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Article

Genetic diversity and structure in Criolla Negra goats in Queretaro, Mexico.

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Abstract:

Since their introduction to Mexico goats have undergone a long process of adaptation and selection, resulting in highly rustic local animals. However, importation of improved breeds has led to the extinction of some regional breeds. For example, the Criolla Negra goat breed is known for its rusticity and high milk quality, but is in decline. A genetic characterization was done of a Criolla Negra population. Hair samples were collected in three goat herds located in different municipalities of the state of Querétaro, Mexico: Cadereyta de Montes (n= 7); El Marqués (n= 11); and San Juan del Río (n= 27). Thirty microsatellites were used to quantify the number of alleles per marker (NA), median number of alleles (MNA), number of effective alleles (NEA), observed heterozygosis (H_o), expected heterozygosis (H_e), polymorphic data content (PDC), the fixation index (F_{IS}) and Hardy Weinberg equilibrium (HWE). The Criolla Negra population was compared to thirteen breeds forming part of the BioGoat project. Genetic diversity was found to be high in this population. A total of 243 alleles were identified with an MNA of 8.1 alleles per marker. The markers were informative (PDC= 0.06) for polymorphism. The H_e (0.71) and H_o (0.62) values indicate a slight imbalance in the population. Reynolds genetic distance results showed the Criolla Negra breed to be genetically furthest from the Anglonubia breed and nearest the Murciano-Granadina breed. The studied Criolla Negra goat population exhibits a breed structure well differentiated from the other breeds in the analysis.

Key words: Genetic characterization, population genetics, Criolla Negra goats.

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Introduction

Goats have closely coexisted with human beings since their domestication began approximately 10,000 years ago[1,2]. One of the first domesticated livestock species, goats formed part of the Neolithic agricultural revolution, development of trade and human migrations[3]. All these events involved some basic evolutionary mechanisms, such as animal migration, selection, gene drift and even mutation. This helps in explaining goats' high capacity for adaptation to different ecosystems and the more than 300 breeds currently in existence[1,4].

First brought to the Americas in 1493, goats were initially propagated by the Spanish although native peoples also learned how to manage them and select for certain traits. New breeds, known as Creoles, consequently arose over time as selection aimed to better adapt them to local environmental conditions[5].

There are currently over 8.7 million goats in Mexico[6]. As in other developing countries goats represent a subsistence resource for people living in arid and semi-arid areas with scarce vegetation and poor rangeland[7,8]. Goats can be found throughout Mexico but are far more common in three main regions: the Mixtec mosaic; central Mexico (El Bajio); and northern Mexico (El Lagunero)[9]. The Criolla Negra (CN) breed is found primarily in the central region, particularly in the states of Querétaro and Guanajuato. Used mostly for dairy production, milk from this breed contains higher total solids content than other goat breeds in Mexico and provides excellent cheese yield[10,11,12]. Long considered a Granadina breed based on its morphological characteristics and origin, over 500 yr of independent evolution have genetically differentiated it from this breed. No studies have been done on the genetic status of the CN breed. This is important because improved goat breeds are increasingly being imported into Mexico and are used in indiscriminate crosses, threatening the CN breed's genetic health[13].

The evaluation of genetic diversity within and between breeds helps to understand a population's genetic structure, and to establish strategies for conservation, genetic improvement and sustainable use of genetic resources[14]. Microsatellite molecular markers are useful in genetic characterization studies within and between populations. They provide genetic codominance, abundance, random distribution across the genome, high reproducibility, neutrality with respect to selection and high levels of polymorphism[14,15]. Numerous genetic diversity studies have been done recently on several cattle species using microsatellite markers and they have become the genetic markers of choice for molecular applications such as genetic diversity[16,17], population structure[18,19], phylogeny[20], paternity evaluation[21], etc. The present study objective was to evaluate genetic diversity and population structure of Criolla Negra goats using microsatellite markers.

