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Morphological and molecular genetic diversity of Syrian indigenous goat populations

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Domestic goats in Syria may provide an interesting source of genetic variability due to its proximity to the centers of domestication. This study aimed to assess the morphological variation, genetic diversity and population substructure of the Syrian goat populations. Commonly, three goat genotypes are distinguished in Syria, namely Jabali or mountain goat, Baladi or local goat and Shami or Damascus (a well-known dairy goat). A pre-tested semi-structured questionnaire was used in recording both qualitative (coat color, eye color, horn length, horn orientation, nose profile) and quantitative (height at wither, chest girth, cannon length, body length, ear length and ear width) morphological data. Data from a total of 5,730 individual goats of the three goat populations reared in ten representative provinces of Syria were collected and analyzed using GenStat version 14 statistical packages. Results of the morphological analysis confirmed that there were clear morphological variations among the three goat populations. The three goat populations are mainly distinguished by their straight (Baladi, 71.1% and Jabali, 82.8%) and curved (Shami, 89.5%) nose profiles. Substantial phenotypic variability was found among and within the breeds suggesting that these goat breeds have not yet undergone an organized breeding program. The genetic variability and population substructures from 398 individual animals of the three breeds were genotyped using 12 DNA microsatellite markers from Food and Agricultural Organization (FAO) panel. All microsatellites typed were found to be polymorphic and a total of 41 distinct alleles were detected on Baladi, Jabali and Shami goat populations. The Syrian goat populations had observed and expected heterozygosity values that ranged from 0.50 to 0.62 and 0.74 to 0.85, respectively, and an average of 13.97 alleles per locus across breeds. For all loci, an average inbreeding values (F_{IS}) of low to moderate level was obtained across the three goat breeds, which ranged from 0.29 (Shami goats) to 0.34 (Baladi goats) indicating the absence of mating between close relatives within these populations. The observed positive F_{IS} coefficients among the studied goat breeds also suggested heterozygote deficiencies. The analyses of the molecular data using STRUCURE program indicated there were two primary populations, which did support the results based on morphological data of the same goat populations that clustered these goat populations into two main groups and confirmed the admixture nature of the Baladi and Jabali goat populations, while the Shami goat breed was well differentiated and grouped into a separate cluster that suggests its evolutionary and genetic uniqueness. The analysis of molecular variance (AMOVA) results detected genetic variations within individuals in a population (96%). The high genetic variability within individuals in a population provides a good base for designing genetic improvement programs under the existing goat management systems.

Key words: Characterization, cluster, genetic differentiation, population structure, Syria.

INTRODUCTION

Syria covers an area of 18.6 million ha and nearly half of Syria's land mass is classified as rangeland. The agriculture sector accounts for about 26% of Syria's Gross Domestic Product. Livestock provides over 34% of the total value of agricultural production, and contributes 17.7% of the value of agricultural exports. The livestock industry also provides employment to about 20% of the national workforce (Hajar, 2006) and is the main source of income and livelihood for Bedouin herders. Goats (*Capra hircus*) are common and the most important livestock species in Syria. They often possess great adaptability to harsh local environmental conditions and represent important genetic resources. These native breeds did not undergo extensive artificial selection by humans and are generally well-adapted to semi-arid or even arid conditions and such adaptive characteristics contribute to a growing interest on indigenous species for conservation and breeding programs.

The majority of Syria's goat population of 2.29 million heads consists of indigenous goats which are distributed all over the country (FAOSTAT, 2011) and raised for multipurpose uses. The economic importance of small ruminants has been increasing in Syria in recent years due to the erratic rainfall and related risk of crop failures. Besides, indigenous goat populations are known in general for heat tolerance, disease resistance, mothering and walking abilities, and the ability to efficiently metabolize low quality feeds (Trail and Gregory, 1984). Thus, indigenous goats are very valuable genetic resources adapted and suited for low-inputs-outputs agricultural production systems of the developing countries like Syria. The Mediterranean countries, namely Lebanon, Syria and Cyprus are considered as the main goat milk and cheese producer next to India (Dubeuf et al., 2004) and the Shami (Damascus) goat is well appreciated for its high milk yield and twinning ability. Recognizing the value of the Shami goats, the Syrian Ministry of Agriculture and Agrarian reform established seven Shami goats' improvement and conservation research and development centers in representative provinces of the country to maintain and improve this unique goat breed. The genetic relationships and differentiation between Shami and other native goat populations available in Syria have not yet been characterized and established in a way to contribute to the declared aim of the Food and Agriculture Organization (FAO) of the United Nations to preserve the genetic diversity of domestic animals including goats.

Phenotypic and molecular characterizations have been widely used to quantify morphological and genetic diversity in small ruminants (Gizaw et al., 2007; FAO, 2012). Morphological polymorphisms are the first to be used to determine the relationship between breeds (Weigend and Romanov, 2002) and considered as an essential component of breed characterization that can be used to physically identify, describe, and recognize a breed, and also to classify livestock breeds into broad categories (FAO, 2012). The magnitude of phenotypic variability differs under different environmental conditions, in which morphometric characters are continuous characters describing aspects of body shape. In addition, microsatellite markers have also been successfully used to study the biodiversity and genetic relationship and differentiation between and within domesticated livestock populations or breeds (Ruane, 1999; Baumung et al., 2006; Toro et al., 2006; Gizaw et al., 2007; Bizhan and Majnoun, 2009; Visser and van Marle-Koster, 2009; Hassen et al., 2012). Their abundance, high level of repeat number of polymorphism, suitability for amplification by polymerase chain reaction (PCR), co-dominant inheritance and random distribution in the organism's genome have facilitated their extensive use for molecular characterization of domestic animals. Therefore, the present study was aimed to analyse the Syrian goat genetic diversity and differentiation using recommended morphological traits (FAO, 2012) and microsatellite markers (FAO, 2004) to inform the design of rational goat breeds improvement and utilization strategies.

MATERIALS AND METHODS

Description of the study area

The Syrian Arab Republic is one of the Mediterranean countries and is located in the Middle East between 32° 19' and 37° 30'N and 35° 45' and 42° E with a total area of 185,400 km^2. Ten out of the fourteen Syrian provinces were selected following purposive sampling techniques by considering agro-ecology, socioeconomic importance of the indigenous goat populations, goat production systems, types of indigenous goats, the main challenges and opportunities of goat keeping. The study areas were also chosen based on previous informal and/or formal studies carried out on Syrian Jabali goats (Wurzinger et al., 2008) and other goat breeds elsewhere in North Africa and West Asia (Iniguez, 2005a, b). The ten targeted provinces were Aleppo, Al-Raqua, Al-Hasakeh, Idleb, Hama, Homs, Damascus Rural, Al-Seweida, Deir Al Zour and Tartous (Figure S1). The districts in each province were randomly selected and fifty-seven districts from the total sixty-four districts were chosen for collecting morphological data and blood samples from the targeted goat populations.

