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Incidence of 1/29 translocation in Bolivian Creole and Brahman Yacumeño cattle

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Abstract

In Bolivia, four different Creole cattle breeds can be found, as well as other European and Zebu breeds adapted to local environments. The relationship between the occurrence of the 1/29 translocation and subfertility is well known, and analysis of Y chromosome morphology is useful to determine a possible introgression with *Bos indicus*. The incidence of the 1/29 translocation was analyzed in four Bolivian Creole cattle breeds and the Brahman Yacumeño population, as well as on four farms with phenotypical Creole-type cattle. In 259 (164 dams and 95 sires) Bolivian Creole cattle, 10.42% of the individuals demonstrated the 1/29 translocation, with a variation from 0 to 28.20% between the breeds. In contrast, 43 (19 dams and 24 sires) Yacumeño Brahman and the Creole-type cattle did not show the centric fusion. The highly significant differences between Creole cattle breeds in relation to the incidence of 1/29 translocation could be a consequence of factors such as founder group, genetic drift, and selection. The low frequency observed in the Saavedreño Creole dairy cattle might be explained by its breeding under a more intensive system, and selection according to milk yield and fertility traits. Finally, no relation between acrocentric Y chromosomes and 1/29 translocation was observed.

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1. Introduction

1.1. American Creole cattle

The first cattle were brought to America by Iberian conquerors in the 16th century [1]. The founding population of Creole cattle, introduced into America by the Spanish and Portuguese during the first 50 years of colonization, consisted of 300–1000 animals of Iberian origin [1,2]. In the course of a few years, these animals were taken to Central and Southern America, and to the southern of United States, and they spread over the South American continent. The Creole cattle were the only bovines bred in Latin America for more than 300 years until the introduction of selected European and Zebu breeds.

American Creole cattle evolved under wild and semiwild conditions low levels of breeding management and, as a result of natural selection, became adapted to different environments, such as tropical rainforest, subtropical dry forest, highland steppe, and Patagonian steppe. Furthermore, American Creole cattle exhibit a high degree of phenotypic variability (e.g. coat color), resistance to tropical disease and high level of fertility.

Today, almost all North, Central and South American countries have Creole cattle breeds. In Bolivia, four different Creole cattle breeds can be recognized and there exist other European and Zebu breeds adapted to local environments. The Brahman Yacumeño is a Zebu breed that adapted to the seasonal flood plain of the El Beni region during more than three decades of selection. The Yacumeño Creole breed is also found in this region of northern Bolivia. The breed population is approximately 1200 animals, raised primarily for beef. Bolivian Chaqueño Creole cattle are found in the southeast area of Bolivia, in a dry forest environment. The Altiplano Creole cattle are adapted to the highland plain of the west of Bolivia. Chaqueño and Altiplano Creole cattle breeds are also raised for beef and their populations are approximately 1200 and 200,000 animals, respectively. Saavedreño Creole cattle breed is found in the Santa Cruz Department, in a tropical plain and is raised primarily for dairy (population ~300 adults).

1.2. Robertsonian fusion in cattle

More than 25 centric fusions in cattle have been reported worldwide [3]. The 1/29 translocation was the first centric fusion reported, identified in Swedish Red and White cattle [4]. This translocation has been reported now in more than 50 breeds, including Spanish and American Creole breeds, and is the most frequent chromosomal aberration in cattle [5–12]. In contrast, other centric fusions are restricted to a few breeds in isolated geographic locations.

Nearly all centric fusions are present in the heterozygous condition. Like other centric fusions, this abnormality reduces fertility as a consequence of genetic excess or deficiency in the germ cells, increasing early embryonic mortality [13–16].

In the present work we analyze the incidence of the 1/29 translocation in four Bolivian Creole cattle breeds and the Brahman Yacumeño population, as well as in four populations of phenotypically Creole-type cattle housed on four farms. These results were evaluated taking into account parameters like the management type (including dairy and meat production, and levels of isolation), geographical region, historical origin, and sex. Furthermore, in order to study the relationship between Zebu introgression and incidence

Breed	Location	Cattle studied		No. of sires	
Saavedreño	Saavedra experimental station	97	51	46	
Yacumeño	Espíritu farm	64	46	18	
Chaqueño	Salvador experimental station	39	24	15	
Altiplano	Patacamaya experimental station	11	10	1	
Creole-like cattle	four private farms from east and southeast of Bolivia	48	33	15	
Brahman Yacumeño	Espíritu farm	43	19	24	
Total		302	183	119	

Table 1 Number of Bolivian Creole and Brahman Yacumeño cattle studied

of the 1/29 translocation, the Y chromosome morphology of 119 bulls belonging to these herds was analyzed.