Material and methods

Biological samples

Hair samples were collected from 45 individual goats distributed in three herds in three municipalities of the state of Querétaro, Mexico: Cadereyta de Montes (n= 7); El Marqués (n= 11); and San Juan del Río (n= 27). Samples were collected following the non-

probabilistic opportunity method. Inclusion criteria were animals must not be related, they must be older than one year of age, have a black coat and erect or semi-lopped ears. Because genealogical data is unavailable for these populations kinship data provided by the producers was utilized.

The analysis included data for 25 microsatellites from 455 individuals from 13 goat populations: Retinta; Verata; Blanca Serrana; Celtibérica; Malagueña; Murciano-Granadina; Florida; Payoya; Serrana; Formentera; Saanen; Alpina; and Anglonubia. All populations form part of the Biodiversidad Caprina Iberoamericana (BioGoat) project[22].

Molecular analysis

Extraction of DNA was done from the hair samples using a chelating resin (Chelex® 100, Bio-Rad Laboratories, Inc. USA)[23]. Thirty microsatellites recommended by the mixed ISAG/FAO committee for analysis of genetic diversity in domestic animals were used[14]. Of these, 25 were found to be held in common among the thirteen BioGoat populations. Marker amplification was done by polymerase chain reaction (PCR) using florescent primers[24]. The amplicons produced with the PCR were separated by capillary electrophoresis (ABI PRISM 3130 Genetic Analyzer, Applied Biosystems) following manufacturer instructions. Allele size was quantified with an internal size standard (GeneScan-400HD ROX, Applied Biosystems), and genotypes were identified with the GENOTYPER 2.5.1. software. Reference samples were included in each sample to confirm the results.

Statistical analysis

The total number of alleles per marker (NA) was determined by direct counts, while the median number of alleles (MNA) was calculated as the sum of all NA data divided by the number of makers used (n= 30). Observed heterozygosis (H_o) was calculated by dividing the number of individual heterozygotes in each marker by the number of individuals positive for each marker. Expected heterozygosis (H_e) was estimated with Nei's formula[25]. Polymorphic data content, an indicator of marker quality[26], was estimated using the MICROSATELLITE TOOLKIT complement for Microsoft Excel 2010[27]. The number of effective alleles (NEA), which is the number of alleles able to pass to the following generation[28], was generated with the POPGENE v. 1.32. software. The exact

test of Hardy-Weinberg equilibrium (HWE), which considers heterozygote deficit, was calculated with the GENEPOP v.4.2 software[29], using the thirty markers for the CN and the Markov chain method (5,000 dememorizations; 100 lots; 10,000 interactions per lot).

A 95%[25,30] confidence interval was used when calculating endogamy coefficients for individuals versus subpopulations (F_{IS}), individuals versus total population (F_{IT}), and subpopulations versus total populations (F_{ST}), as well as the genetic differentiation coefficient (G_{ST}). All were generated with the GENETIX v. 4.05 software[31].

A matrix for Reynolds genetic distance[32], the minimum normalized Nei distance with a heterozygosis value in the founding population, was calculated with the POPULATIONS v.1.2.28 software. Split Graphs were then generated with the "NeighborNet" algorithm in the SPLITSTREE4 program[33].

Genetic structure origin of the populations included in the study was analyzed with cluster (K) techniques, which represent the number of populations. These use a Bayesian algorithm employing a model based on the Montecarlo Markov Chains (MCMC) method, which estimates the *a posteriori* distribution of each mix coefficient for each individual. This was done with the STRUCTURE v.2.3.4 software[34]. The MCMC burn-in was 50,000 iterations and 200,000 repetitions, and results were viewed with the DISTRUCT program[35]. Optimum K was estimated by fixing values of K2 to K15 and running the analysis with fifteen repetitions for each K value, following the method of Evanno[36] and using the STRUCTURE HARVESTER program[37].

Results

Genetic variation in Criolla Negra population

A total of 243 alleles were identified with the thirty markers used in the analyses. Median number of alleles (MNA) was 8.1 per locus in this population (Table 1). The highest NA (13) was observed for markers MM12 and SRCRSP23, followed by BM6526 and HSC with twelve alleles. The lowest NA (2) was observed in MAF209. The HSC marker had the highest NEA (9.14) while MAF209 had the lowest (1.25). This may have occurred due to the proportion of polymorphic markers, the number of alleles per marker and their frequencies, and sample size. Average population H_e was 0.71, but varied from 0.20 in MAF209 to 0.90 in HSC. Average H_o was 0.62, and ranged from 0.18 in MAF209 to 0.93 in HSC.