Goat populations and morphometric measurements

The agricultural development experts who were involved in the

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actual field survey were trained on characterization of the indigenous goat populations at morphological levels. The targeted goat populations were Baladi, Jabali and Shami, which are raised and distributed almost all over the country. The populations were varied on their physical appearance and in population sizes. The Baladi goats were the most dominant followed by the Jabali goats, while the Shami goats were the least in number per flock in each targeted study areas. These goats' breeds were normally kept together by smallholder farmers, which were managed under extensive management practices and studied goat populations were sampled from farmers' flocks. To capture the largest possible representation of the existing genetic diversity, we sampled relatively unrelated animals from several flocks in each population for morphological and molecular characterizations of the aforementioned goat breeds. In these flocks, veterinary health care and proper small ruminant feeding are rarely practiced, mating was uncontrolled and performance recording scheme was also not existing.

Field surveys were carried out in ten representative and accessible provinces across Syria covering all agro-ecological zones for generating socioeconomic data, goat herd structure (results of the goat production system analysis and goat management systems are not presented here), and recording the physical appearances and also for measuring selected phenotypic traits. In addition, in each of the study provinces, goat owners, key informants and extension agents were interviewed using a pre-tested semi-structured questionnaire and 3 to 5 mature unrelated animals per herd were randomly selected (that would help to avoid sampling of closely related individuals) and used to measure morphological traits. In addition, a list of physical descriptors was used to record morphological variations on goats coat color, eye color, horn length, horn orientation and nose profile. Moreover, quantitative data on linear body measurements (cm) such as height at wither, chest girth, cannon length, body length, ear length and ear width were measured using a measuring tape following the descriptor list of the Food and Agriculture Organization of the United Nations FAO (1986). Besides, focus group discussions were held with livestock keepers and knowledgeable key informants for generating general information regarding the history of the various goat types and special distinguished features of the targeted goats. These descriptors were used for identifying and refining the goat populations available in Syria. Depending upon the number of each goat population within a flock (data not shown in this paper) data on a total of 5,730 individual goats of both sexes (male, n=1,071 and female, n= 4,659): 409, 2,071 and 3,250 goats of Shami, Jabali and Baladi, respectively were recorded from ten provinces following the FAO goat descriptor manual (FAO, 1986).

Blood sampling and DNA extraction

The blood samples were collected from eight representative provinces, namely Aleppo, Al-Raqua, Al-Hasakeh, Idleb, Hama, Homs, Damascus Rural and Al-Seweida which followed the distribution and the density of the Baladi, Jabali and Shami goat populations across the country (Figure S1). A total of 398 blood samples from the three targeted goat populations (Baladi, n=236, Jabali, n= 90 and Shami, n= 12) were collected from different villages and herds (one blood sample per herd). Samples were also collected from 60 Shami goats (30 samples from each station) captured in Hmemeh Shami research station in Aleppo and Karahta Shami goat research station in Damascus provinces. Samples were taken from mature genetically unrelated herds that represented the three morphologically identified goat populations. The samples were collected by puncturing the jugular vein of each animal using the 10 ml vacutainer tubes having K3-EDTA as anticoagulants, field collection, all samples were extracted following the DNA extraction procedure described for peripheral blood lymphocytes (PBL) stored with Urea (Tapio et al., 2007). Subsequently, DNA concentrations were estimated by a Nano-DNA spectrophotometer (Pharmacia LKB-Ultraspec III) in which the quality of DNA was assessed using the ratio of A260/A280.

PCR amplification and genotyping

The DNA was amplified by PCR in a thermal cycler (GeneAmp PCR System 2700 96-well cyclers) using 12 microsatellite markers selected from FAO/ISAG panel list (FAO, 2004) described in Table 3. The forward primers of each pair were labeled with either NED (Yellow), FAM (Blue), and VIC (Green) dyes, which were supplied by Applied Biosystems Company, Warrington, UK. The primers were screened from the list of microsatellite markers recommended by FAO/ISAG in which only 12 fluorescently labelled microsatellite markers were chosen based on the degree of polymorphism obtained using genomic DNA extracted from Syrian goats. These markers were also used by different researchers for livestock genetic variability studies such as on Ethiopian goats (Hassen et al., 2012), Hamdani sheep (Al-Barzinji et al., 2011) and the characterization of other goat populations elsewhere (Visser and van Marle-Koster, 2009; Martinez et al., 2006). The 20 µl amplification reactions contained genomic DNA, 10× standard polymerase chain reaction (PCR) buffer, dNTPs, Amplicon *Taq* DNA polymerase, forward and reverse primer mix and double-distilled sterilized water, which was formulated following a standard protocol (Sambrook et al., 1989) and were performed in a single PCR amplification for each locus. The reactions were processed on a thermal cycler following a step down amplification method. The PCR products were initially visualized in agarose gels stained with Ethidium bromide to identify possible imperfections and to decrease the rate of failure in capillary electrophoresis. Only the amplified PCR products were multiplexed based on their reported allele size range and the type of fluorescent labels used for each locus which were finally analyzed by capillary electrophoresis using an automated ABI Prism® 3100 DNA genetic analyzer. The data was captured using GeneScan version 3.1 software with 350 ROX labeled internal size standards and the allele sizes (bp) were determined using GeneMapper version 3.7 software (Applied Biosystems, Foster City, CA, USA). Finally, an allelic table was created from this dataset and exported to Microsoft Excel for further statistical analysis using appropriate molecular genetic analyses software.

Statistical data analyses

The General Linear Model (GLM) procedures of GenStat (version 14) statistical package were employed to analyze the quantitative data collected from Syrian goat breeds in which breed, sex, age and their interactions were fitted as fixed effects. In other words, the goat breeds, sex and age were fitted as independent variables, whereas body weight and other linear body measurements were fitted as dependent variables. The qualitative traits were analyzed in GenStat as descriptive statistics (as percentage). The interactions between breed, age and sex were found to be statistically non-significant; hence, the statistical analysis results for breed by age and sex interactions are not presented in this paper. As farmers did not have birth record of their animals, age of each sampled goat was estimated using dentition as described by Wilson and Durkin (1984); hence, four age groups were identified (Table 2). For each goat population, morphometric data from different villages and flocks across the different districts in the targeted

provinces were collected from unrelated goats of both sexes and breeds. The quantitative traits considered were height at withers, chest girth, cannon length, ear width, body length, ear length and ear width while the qualitative traits recorded were coat color, eye color, horn length, horn orientation and nose profile. Hierarchical cluster analysis was conducted and a dendrogram constructed based on Euclidean distances between populations derived from morphological variables using the unweighted pair-group method to describe morphological clustering pattern of the targeted goat populations. In the hierarchical cluster analysis, the major quantitative (height at wither, chest girth, cannon length, body length, ear length and ear width) and qualitative (coat color, eye color, horn length, horn orientation and nose profile) morphometrical variables were included, in which the data for individual traits were pooled for both sexes in each breed.

