 5.8 for Simmental. All the analyzed loci showed high polymorphism and sufficient informativeness, though *ETH10* in Charolais cattle showed very low heterozygosity. The highest polymorphism for *TGLA227* and *INRA023* loci had also been found by Radko et al. (2005) in Polish Red cattle and Hereford.

Table 5 presents a list of *B.indicus*- and *B.taurus*-specific alleles across the different microsatellite loci. The two groups (zebu and *B.taurus*) breeds have shown separate and characteristic distributions of alleles in *ETH225* locus tested (Table 5). Alleles with high molecular weight (154, 158 and 160 bp) were more frequent in zebu animals while taurine animals exhibited low weight (≤ 150 bp) (Hall, Bradley, 1995).

Table 5. A list of *B. indicus*- and *B. taurus*-specific alleles across the different microsalellite loci.

Locus / alleles	Species	Literature
ETH225 (154, 158 and 160 bp)	*B. indicus*	Hall, Bradley, 1995
ETH152 (191 and 193 bp); *ILSTS001* (77 bp); *ETH225*; *HEL1*; *HRHl*; *ILSTS005*; *ILSTS014*; *OCAM* (182 bp); *RASA*; *TGIA48*	*B. indicus*	MacHugh et al., 1997
ETH10 (207, 209 and 211 bp); *ETH152* (191 bp); *ETH225* (153, 155, 157 and 159 bp); *Hel13*; *ILSTS005*; *INRA005*	*B. indicus*	Loftus et al., 1999
INRA124 (130 bp)	*B. indicus*	Hanotte et al., 2000
INRA189 (88 bp), *BMS861* (156 bp)	*B. indicus*	Edwards et al., 2000
BM2113; *ILSTS001*	*B. indicus*	Magee et al., 2002
BM2113 (130 and 142 bp); *CSSM66* (181 bp); *ETH10* (207, 209 and 211 bp); *ETH152* (191 bp); *HEL1* (101, 107 and 117 bp); *HEL13* (182 and 186 bp); TGLA122 (144 bp).	*B. indicus (Asian)*	Ibeagha-Awemu et al., 2004
ETH225 (153, 157, 159 bp); *TGLA227* (79 bp); TGLA122 (136 bp)	*B. indicus*	Liron et al., 2006
TGLA227 (77 and 79 bp)	*B. indicus*	our results
ETH10 (209 and 211 bp)	*B. indicus*	our results
ETH225 (144, 146, 148 and 150 bp)	*B. taurus*	Hall, Bradley, 1995
INRA124 (132 bp)	*B. taurus*	Hanotte et al., 2000;
INRA189 (98 bp)	*B. taurus (European)*	Edwards et al., 2000
BMS861 (158 bp)	*B. taurus*	Edwards et al., 2000
BM1824 (189 bp); *CSSM66* (183 bp); ETH10 (215 bp); *HEL1* (113 bp); HEL13 (188 bp); *ILSTS6* (289 bp); TGLA122 (150 bp).	*B. taurus (European)*	Ibeagha-Awemu et al., 2004
BM1824 (181 bp); *BM2113* (122 bp); ETH10 (219 bp); *ETH152* (195 bp); HEL1 (109 bp); *HEL13* (190 bp); INRA023 (199 bp).	*B. taurus (African)*	Ibeagha-Awemu et al., 2004
TGLA227 (89 and 91 bp)	*B. taurus*	our results
ETH10 (217 and 219 bp)	*B. taurus*	our results

As suggested by MacHugh et al. (1997), substantial differences in the distribution of alleles at 10 microsatellite loci have been observed between zebu and taurine cattle: *ETH152* (191 and 193 bp), *ILSTS00*1 (77 bp), *ETH225, HEL1, HRHl, ILSTS005, ILSTS014, OCAM* (182 bp), *RASA* and *TGIA48*. In total, 18 alleles from the 10 diagnostic loci were classified as zebu-diagnostic.

On the other hand, six microsatellite loci – *ETH10* (207, 209 and 211 bp), *ETH152* (191 bp), *ETH225* (153, 155, 157 and 159 bp), *HEL13, ILSTS005* and *INRA005* – displayed alleles that were present at high frequency in the Asian zebu populations (Table 5). In total, 13 alleles from the six loci were classified as diagnostic of zebu ancestry (Loftus et al., 1999). A Y-specific (*INRA124*) microsatellite polymorphism has been recently described (Hanotte et al. 2000). This locus shows two alleles. The 132 bp allele is specific to cattle of taurine origin (African or European taurine) and the 130 bp allele is specific to cattle of indicine origin (Hanotte et al., 2000).

Additionally, both *BM86*1 (a similar marker to *INRA124*) and *INRA189* loci seem to show allele size variants specific to taurine and zebu in the cattle breeds studied (Edwards et al., 2000). The *BM2113* and *ILSTS001* loci have been described previously as displaying a total of four alleles specific to West African *B.taurus* breeds (MacHugh et al., 1997), whereas three alleles across the *HEL1* and *ILSTS001* loci are considered to be exclusive to populations exhibiting *B.indicus* ancestry (Magee et al., 2002).

Ibeagha-Awemu et al. (2004) reported that microsatellite allelic distribution displayed groups of alleles specific to the Indian zebu, African taurine and European taurine. Zebu alleles were identified at seven of the ten loci and their mean frequency distribution was the highest in Indian zebus (63.1%) followed by African zebus (45.2%) while being less than 10.0% in both African and European taurines. Identified European taurine specific alleles were seven at seven loci (see Table 5). Their distribution was the highest as expected in the European taurines (32.5%) while being less than 4.0% in breeds in the other bio-geographical groups.

Conclusion

In this study we used microsatellite data to study the genetic constitution of the SM cattle by considering introgression of *B. indicus* and *B. taurus*. In the SM cattle zebu and taurine alleles were identified at two of the 10 loci studied, *TGLA227* and *ETH10*. It can be assumed that the *TGLA227* (77 bp) and *ETH10* (209-211 bp) alleles among the SM cattle examined individuals were inherited from a *B. indicus* ancestor. On the other hand, the *TGLA227* (89 bp) and *ETH10* (217-219 bp) alleles were inherited from a *B.taurus* ancestor. Thus, the SM cattle presented with high level of taurine/zebuine admixture, which is consistent with the breeding history.

Acknowledgements

Financial support was received from the Ministry of Education and Science of Ukraine (state registration number 0117U000485) to Dr. Anna V. Lykhach and Dr. Alexander S. Kramarenko.

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Citation: Kramarenko, A.S., Karatieieva, O.I., Lykhach, A.V., Lugovoy, S.I., Lykhach, V.Ya., Pidpala, T.V., Patryeva, L.S., Kramarenko, S.S. (2019). Assessing genomic taurine/zebuine admixture in the southern meat cattle based on microsatellite markers. Ukrainian Journal of Ecology, 9(1), 251-261.