Average PDC in the CN population was 0.66. The least informative marker (PDC<0.25) was MAF209 (PDC= 0.18), followed by ETH225 (PDC= 0.26) and SPS115 (PDC= 0. 44). The remaining 27 markers were the most informative (CIP >0.5). Fourteen of the thirty tested microsatellites exhibited significant deviation for the HWE ($P \leq 0.05$).

Table 1: Analyzed microsatellites, number of alleles detected (NA), number of effective alleles (NEA), expected heterozygosis (H_e), observed heterozygosis (H_o), polymorphic data content (PDC) and Hardy-Weinberg equilibrium (HWE) deviations

Microsatellites	NA	NEA	H_e	H_o	PDC	HWE (*P*)
BM1329	8	3.44	0.72	0.67	0.68	0.20
BM1818	8	4.63	0.79	0.71	0.76	0.12
BM6506	9	3.26	0.70	0.55	0.66	0.02
BM6526	12	4.93	0.81	0.86	0.78	0.90
BM8125	6	3.64	0.73	0.62	0.68	0.02
CRSM60	8	4.32	0.78	0.71	0.73	0.03
CSRD247	6	3.25	0.70	0.77	0.66	0.97
CSSM66	11	7.06	0.87	0.34	0.84	0.00
ETH010	4	2.69	0.63	0.56	0.56	0.19
ETH225	4	1.41	0.29	0.25	0.26	0.22
HAUT27	8	4.11	0.77	0.71	0.72	0.28
HSC	12	9.14	0.90	0.93	0.88	0.31
ILSTS011	6	2.87	0.66	0.59	0.59	0.33
INRA063	5	2.46	0.60	0.64	0.51	0.72
MAF065	11	5.78	0.84	0.87	0.81	0.24
MAF209	2	1.25	0.20	0.18	0.18	0.43
McM527	8	5.33	0.82	0.82	0.79	0.58
MM12	13	7.00	0.87	0.75	0.84	0.03
OarFCB011	10	5.73	0.83	0.75	0.80	0.12
OarFCB048	10	7.14	0.87	0.78	0.84	0.01
OarFCB304	10	3.72	0.74	0.61	0.69	0.00
SPS115	3	2.02	0.51	0.27	0.44	0.00
SRCRSP08	10	3.76	0.74	0.70	0.69	0.23
TGLA122	8	2.20	0.55	0.49	0.52	0.02
SRCRSP05	7	3.09	0.68	0.59	0.63	0.05
SRCRSP23	13	8.49	0.89	0.68	0.87	0.00
SRCRSP24	10	3.59	0.73	0.56	0.69	0.00
ILSTS019	6	2.27	0.57	0.51	0.53	0.04
INRA005	5	2.23	0.56	0.45	0.51	0.03
INRA006	10	5.29	0.82	0.77	0.79	0.18
Average	8.1	4.20	0.71	0.62	0.66	

P>0.05= Not significant

Interpopulation genetic differentiation

The endogamy coefficients (F_{IS}, F_{IT} and F_{ST}) and G_{ST} were estimated for each of the 25 microsatellites shared between the CN and the thirteen breeds included in BioGoat[22]

(Table 2). Average F_{IS} was 0.067. Negative values for the markers BM8125 (-0.002) and MAF209 (-0.006) indicate these heterozygotes were present in excess[18,19]. Of the 25 markers eleven had a F_{IS} greater than 0.05. Values for G_{ST} generally followed a similar trend to those for F_{ST}. The marker with the highest G_{ST} value was BM6526 (0.114) while the lowest was MAF209 (0.037).