The Genetic Analysis in Excel (GenAlEx) version 6.5 (Peakall and Smouse, 2012) program and PowerMarker version 3.25 (Liu and Muse, 2005) statistical package were used to generate population genetic diversity parameters (total and average number of alleles, allele frequency, observed and expected heterozygosity). The Genetic diversities within and among goat populations were measured as the mean number of alleles (MNA) per locus and breeds as well as effective number of alleles (Ne). The effective number of alleles (Ne) per locus and breed were computed using PopGene version 1.32 software (www.ualberta.ca/~fyeh/popgene). The observed mean number of alleles (MNA), observed (H_o) and expected heterozygosity (gene diversity) (H_e) values were also computed. Using the variance-based method of Weir and Cockerham (1984) fixation indices (F_{IS}, F_{IT}, F_{ST}), estimated genetic differentiation (Gst), Shannon diversity index (I) and gene flow (Nm) values for each locus and overall loci were calculated based on GenAlEx software. P-value for inbreeding coefficients (F_{IS}) within samples was calculated on FSTAT version 2.9.3.2 (Goudet, 2001). The MNA detected in each population and the H_e values are in general good indicators of genetic polymorphism. MNA was counted as the average number of alleles observed in a population, while the H_e value is estimated as the proportion of heterozygote expected in a population. The GenAlEx program was used for testing deviation or departure from Hardy-Weinberg Equilibrium (HWE) at each locus for each studied goat populations.

Pair-wise Reynolds' linearized standard genetic distances between populations were calculated from allele frequencies following Nei et al. (1983) procedure in GenAlEx package. Distances obtained were used to construct a dendrogram following unweighted pair group method with arithmetic mean (UPGMA). Bootstrap (n=1,000) re-sampling was carried out to check the robustness of the phylogenetic tree and the resulting tree was visualized in TREEVIEW version 1.6.6 software. The analysis of molecular variance (AMOVA) was also performed by the GeneAlEx using the codominant allelic distance matrix with 999 permutations to partition the total covariance components into inter-group, inter-populations within group and within population components.

The Bayesian cluster analysis using STRUCTURE version 2.3.4 software (Pritchard et al., 2000) was run to infer the genetic relationships between the Syrian goats and also to assess level of admixture. To estimate the number of subpopulations (K), ten independent runs of K = 1 to 15 were carried out with a 100,000 burn-in period at 100,000 Markov Chain Monte Carlo iterations by considering correlated allele frequencies and an admixture model. The averaged likelihood at each K was used to calculate ΔK (Evanno et al., 2005) to further investigate results from STRUCTURE using STRUCTURE HARVESTER version 0.6.94 website based program (Earl and vonHoldt, 2012), which was used as an *ad hoc* indicator of population number or cluster number. Results from replicate runs at the optimal K were combined in CLUMPP (Jakobsson and Rosenberg, 2007) and then CLUMMP results were used to plot bar graphs based on DISTRUCT (Rosenberg, 2004) program.

RESULTS AND DISCUSSION

It is not possible to provide research results on the characterization of Syrian indigenous goat production and management systems. Rather, this part will be attempted to cover as a separate manuscript. This paper provides a range of research results on phenotypic and molecular characterization of Syrian goat populations (Baladi, Jabali and Shami) which identified substantial phenotypic and genotypic variability among and within the targeted breeds. As mentioned earlier in the methodology part, agro-ecological zones, distributions and goat densities were the main criteria used for collecting morphological data and blood samples from the purposely targeted goats breed of the Baladi, Jabali and Shami goat populations across the country (Figure S1).

Qualitative variations

The physical body characteristics for Syrian goat breeds and their coat colors as well as their appearances are presented in Table 1. The majority of the Syrian indigenous goat populations had varying percentages of different coat color types and compositions, which could be used in most cases to distinguish the three goat populations (Figure 1). Commonly, three goat genotypes are distinguished in Syria, namely Jabali, Baladi and Shami. The majorities of the Baladi, Jabali and Shami goat populations of both sexes have predominant brown, black and brown coat colors, respectively. The most common and frequent body coat colors for these goats were black (32.23%) and brown (31.93%). Most Syria male (29.3%) and female (32.83%) goats had black coat color followed by brown. In addition, goats with crème and admixture of black, grey and brown coat colors were also observed. Such colors might have resulted from continuous selection practiced by goat owners for developing breeds with preferred colors. The most common eye color observed on Syrian goat breeds of Baladi, Jabali and Shami were crème (35%), brown (23.9%) and crème (76.9%), respectively along with the presence of various percentages of other eye colors.

Most Syrian Baladi (62.1%) and Shami (81.2%) goat breeds were polled (hornless) (Table 1), while the remaining goats have horns of short to long size orienting upward, backward and sideward. Moreover, the majority of the Syrian Jabali goats had backward horn-orientation (41.3%) with the presence of various percentages of other horn-orientation types. Most Baladi (71.1%) and Jabali (82.8%) goats' populations have had straight nose profile, which is in line with the findings reported for Syrian Jabali goats (Wurzinger et al., 2008). Most of the Shami goats had curved nose structure (89.5%) and similar nose profile of a Roman nose structure was also reported by Hancock and Louca (1975) for Shami goat breed. Most of the Syrian goat breeds have long and drooping ears and the owners of the goats practice ear

Table 1. Observed mean frequency (%) values for selected qualitative traits on Syrian goat populations.

Qualitative traits		Breed			Sex by breed					
					Male			Female		
		Baladi (3250)*	Jabali (2071)	Shami (409)	Baladi (512)	Jabali (487)	Shami (87)	Baladi (2738)	Jabali (1584)	Shami (322)
Coat color	Black	25.4(826)	52.9(1096)	18.4(76)	17.2(88)	50(244)	20.7(18)	26.9(737)	53.7(851)	17.9(58)
	Brown	34.1(1109)	17.2(356)	44.5(182)	39.1(200)	18.1(88)	41.5(36)	33.2(909)	17(269)	45.2(146)
	Crème/Grey	26.2(852)	18.8(389)	27.5(113)	28.7(147)	20.3(99)	26.8(23)	25.7(704)	18.4(291)	27.7(89)
	Mixed	0.4 (13)	0.7(15)	0.7(3)	0.6(3)	0.2(1)	1.2(1)	0.4(11)	0.8(13)	0.6(2)
Eye color	Crème	35.0(1138)	23.9(495)	76.7(314)	43.8(224)	31.1(151)	76.8(67)	33.4(914)	21.7(344)	76.7(247)
	Brown	28.2(917)	46.9(972)	7.8(32)	21(108)	39.4(192)	7.3(6)	29.5(808)	49.2(779)	8(26)
Horn length	No horn (polled)	62.1(2018)	34.7(719)	81.2(333)	77.3(396)	41(200)	75.5(66)	59.1(1618)	32.8(520)	82.1(264)
	Cut	4.3(140)	1.6(34)	7.0(29)	2(10)	0.6(3)	11.3(10)	4.7(129)	1.9(30)	6(19)
Horn orientation	Backward	27.9 (907)	41.3(855)	10.9(45)	11.5 (59)	16.3(79)	5.3(5)	30.8(843)	49.0(776)	12.2(39)
Nose profile	Straight	71.1(2311)	82.8(1715)	10.5(43)	56.9(291)	76.6(373)	15.9(14)	73.7(2018)	83.7(1326)	9.2(30)
	Curved	28.9(939)	17.2(356)	89.5(366)	43.1(221)	23.4(114)	84.2(73)	26.3(720)	16.3(258)	90.8(292)

*- numbers in bracket refers to sample sizes taken for each qualitative trait per breed.

cutting to avoid the damage of goat ears during browsing and/or grazing. A set of distinguishable and unique characters to each goat breed is presented in pictures (Figure 1).