2. Materials and methods

2.1. Cytogenetic analysis

Forty-eight Creole-like cattle (33 dams and 15 sires), corresponding to four private farms from east and southeast of Bolivia, were analyzed (Table 1). Furthermore, 211 (131 dams and 80 sires) Bolivian Creole cattle and 43 (19 dams and 24 sires) Brahman Yacumeño were studied (Table 2). All the animals were phenotypically normal. Eighty-seven (40 bulls and 47 dams) out of 97 analyzed Saavedreño Creole cattle included in the present study were previously studied by De Luca et al. [16]. Chromosomal preparations were made by conventional techniques as described in De Luca et al. [16]. Thirty metaphases per animal were scored to analyze the incidence of 1/29 translocation and Y chromosome morphology.

Table 2
Incidence of 1/29 translocation in Bolivian Creole and Creole-like cattle and Brahman Yacumeño cattle, located on the Saavedra, El Salvador and Patacamaya Experimental Stations (Saavedreño, Chaqueño, and Altiplano breeds respectively), Espíriru Farm (Yacumeño breed), four private farms (Creole-like cattle) and Espíritu farm (Brahman Yacumeño)

Breed	Cattle studied <i>n</i>	Carriers of 1/29 translocation	Sire carriers		Dam carriers		Gene
			n	%	n	%	frequencies
Saavedreño	97	1 (1.03%)	0	0	1	100	0.005
Yacumeño	64	13 (20.31%)	5	38.5	8	61.5	0.101
Chaqueño	39	11 (28.20%)	4	36.4	7	63.6	0.141
Altiplano	11	2 (18.18%)	0	0	2	100	0.090
Creole-like cattle	48	0 (0%)	0	0	0	0	0.000
Brahman Yacumeño	43	0 (0%)	0	0	0	0	0.000
Total	302	27 (8.91%)	9	33.33	18	66.66	

2.2. Population genetic analysis

Gene considered as the number of 1/29 chromosomes and genotype considered as the number of carrier animals frequencies within each population were studied in the entire Creole sample and calculated by direct count.

Hardy–Weinberg equilibrium H–W of the 1/29 translocation within population was estimated through an exact test, taking into account three different H₁ hypothesis (heterozygote deficit, heterozygote excess, or both). The *P*-value estimation of exact test was performed through the Markov Chain method proposed by Gou and Thompson [17]. Hardy–Weinberg equilibrium in the entire Creole sample was tested using the chi-square Fisher's method.

Population differentiation and genetic structure analysis for the studied translocation was evaluated through Fisher's exact test as described by Raymond and Rousset [18]. Gene differentiation between regions was evaluated through the analysis of pairwise $F_{\rm ST}$ parameters, using a weighted analysis of variance [19,20]. In these analyses, only the four pure Bolivian Creole cattle breed populations Saavedra, Chaqueño, Yacumeño, and Altiplano were included due to the fact that these populations belong to different geographical regions, historical origins and management types. These estimations were performed using Genepop [18] and Arlequin [21] programs.

Finally, the incidence of 1/29 translocation was evaluated taking into account the sex of the animals and the percentage of acrocentric Y chromosomes Zebu gene introgression in studied populations. Differences in the incidence of 1/29 translocation between sexes within each population as well as a global sample were analyzed through chi-square analysis.

3. Results

The cytogenetic analysis showed that 10.42% (27 of 259) of studied Creole cattle contained the 1/29 translocation, giving a gene frequency of 0.052 for the 1/29 chromosome. These values varied from 0 to 28.20 and 0.00 to 0.141% between Creole cattle populations (Table 2). All studied animals exhibited the translocation in heterozygous condition 2n = 59. In contrast, the Yacumeño Brahman population and Creole-like cattle did not show the centric fusion.