Table 2: Genetic differentiation coefficient and endogamy coefficients for each microsatellite compared between the Criolla Negra breed and breeds in BioGoat (Retinta, Verata, Blanca Serrana, Celtibérica, Malagueña, Murciano-Granadina, Florida, Payoya, Serrana, Formentera, Saanen, Alpina and Anglonubia)

Microsatellite	G_{ST}	F_{IS}	F_{IT}	F_{ST}
BM1329	0.081	0.024	0.078	0.056
BM1818	0.077	0.024	0.085	0.062
BM6506	0.074	0.044	0.094	0.053
BM6526	0.114	0.045	0.111	0.069
BM8125	0.076	-0.002	0.065	0.067
CRSM60	0.041	0.064	0.091	0.029
CSRD247	0.082	0.026	0.095	0.071
CSSM66	0.083	0.271	0.316	0.062
ETH010	0.058	0.032	0.076	0.047
ETH225	0.057	0.015	0.058	0.044
HSC	0.068	0.095	0.141	0.050
ILSTS011	0.058	0.068	0.114	0.049
INRA063	0.051	0.164	0.195	0.038
MAF065	0.073	0.025	0.084	0.060
MAF209	0.037	-0.006	0.018	0.024
McM527	0.081	0.087	0.151	0.070
MM12	0.060	0.059	0.098	0.042
OarFCB011	0.084	0.065	0.134	0.073
OarFCB048	0.060	0.058	0.103	0.049
SPS115	0.097	0.187	0.257	0.086
SRCRSP08	0.106	0.049	0.143	0.099
TGLA122	0.091	0.070	0.146	0.082
Promedio	0.073	0.067	0.121	0.058

G_{ST}= genetic differentiation coefficient; F_{IS}= endogamy coefficient of individuals vs. subpopulations; F_{IT}= endogamy coefficient of individuals vs. total population; and F_{ST}= endogamy coefficient of subpopulations vs. total population.

Interpopulation genetic distance and its graphic representation

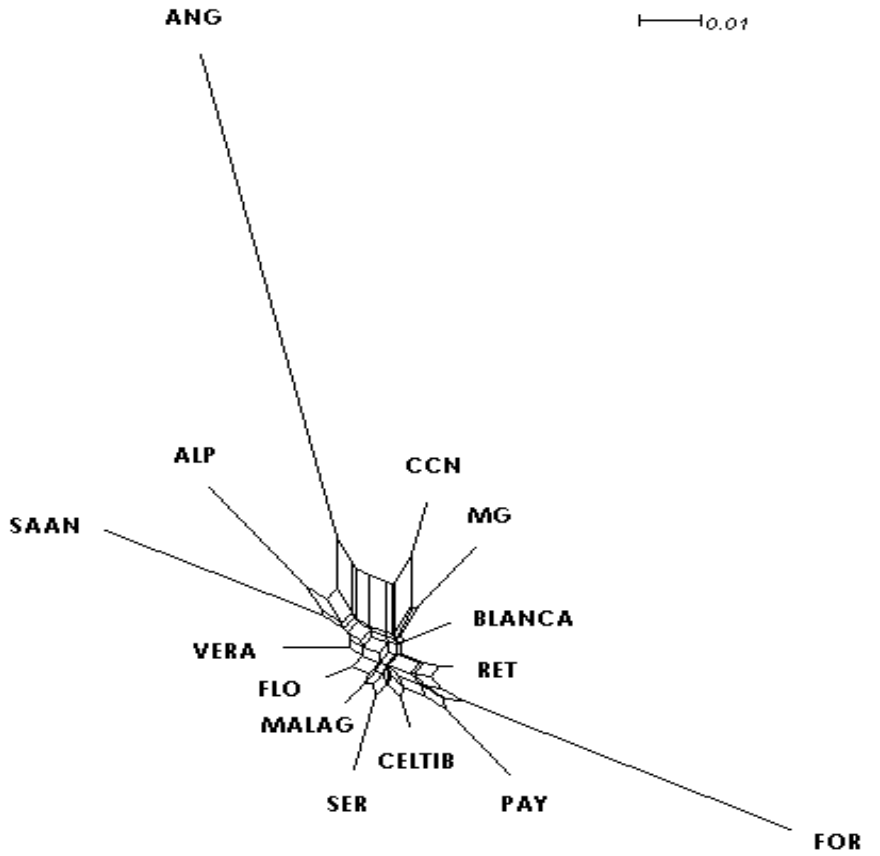
Genetic distance analysis between the fourteen compared breeds showed the shortest distance to be between the CN and Murciano-Granadina breeds (MG) (0.133), and the longest to be between CN and Anglonubia (ANG) (0.420) (Table 3). A neighbor-net dendrogram was built to assist in interpreting values in the genetic distance matrix (Figure 1).