Quantitative variations

Least squares means (± SE) of the body measurements (cm) for Syrian goat breeds are depicted in Table 2. Age, breed and sex consistently showed a highly significant ($p<0.001$) effect on height at wither, chest girth, cannon and body length. In addition, a highly significant difference was obtained ($p<0.001$) among goat breeds on ear length and difference on ear width were obtained on age and breed. The linear body measurements like height at wither, chest girth, cannon, and body length and ear width of the Syrian Shami goats were the highest followed by Baladi goats, while the Jabali goats were the smallest for all the aforementioned measured traits. Mavrogenis et al. (2006) reported comparable results regarding the body length of the Damascus (Shami) goats, which were imported into Cyprus more than 70 years ago with the aim to upgrade the local Cypriot goat population.

Majority of the Shami, Baladi and Jabali goat breeds can be distinguished by their dominant qualitative and quantitative traits. For instance, most of the Shami goats have brown coat color, no horn and curved nose profile, while the Jabali goats have black coat, and brown eye color, no horn and have straight nose structure (Table 1 and Figure 2).

Microsatellite marker polymorphism and allelic variations

The present work investigated for the first time the genetic variability and the population structure of the Syrian indigenous goat populations using microsatellite markers from FAO panel. The

Figure 1. Physical appearance of indigenous Syrian goat populations

Table 2. Least squares means (± SE) for effects of breed, sex and age of Syrian goat breeds on quantitative traits.

Effect and level	Height at withers	Chest girth	Canon length	Body length	Ear length	Ear width
N	5730	5730	5730	5730	5730	5730
Overall	74.67±0.31	85.42±0.42	10.81±0.08	70.82±0.54	20.46±0.45	9.22±0.15
CV (%)	7.6	8.88	14.86	13.84	27.87	21.2
Age group	***	***	***	***	NS	***
G1	75.52 ±0.23	85.16±0.31	11.26±0.06	70.7±0.39	20.15±0.26	9.65±0.08
G2	77.58 ±0.2	87.89±0.29	11.41±0.05	73.69±0.37	20.1±0.23	9.49±0.08
G3	78.25 ±0.21	89.08±0.28	11.46±0.05	74.4±0.37	20.52±0.23	9.43±0.08
G4	77.55±0.02	89.05±0.21	11.22±0.04	73.76±0.27	20.15±0.2	9.27±0.07
Breed	***	***	***	***	***	***
Baladi	76.99±0.29	87.41±0.4	11.40±0.08	73.54±0.52	21.04±0.44	9.48±0.15
Jabali	74.68±0.31	85.16±0.41	10.89±0.09	69.81±0.53	19.25±0.46	8.79±0.16
Shami	80.01±0.21	90.82±0.37	11.73±0.07	76.03±0.32	20.38±0.4	10.12±0.11
Sex	***	***	***	***	NS	NS
Male (M)	80.04±0.19	90.22±0.26	12.04±0.05	75.75±0.34	20.03±0.23	9.49±007
Female (F)	74.42±0.17	85.38±0.22	10.67±0.03	70.51±0.25	20.41±0.21	9.44±0.06

***, p<0.001; NS, Non-significant; *- G1, G2, G3 and G4 are referred to the age of the goats from 1 to 2, >2 to 3, > 3 to 4 and > 4 years old, respectively.

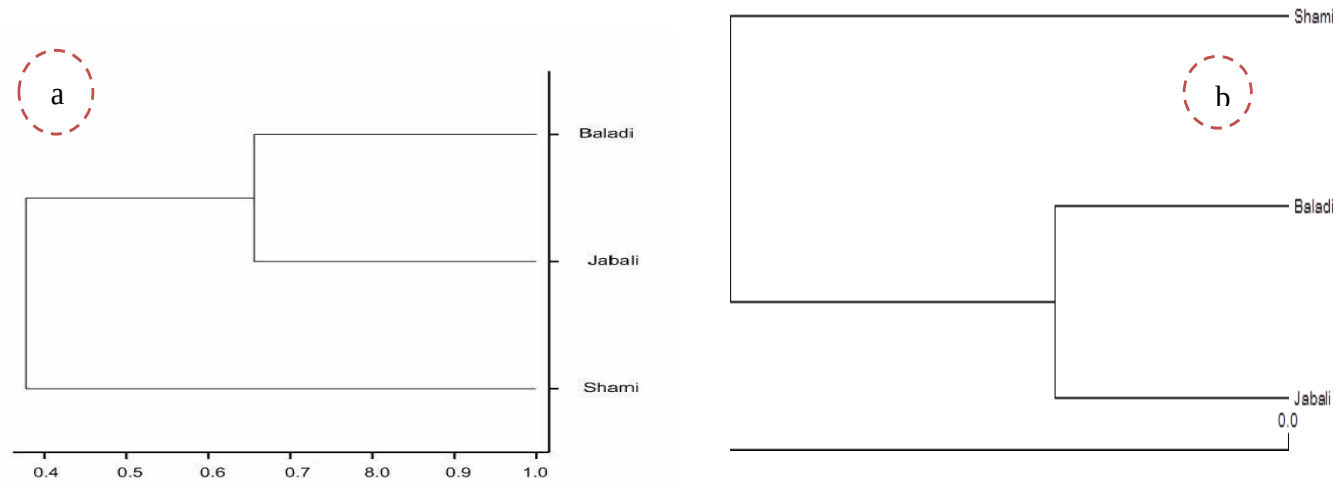

Figure 2. (a) Dendrogram showing morphological and **(b).** molecular variabilities among Syrian goat populations.

Table 3. Basic characteristics of each microsatellite loci used, annealing temperature (AT), observed allele size (AS) range, major allele frequency (AF), total number of alleles (TNA), mean number of alleles (MNA), effective number of alleles (Ne), polymorphic information content (PIC), Observed heterozygosity (Ho), Expected Heterozygosity (He), Wright's F-statistics (F_{IT}, F_{IS}, F_{ST}), observed genetic differentiation (G_{ST}), Shannon diversity index (I) and gene flow (Nm) values by locus across studied Syrian goat populations

Locus	AT (°C)	AS (bp)	AF (%)	TNA	MNA	Ne	PIC	Ho	He	FIS	FIT	FST	GST	I	Nm
ILSTS044	65-55	138-172	0.38	20	11.33	4.38	0.68	0.31	0.72	0.47	0.50	0.06	0.05	1.66	4.33
ILSTS087	68-58	114-167	0.25	27	15.33	6.19	0.83	0.59	0.85	0.34	0.38	0.06	0.05	2.31	4.24
SRCRSP8	65-55	112-255	0.47	22	12.00	4.36	0.72	0.25	0.74	0.70	0.73	0.09	0.08	1.9	2.66
ILST019	65-55	118-176	0.37	22	13.67	6.70	0.80	0.29	0.82	0.57	0.58	0.04	0.03	2.16	6.99
OARFCB48	68-58	96-180	0.25	23	14.00	6.17	0.83	0.62	0.85	0.22	0.26	0.04	0.04	2.27	5.76
ILSTS005	68-58	96-196	0.56	20	9.67	4.05	0.58	0.19	0.62	0.59	0.63	0.09	0.09	1.41	2.47
BM6444	68-58	118-182	0.12	34	23.67	13.08	0.94	0.61	0.94	0.34	0.37	0.04	0.03	3.08	6.05
ETH10	68-58	121-212	0.41	13	7.33	3.50	0.63	0.60	0.69	0.11	0.19	0.09	0.08	1.43	2.55
MAF209	68-58	89-122	0.51	12	6.33	3.15	0.64	0.55	0.68	0.11	0.21	0.11	0.11	1.52	1.96
MAF70	68-58	95-182	0.19	41	23.33	11.74	0.89	0.75	0.90	0.11	0.13	0.03	0.02	2.67	9.68
P19(DYA)	65-55	116-203	0.18	24	16.33	8.50	0.90	0.81	0.91	0.02	0.06	0.04	0.03	2.57	6.86
SRCRSP9	68-58	92-144	0.14	23	14.67	8.68	0.90	0.68	0.91	0.17	0.21	0.04	0.03	2.56	6.04
Mean/Breed			0.32	23.42	13.97	6.71	0.78	0.52	0.80	0.32	0.35	0.06	0.05	2.13	4.97