Table 3: Reynolds genetic distance matrix between the fourteen studied goat breeds

	RET	VERA	BLANCA	CELTIB	MALAG	MG	FLO	PAY	SER	FOR	SAAN	ALP	ANG
VERA	0.025												
BLANCA	0.025	0.032											
CELTIB	0.025	0.036	0.027										
MALAG	0.021	0.025	0.023	0.021									
MG	0.044	0.045	0.031	0.034	0.041								
FLO	0.023	0.023	0.028	0.026	0.015	0.041							
PAY	0.034	0.044	0.047	0.036	0.046	0.061	0.038						
SER	0.034	0.038	0.035	0.028	0.024	0.048	0.027	0.045					
FOR	0.071	0.094	0.081	0.078	0.083	0.099	0.083	0.081	0.107				
SAAN	0.071	0.061	0.070	0.069	0.070	0.069	0.061	0.077	0.078	0.119			
ALP	0.063	0.056	0.052	0.062	0.055	0.076	0.049	0.064	0.073	0.119	0.071		
ANG	0.124	0.125	0.130	0.151	0.132	0.146	0.126	0.178	0.149	0.221	0.161	0.142	
CN	0.039	0.052	0.045	0.044	0.046	0.038	0.048	0.067	0.053	0.102	0.083	0.073	0.130

RET= Retinta, VERA= Verata, BLANCA= Blanca Serrana, CELTIB= Celtibérica, MALAG= Malagueña, MG= Murciano Granadina, FLO= Florida, PAY= Payoya, SER= Serrana, FOR= Formentera, SAAN= Saanen, ALP= Alpina, ANG= Anglonubia, CN= Criolla negra.

Figure 1: Neighbor-net dendrogram built using Reynolds genetic distance data for the fourteen studied goat breeds.