characteristics and the nature of the twelve selected microsatellite markers used in this study are summarized in Table 3. Results of molecular genetic analysis showed that all twelve loci were polymorphic; none of the markers were monomorphic and were adhered to the parameters for studying genetic diversity. A total of 281 alleles were detected at the 12 microsatellite loci on three studied goat breeds. The observed mean number of alleles per locus ranged from 6.33 (MAF 209) to 23.67 (BM6444), with an average of 13.97 alleles per locus across breeds. The observed number of alleles at a locus (Table 3) and the genetic distance values (Table 5) indicated genetic variability at that locus, which suggested the appropriateness of the loci to be used to analyze genetic diversity on goats. It was also suggested that for studies of genetic diversity and genetic distance within and among populations, microsatellite markers should have no fewer than four alleles which could help to reduce standard errors of distance estimate (Barker et al., 2001).

The effective number of alleles (Ne) ranged from 3.15 (MAF209) to 13.08 (BM6444), with an overall mean of 6.71 alleles per locus. All the loci used to analysis the Syrian goat diversity were highly informative which make them useful in genetic diversity studies. This is due to the fact that if a locus has PIC value > 0.5 that locus is considered as highly polymorphic loci; while a locus with PIC values ranging from 0.25 to 0.5 is clustered as a medium polymorphic marker (Vanhala et al., 1998). In this investigation, all loci were highly polymorphic, with PIC value range from 0.58 (ILSTS005) to 0.94 (BM6444),

Table 4. Breed level allelic and genetic diversity: mean number of alleles (MNA), Polymorphic Information Content (PIC), effective number of alleles (Ne), Shannon's diversity index (I), observed (Ho), and expected (He) heterozygosity and inbreeding coefficient (F_{IS}) values for Syrian goat populations.

Breed	Allelic diversity			Genetic diversity			
	MNA	Ne	PIC	Ho	He	I	FIS
Baladi	15.33±1.92	6.32±1.22	0.75	0.52±0.06	0.78±0.04	1.92±0.17	0.34±0.06*
Jabali	12.50±1.80	5.93±1.27	0.71	0.50±0.07	0.74±0.04	1.84±0.17	0.33±0.09*
Shami	14.08± 1.70	7.87±1.09	0.83	0.62±0.07	0.85±0.01	2.26±0.11	0.29±0.07*
Mean	13.97±1.87	6.71±1.19	0.78	0.52±0.07	0.80±0.03	2.01±0.15	0.32±0.07

*$p < 0.05$.

with a mean of 0.78 per locus. The average expected heterozygosity value ranged between 0.62 (ILSTS005) and 0.94 (BM6444) with an overall mean of 0.80, whereas the observed heterozygosity value ranged from 0.19 (ILSTS005) to 0.81 (P19) with an average value of 0.52 (Table 3).

Genetic diversity and differentiation

The genetic variability of each subpopulation was initially studied in terms of observed and effective number of alleles, as shown in Table 3 and the three goat breeds were having varied mean number of alleles. Genetic diversity analyses also suggested substantial genetic variability within the studied goats breeds (96%) (Table S2) in which its value supported by the morphological characterization study carried out on the same goat populations (Tables 1 and 2). The genetic diversity of each goat breed also showed considerable differences when measured in MNA per breed across all loci that ranged between 12.50 for Jabali goat and 15.33 for Baladi goat breeds. The Syrian Jabali goats had less than the average number of allele, while the Shami and Baladi goat breeds had higher mean number of alleles (Table 4). It was suggested that the observed MNA over a range of loci across different population is considered to be a good indicator of genetic variation within a given animal population (MacHugh et al., 1997).

Observed mean heterozygosity value was lower than the expected mean heterozygosity for all studied goat populations. The average observed and expected heterozygozity values ranged from 0.50 to 0.62 and 0.74 to 0.85, respectively. Moreover, the mean observed and expected heterozygosity values across all loci on studied goat populations were 0.52 and 0.80, respectively (Table 4), which were comparable with studies carried out on other domestic goat breeds (Kumar et al., 2005; Aggarwal et al., 2007; Dixit et al., 2008; Hassen et al., 2012). Due to its geographical location, Syria is considered as one of the countries believed to be home for small ruminant populations including the present domesticated goat breeds. The presence of long term natural selection for adaptation and the existence of interbreeding as result of the free movement of animals in the area are thought to contribute at large to the broad genetic diversity of the Syrian goats. The genetic diversity observed in Syrian goat breeds was comparable with the results reported on South-East Asian goats (Barker et al., 2001), Chegu goats (Behl et al., 2003), Indian goats (Kumar et al., 2009) and Ethiopian goats (Hassen et al., 2012). In addition, the PIC values across all loci ranged from 0.71 (for Jabali goats) to 0.83 (for Shami goats), with an average PIC value of 0.78 (Table 4), which suggested that all loci used in this study showed relatively high polymorphism for analyzing genetic diversity in goats.

Populations genetic differentiation were evaluated base on fixation indices (F_{IS}, F_{IT} and FST) according to Weir and Cockerham (1984), genetic differentiation (G_{ST}), Shannon diversity index (I) and gene flow (Nm) values using 12 microsatellite markers across three goat breeds (Table 3). The mean estimates of F-statistics obtained over loci were $F_{IS} = 0.32$, $F_{IT} = 0.35$ and $F_{ST} = 0.06$. The within breed deficit or excess in heterozygosity value was assessed by the inbreeding coefficients (F_{IS}), ranged between 0.02 (P19) to 0.70 (SRCRSP8), with an average of 0.32 across all loci, while the degree of differentiation within breed was estimated by the F_{IT} value, which was 0.35 and the extent of differentiation among subpopulations was measured by F_{ST} that was 0.06. All loci having positive F_{IS} values indicate an excess of homozygotes across the studied goat breeds. The highest value of F_{ST} (0.11) was observed for MAF209, while the lowest value of 0.03 was obtained at MAF70. The mean F_{ST} value (0.06) indicates that most of the total genetic variation corresponds to differences among individuals within goat populations (Table S2). Both high F_{IS} and F_{ST} values imply considerable degree of inbreeding and genetic differentiation among goat populations, respectively. Values of G_{ST} ranging from 0.02 (MAF70) to 0.11 (MAF209), with a mean of 0.05 (Table 3), reveal that genetic variation among the studied goat breeds was relatively low (5%).

At goat breed level, the inbreeding coefficients (F_{IS} values) showed heterozygote deficiencies occurring in all

Table 5. Pair wise estimate of genetic identity (above diagonal) and genetic distance (below diagonal) values for Syrian goat populations.

Breed	Baladi	Jabali	Shami
Baladi	***	0.961	0.458
Jabali	0.043	***	0.466
Shami	0.780	0.763	***

the three goat breeds. The mean F_{IS} value ranged from 0.29 for Shami to 0.34 for Baladi goat breeds that represented an average increase in the number of homozygous loci of 29% and 34% in Shami and Baladi goat populations (Table 4), respectively. It was suggested that less inbreeding values of less than 0.5 or closer to zero (Wang, 1996) might have happened due to the absence of mating between close relatives and/or within individuals. Similarly, such comparable inbreeding values were also reported for Asian (Barker et al., 2001), Indian goat populations (Kumar et al., 2005; Aggarwal et al., 2007; Dixit et al., 2008; Dixit et al., 2010) and local Albanian goat breeds (Hoda et al., 2011).

The HWE test results revealed that most of the markers used to study Syrian goats were not in HWE, except one locus (that is, ETH10) did show adherence to HWE for Jabali goats (Table S1). Several researchers (Laval et al., 2000; Barker et al., 2001) reported similar results of deviation from HWE for goat diversity studies using microsatellite markers. A population is considered to be within HWE when it is able to maintain its relative allele frequencies. Departure from HWE occurred when there is no excess heterozygotes due to the presence of null alleles (Pemberton et al., 1995), small sample size, migration, selection intensity, uncontrolled goat breeding practices, presence of less heterozygosity (Wahlund effect) and decreased heterozgosity due to inbreeding (Kumar et al., 2006).

Genetic relationships and phylogenetic analyses based on morphological and molecular data

The mean morphological values of both qualitative and quantitative characters were used as classifying variable, and the three goat populations were grouped into two main clusters as indicated in the dendrogram (Figure 2a). Cluster one contains Baladi and Jabali goat populations, while cluster two contains the Shami goats indicating that the Shami goats is relatively different from the two goat populations and was consistent with our earlier assumptions. Further subdivisions between Baladi and Jabali goats showed that these subpopulations were developed from different but closely related goat populations which were also consistent with our earlier hypothesis. Substantial phenotypic variability was found among and within these breeds suggesting that these goat breeds are not under an-organized breeding program.

The Syrian goat populations genetic dissimilarity was computed using molecular data and the smallest genetic distance value was detected between Baladi and Jabali goat populations (0.043), while the largest genetic distance value was recorded between the Baladi and Shami (0.780) and also between Jabali and Shami (0.763) goat populations (Table 5). These genetic distance values were used to construct a phylogenetic tree using UPGMA method and the results revealed the clustering of the three goat populations into two major separate groups. The first cluster contains the Shami goat breed, while the second group includes the Baladi and Jabali goat subpopulations (Figure 2b), which was also supported by classification based on the morphological dataset from the same goat populations.

Population genetic structure analyses

The AMOVA indicated that 4 % of the total variation was present among goat populations, and the majority of genetic variation was found within the goat population (Table S2), hence, similar partitioning of variance has also been reported (Vahidi et al., 2014). The population genetic structure of the Syrian goat populations was analyzed using STRUCUTRE program (Pritchard et al., 2000) with the number of expected clusters (K) ranging from 1 to 15 and bar plots were generated (Figure 3). Such analysis was carried out to detect the potential presence of substructures within breeds. Figure 3 shows the admixture plot of all individuals revealing the admixture patterns of the Syrian goat breeds ranging from K = 2 to 5. At K = 2, the admixture plot of all goat breeds reveals two distinct population patterns, which show strong support for a true subpopulation structure. Particularly, the Shami admixture plot represents a different pattern from those of Baladi and Jabali goat breeds show some degree of genetic dilution with these goat breeds. The true population substructure could be hindered by the sample sizes considered. At K = 3, the Shami goat exhibited similar admixture pattern as observed at K=2 showed more admixture pattern with Jabali goats (Table 5). Whereas, Baladi and Jabali goat breeds revealed different admixture pattern indicate substantial gene flow between the Syrian Baladi and Jabali goat breeds. At K = 4, Shami goats were clearly separated from the other goat breeds as before, while the Baladi and Jabali goat breeds admixture pattern was inseparable and additional unclear subpopulation were observed. The number of blood samples taken for both Jabali and Shami goats might hinder to point out the true population structures of these goat breeds. These were represented as admixture individuals without showing any notable subdivision among the different groups when K = 4. At K = 5 the admixture patterns revealed relatively similar patterns to that of K = 4, however, further