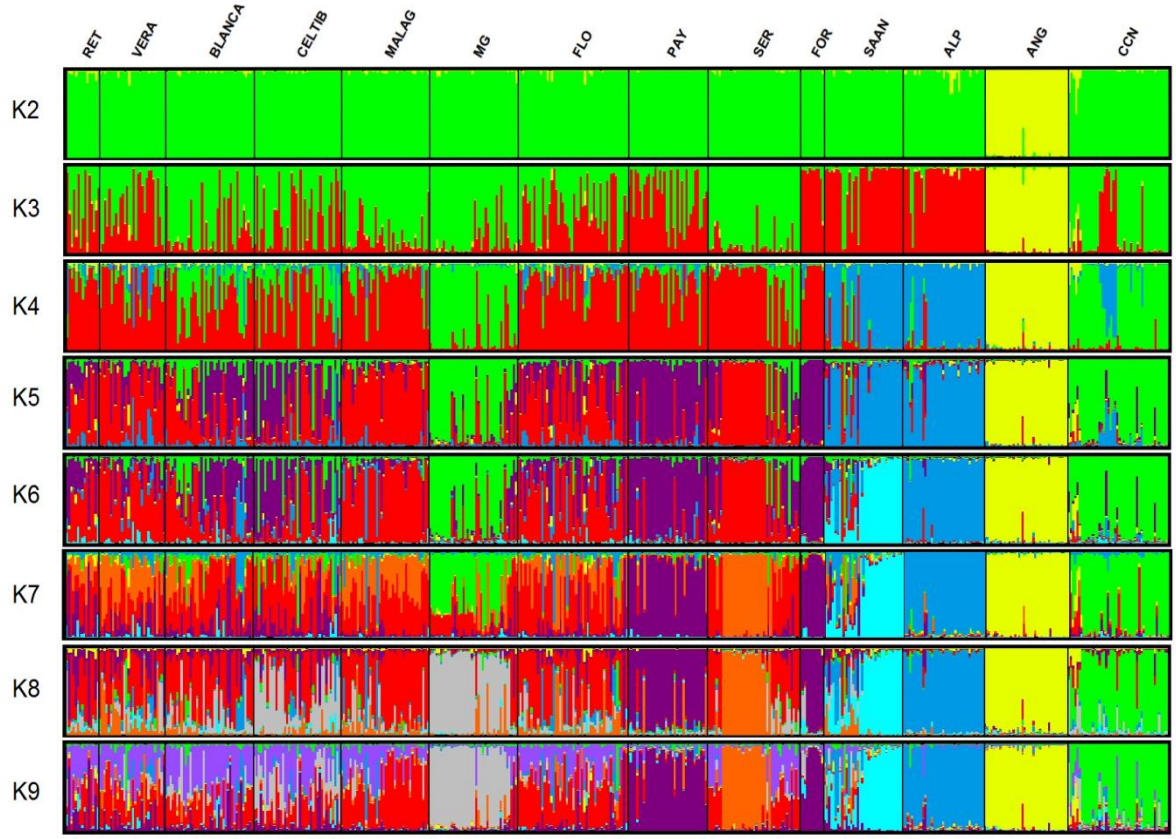


RET= Retinta, VERA= Verata, BLANCA= Blanca Serrana, CELTIB= Celtibérica, MALAG= Malagueña, MG= Murciano-Granadina, FLO= Florida, PAY= Payoya, SER= Serrana, FOR= Formentera, SAAN= Saanen, ALP= Alpina, ANG= Anglonubia, CCN= Criolla Negra.

Genetic structure analysis

Optimum K for the genetic structure of the studied populations was 9. When shown graphically (Figure 2), each individual is represented by a vertical line divided into color segments indicating to what extent the individual belongs to each group (K).

Figure 2: Graphic representation of genetic structure in the fourteen studied goat breeds, assuming an ancestral populations number ranging from 2 to 9



RET= Retinta, VERA= Verata, BLANCA= Blanca Serrana, CELTIB= Celtibérica, MALAG= Malagueña, MG= Murciano-Granadina, FLO= Florida, PAY= Payoya, SER= Serrana, FOR= Formentera, SAAN= Saanen, ALP= Alpina, ANG= Anglonubia, CCN= Cabra Criolla Negra.

Discussion

Genetic variation in Criolla Negra population

When running analyses with the microsatellites used in the present study it is recommended to have at least four alleles, and that the NEA be greater than two to be included in diversity studies and reduce standard error when estimating genetic distances[38]. Only two markers (MAF209 and SPS115) had 2 and 3 alleles in the present

results. Values for NEA were lower than two in the markers ETH225 (1.41) and MAF209 (1.25). This indicates how appropriate the markers were for genetic diversity evaluation of NA and NEA. The MNA value for the CN population (8.1) provided information on genetic diversity in this population. When MNA values are higher diversity is greater and vice versa. For the studied CN population MNA was high compared to other characterization studies done with breeds such as the Criollo Cubano[39]; Saudi goats[19]; cashmere goats in China[40,41], and some Iranian goat breeds[42]. However, the MNA values for CN were similar to those reported for dairy goats in South Africa[43]. Average PDC value for the markers used here was 0.66, which is similar to values reported for the Retinta Extremeña goat breed[44].

Heterozygosity values can also help to understand genetic diversity since they depend on allele number and relative frequency[45]. The average heterozygosis values in the present results (H_e = 0.71, H_o = 0.62) are very similar to those reported for the Blanca Andaluza[46] and Retinta Extremeña goat breeds[44], though the latter has a higher MNA than the CN. These H_e and H_o values indicate the presence of notable genetic variability in the CN considering that the population is shrinking in the studied area, which would be expected to promote marked consanguinity. The HWE test identified fourteen markers with significant deviations ($P \leq 0.05$), indicating there to be a heterozygous deficit. The fact that some of these markers behave homozygously may be due to actions such as management conditions (e.g. sire loan), low genetic flow in each flock, and markers that could be linked to productive traits due to production-focused selection of milk and weight gain traits regardless of kinship relations[47].