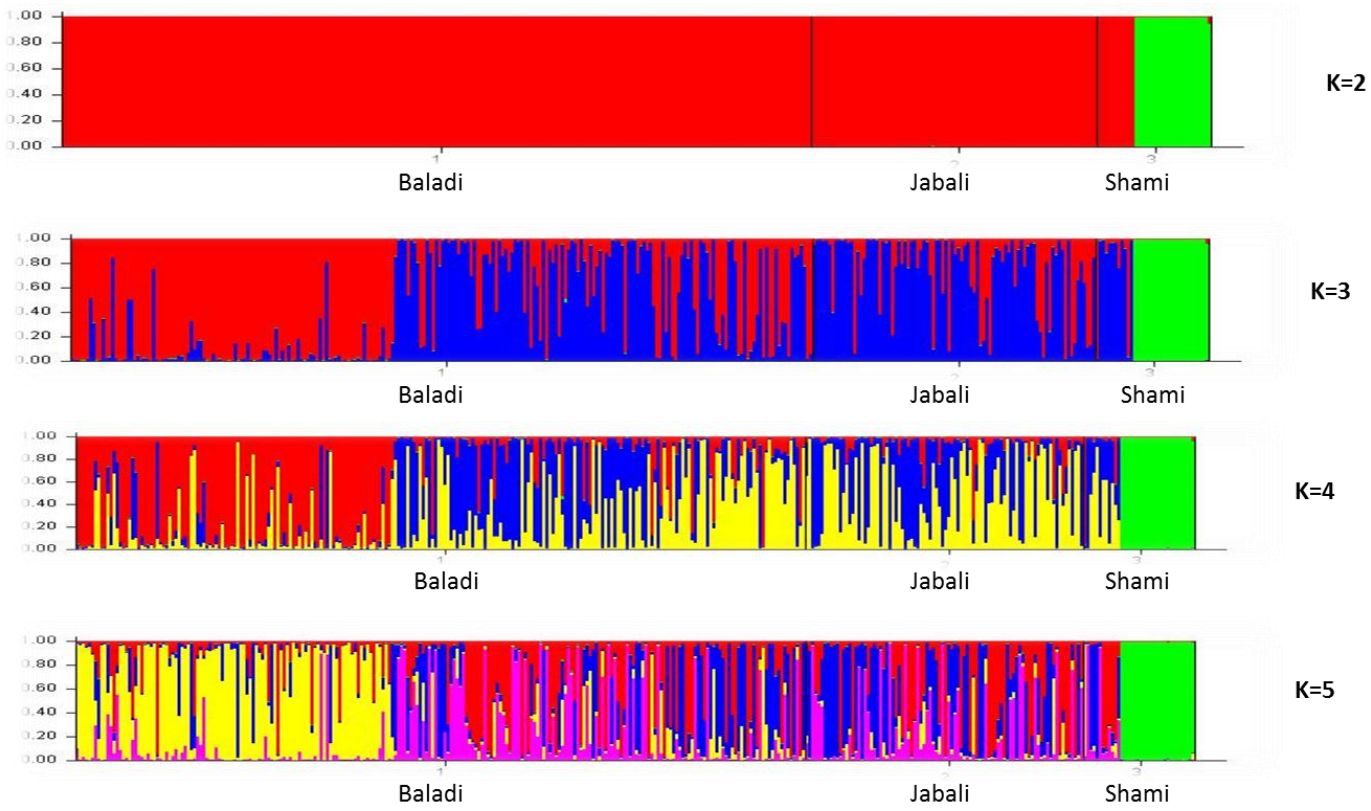

Figure 3. Depicts the clustering of all samples at k= 2, k=3, k= 4 and k=5, and each individual is represented by a vertical bar and partitioned into different colored segments with the length of each segment representing the proportion of the individual's genome, and populations are separated by backlines and each population is labeled.

inseparable subpopulation were also created. Hence, at K = 3, all three goat breeds appeared to have distinguishable admixture patterns, especially the Shami goat population was clearly separated from the rest of the Syrian goat populations at K= 2 to K= 5 with some levels of genetic dilution present with other Syrian goats. The Shami goat population had the least cases of genome admixtures, which is consistent with the phylogenetic tree constructed using the morphological data generated from the same goat populations (Figure 2a). This might be due to the fact that the Shami goats are raised mainly for milk and used as a milk-improver breed for crossing with other goat breeds in Syria and beyond (for example, in Cyprus). This might be due to the fact that the Shami goat owners might not erode and dilute the genetic identity of this goat breed by crossing with other goats breeds kept in a flock, which actually needs further investigation. The admixture plot at K = 3 could best describe the Syrian goat structure in which the three indigenous goat populations were represented by three predominating colors and distinct admixture patterns. These results suggest that Syrian indigenous goat breeds may descend from the same ancestor(s).

Further, to elucidate the relationships between the Syrian goat populations and provide finer quantification of the different ancestral contributions, STRUCTURE HARVESTER analysis was conducted by evaluating replicate likelihoods and resultant ΔK statistics for different values of K (K= 1 to 15). The Ln (K) values increased from K= 1 to K=2, and somewhat less quickly from K= 2 to K= 3, before reaching a plateau at successive values (Figure S2a). The largest value of ΔK occurred for K= 2 (ΔK = 488.67) and, secondarily, for K= 3 (ΔK =85.26) (Figure S2b).

Conclusion

This paper describes the first attempt to compare the morphological and molecular genetic variability of the Syrian indigenous goat populations. The Syrian goats were well differentiated into two major groups by their morphological appearances, genetic distance and population structure values, suggesting the genetic diversity of these groups. Phenotypically, the three goat breeds can be distinguished by their coat color, nature of their horn orientation and nose profile. It is remarkable that the Baladi (local) and Jabali (mountain) goats have higher genetic similarity both at morphological and molecular levels even though they have sub-grouped into

separate subpopulations. However, only the Shami goat population was structurally different and clustered into a separate group as a result of its high genetic distance compared to the other two goat breeds of Syria. The higher genetic variability in Shami goats may mean the presence of private or unique alleles suggesting the presence of certain functional genes which may result to better adaptability and performances. The results also reveal the presence of higher genetic variability within the goat population (96%) and such high variation within breed provides an excellent base for designing genetic improvement program.

Conflict of Interests

The authors have not declared any conflict of interests.

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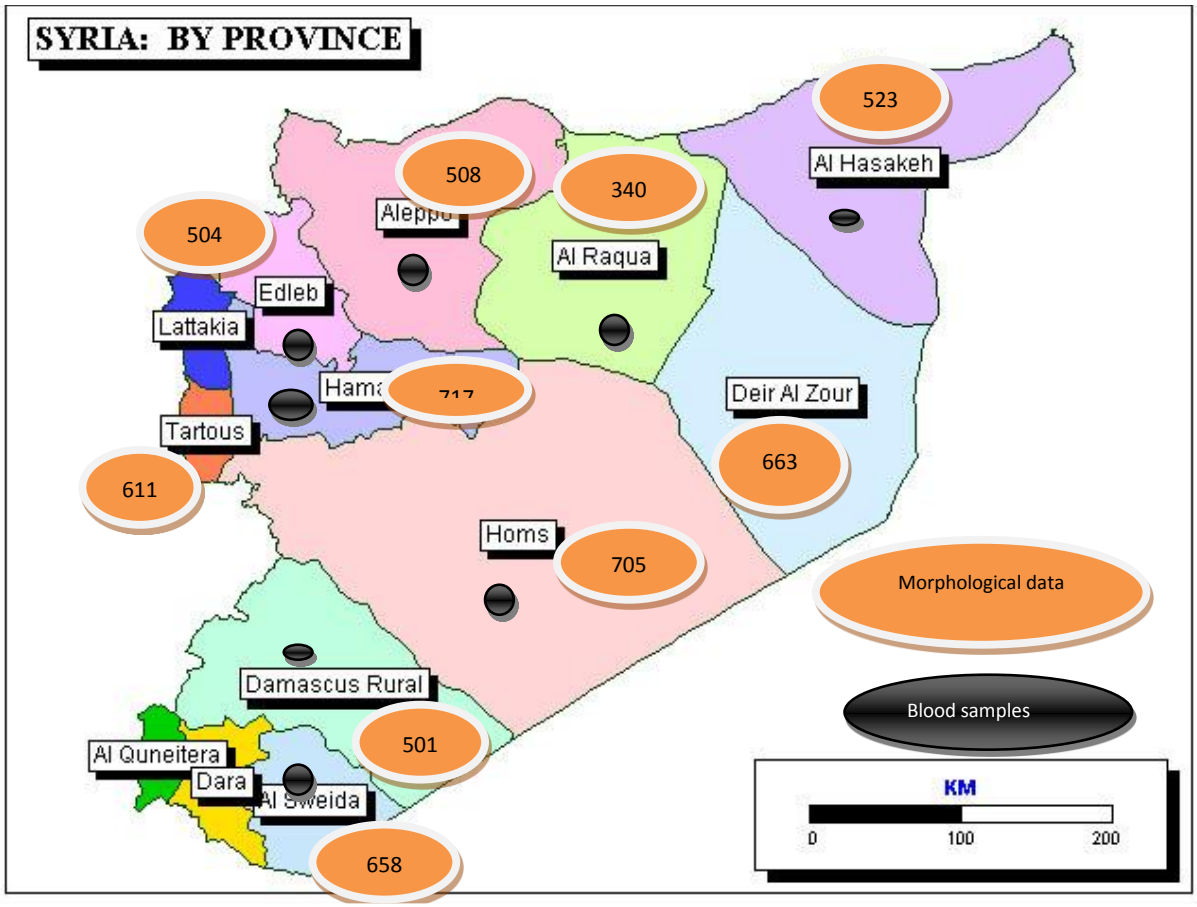

Figure S1. Map of Syria showing sampled provinces.

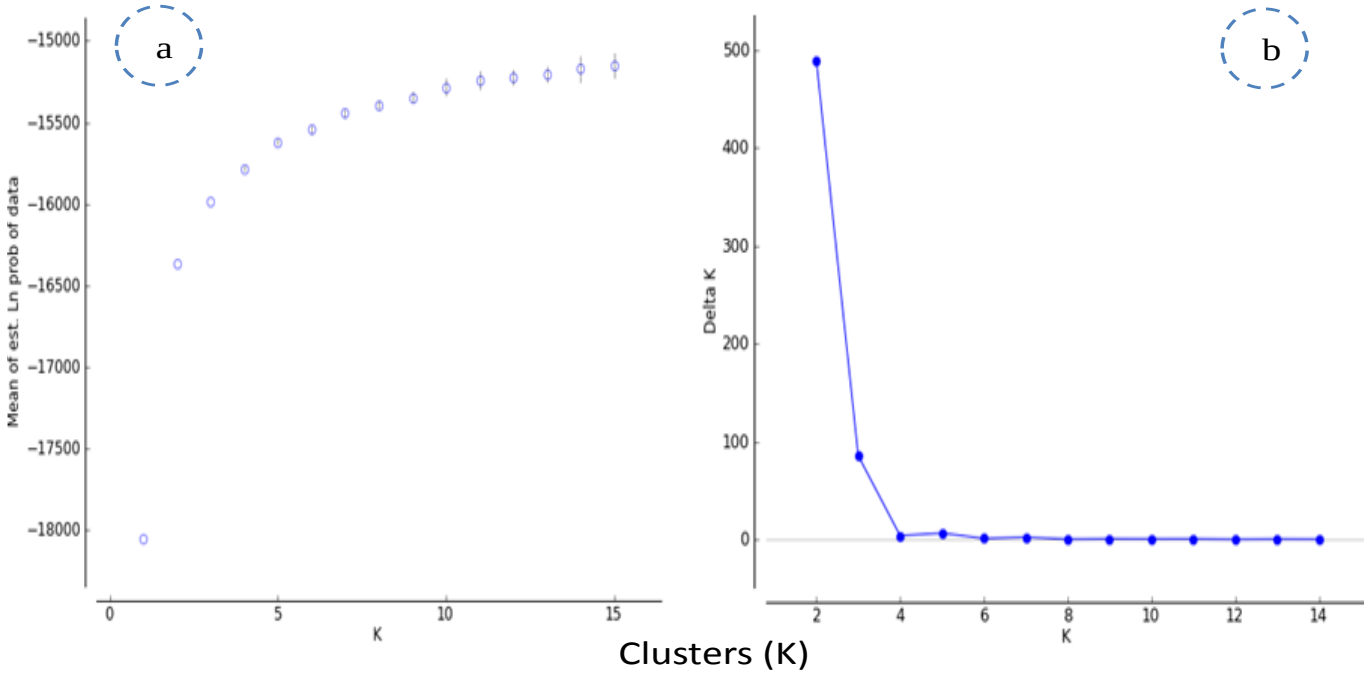

Figure S2 (a, b). Mean Log-likelihood (left-a) and ΔK (right-b) based on 10 replicated STRUCTURE runs for Syrian goat breeds.

Table S1. Analyzed mean number of alleles (MNA), effective number of alleles (Ne), Polymorphic Information Content (PIC), expected (He) and observed heterozygosity (Ho) values, Shannon diversity index (I), inbreeding coefficient (F_{IS}) and Hardy Weinberg equilibrium (HWE) p-values.

Locus	Baladi							Jabali							Shami						
	MNA	Ne	PIC	He	Ho	I	HWE	MNA	Ne	PIC	He	Ho	I	HWE	MNA	Ne	PIC	He	Ho	I	HWE
ILSTS044	10	3.16	0.65	0.69	0.30	1.41	0.000***	12	3.52	0.62	0.67	0.26	1.54	0.000***	12	6.46	0.82	0.84	0.56	2.14	0.000***
ILSTS087	18	5.46	0.8	0.82	0.61	2.02	0.000***	15	5.72	0.79	0.81	0.60	2.11	0.000***	13	7.38	0.84	0.86	0.39	2.26	0.000***
SRCRSP8	14	3.41	0.72	0.74	0.30	1.66	0.000***	10	2.88	0.53	0.56	0.20	1.53	0.000***	12	6.80	0.81	0.83	0.09	2.26	0.000***
ILST019	17	4.85	0.79	0.80	0.26	1.97	0.000***	10	4.70	0.74	0.76	0.19	1.87	0.000***	14	10.56	0.89	0.89	0.69	2.52	0.000***
OARFCB48	14	6.20	0.8	0.82	0.59	2.11	0.000***	13	5.00	0.81	0.83	0.63	1.90	0.003**	15	7.32	0.87	0.88	0.86	2.18	0.000***
ILSTS005	9	2.15	0.5	0.54	0.14	1.09	0.000***	7	2.52	0.5	0.58	0.19	1.09	0.000***	13	7.49	0.85	0.86	0.50	2.22	0.000***
BM6444	31	15.99	0.94	0.94	0.61	2.99	0.000***	26	18.08	0.92	0.93	0.69	3.05	0.000***	14	5.17	0.77	0.78	0.47	2.27	0.000***
ETH10	7	2.79	0.58	0.65	0.58	1.17	0.030*	7	2.93	0.57	0.64	0.72	1.22	0.948ns	8	4.77	0.76	0.79	0.46	1.80	0.000***
MAF209	8	2.85	0.63	0.67	0.58	1.34	0.000***	4	2.27	0.42	0.47	0.39	0.97	0.000***	7	4.32	0.73	0.77	0.76	1.62	0.000***
MAF70	21	7.92	0.86	0.87	0.73	2.36	0.000***	21	8.64	0.88	0.89	0.75	2.46	0.000***	28	18.65	0.94	0.94	0.86	3.16	0.000***
P19(DYA)	18	10.57	0.9	0.91	0.81	2.48	0.000***	15	6.93	0.85	0.86	0.80	2.20	0.001***	16	8.00	0.87	0.88	0.89	2.31	0.000***
SRCRSP9	17	10.51	0.89	0.90	0.67	2.47	0.000***	10	8.00	0.86	0.88	0.61	2.14	0.000***	17	7.54	0.87	0.88	0.89	2.34	0.000***
Mean	15.33	6.32	0.75	0.78	0.52	1.92		12.5	5.93	0.71	0.74	0.50	1.84		14.08	7.87	0.83	0.85	0.62	2.26	

ns = not significant, *p < 0.05, **p < 0.01, ***p < 0.001 did not adhere to HWE.

Table S2. Analysis of molecular variance (AMOVA) for Syrian goat populations using genotyped data from twelve microsatellite markers.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Explained variation (%)
Among populations	2	90.452	0.212	4
Among individuals within populations	359	2347.857	1.763	35
Within individuals	362	1091.000	3.014	61
Total	723	3529.309	4.989	