Interpopulation genetic differentiation

Estimated values for F_{IS} and F_{IT} vary from 1 to -1, with positive values indicating heterozygote deficiency and negative values an excess. The present results for both indices (F_{IS}= 0.067 and F_{IT}= 0.121) indicate that some of the markers were homozygous. Although the values were near zero, they indicate possible mating between genetic relatives, which is consistent with values reported for native goats in China[48], India[47], Spain and Portugal[24]. The F_{ST} indicated that 94.2% of the genetic variability in the studied breeds was due to differences between individuals within the breed and 5.8% due to genetic differences between breeds. This genetic differentiation coefficient (G_{ST} = 0.073) confirmed this result in that it showed 92.7% of variability of total genetic diversity to be intrabreed and 7.3% to be interbreed. The discrepancy between these indicators exists because F_{ST} reflects the properties of interpopulation allelic frequency distribution while G_{ST} is defined in terms of intrapopulation frequencies[49]. Both the F_{ST} and G_{ST}

values suggest that the level of genetic variation in the studied breeds has remained relatively constant. Percentages like those in the present study have been reported for other goat populations[17,42,50].

Interpopulation genetic distance and its graphic representation

The neighbor-net dendrogram showed that the Spanish goat breeds included in the study (Retinta, Verata, Blanca Serrana, Celtibérica, Malagueña, Murciano-Granadina, Florida, Payoya, Serrana and Formentera) remain grouped. Reported in previous studies[51], this effect is caused by the close genetic and geographical relationships between these breeds. The Saanen and Alpina breeds formed another group towards one end of the dendrogram. Of particular note is the Anglonubia breed's large genetic distance from the other studied breeds. These kinds of relationships have also been observed in a comparison between Brazilian goat breeds[52]. This effect can be attributed to a greater genetic distance between a breed when compared to others and not necessarily to origin or kinship relations. Another important factor in any goat population is that individuals within it have also been selected based on morphological characteristics. Estimates generated from the Reynolds genetic distance data showed the shortest distance (0.038) to be between the CN and MG breeds, suggesting a possible genetic relationship between them.

Genetic structure analysis

Genetic structure analysis was used to evaluate the degree of kinship between the different studied populations, using optimum K (K= 9) to identify interbreed differences. No crossings were found between CN and the other studied breeds. The ANG population separated from the others beginning at K2 and remained so thereafter. Apparently, this population is more genetically distant from the other populations, a phenomenon reported for the population structure of other Creole goats in the Americas[53]. The ANG population also preserved its genetic structure, having a low level of mixing of individuals from the other thirteen studied populations. Genetic structure in the Spanish breeds included in this study was more intermixed, similar to the results reported in a study on goat biodiversity[24]. Intermixing is often due to geographical proximity between

populations, which facilitates migration of individuals between populations. The genetic nearness of the CN breed to the MG breed confirm the supposed origin of the studied CN population. However, analysis using optimal K (K9) showed the CN population to have a totally different structure than the MG breed and the other studied breeds. This supports the distances shown in the neighbor-net dendrogram and suggests that the CN breed maintains a unique genetic structure that is differentiated from the populations that may have contributed to its origin.

Conclusions and implications

These are the first published data on genetic diversity and structure in a Criolla Negra goat population. The studied population has a certain degree of genetic diversity based on its level of polymorphism. The genetic distances between the Criolla Negra population and the other races included in the study indicate that this population is clearly differentiated from them and should thus be considered a distinct Mexican goat breed. The relatively short genetic distance between the Murciano-Granadina and Criolla Negra breeds suggests that both have a common ancestor, most probably the Granadina breed. The Criolla Negra goat has a defined breed structure and is differentiated from its possible precursor breeds. The Criolla Negra breed is the first breed of goat in central Mexico to be genetically described.

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