The $F_{\rm IS}$ showed that the 1/29 translocation was in H–W equilibrium within each population, as well as in the entire Creole cattle sample ($-0.162 < F_{\rm IS} < -0.053$, P > 0.952). Furthermore, when excess or deficit of heterozygous animals was considered, non-significant differences were observed in the populations studied ($P_{\rm excess} > 0.43$; $P_{\rm deficit} = 1$).

The Genetic Differentiation test between analyzed populations for the 1/29 translocation showed a highly significant degree of subdivision in the Bolivian Creole cattle (P = 0.000). This result was confirmed by the $F_{\rm ST}$ index ($F_{\rm ST} = 0.0678$, P = 0.00098). In accordance with this data, when the sources of variation for the 1/29 translocation were studied, the ANOVA test showed that the variation among and within populations accounted for 6.78 and 93.22% of the total variability, respectively. Gene differentiation between pairs of

Table 3
Incidence of Y chromosome morphology in Creole and Creole-like cattle and Brahman Yacumeño cattle, located on the Saavedra, El Salvador and Patacamaya Experimental Stations (Saavedreño, Chaqueño and Altiplano breeds respectively), Espíriru Farm (Yacumeño breed), four private farms (Creole-like cattle) and Espíritu farm (Brahman Yacumeño)

Breed	Bulls studied	Acrocentric Y chromosome		Submetacentric Y chromosome	
		\overline{n}	%	\overline{n}	%
Saavedreño	46	10	21.73	36	78.27
Yacumeño	18	3	16.66	15	83.34
Chaqueño	15	4	26.66	11	73.34
Altiplano	1	0	0	1	100
Creole-like cattle	15	3	20	12	80
Total	95	20	21.05	75	78.95
Brahman Yacumeño	24	24	100	0	0

populations corresponding to different regions showed that the pairwise $F_{\rm ST}$ value ranged from 0.003 to 0.203. However, only the Saavedra population exhibited significant differences (P < 0.035), while Yacumeño, El Salvador (Chaqueño breed) and Patacamaya (Altiplano breed) populations did not show significant gene differentiation (0.471 < P < 0.699).

Comparison between the percentage of 1/29 translocations obtained in males and females did not show significant differences between sex within population and in the entire sample ($\chi^2 \le 0.862$, $P \ge 0.99$).

Results of Y chromosome cytogenetic analysis are summarized in Table 3. Both types of Y chromosome morphology (acrocentric and submetacentric) were found in the Creole bulls, whereas, as was expected, only acrocentric Y chromosome was detected in Brahman Yacumeño bulls. Finally, the percentage of acrocentric Y chromosome (Zebu gene introgression) in the populations was compared with the incidence of 1/29 translocation. This comparison did not indicate a relation between the two characteristics.

4. Discussion

In the present work, the incidence of 1/29 translocation in four Bolivian Creole cattle breeds, in Creole-like cattle and in the Brahman Yacumeño was analyzed. The results obtained showed the presence of 1/29 translocation in the Bolivian Creole cattle, with an average frequency of 10.42%, as well as its absence in the Brahman Yacumeño. Furthermore, our results did not show the presence of 1/29 translocation in the Creole-like cattle populations.

This translocation has been studied in several breeds from all continents, being reported in more than 50 breeds [23]. However, the incidence of this translocation varied significantly according to bovine breeds and groups of breeds. High frequency has been reported in Portuguese and Spanish breeds, in British White cattle, in Swedish Red and White cattle, in Italian breeds, in Continental breeds and in *Bos taurus* from Africa and

Asia cattle breeds [6,13,24–28]. In contrast, it has been well documented that most British beef breeds, Holstein–Friesian, Jersey, Normandy, and Zebu cattle breeds do not show the translocation [28,29].

The absence of the 1/29 translocation in the Brahman Yacumeño cattle is in agreement with data reported in other *Bos indicus* breeds, like Nelore cattle. On the other hand, the results obtained in the four Bolivian Creole cattle breeds are in agreement with those obtained in several American Creole cattle breeds, such as the Venezuelan, Uruguayan, Cuban and Saavedreño Creole [11,12,16,30]. As such, the Argentine Creole cattle seem to be an exception within the American Creole cattle population [31,32].

Spanish and Portuguese breeds exhibit one of the highest frequency reported for the centric fusion [6,7,9,27]. This suggests that the widespread distribution of 1/29 translocation in American Creole cattle might be explained through their Iberian origin. Considering that several authors proposed an ancient origin of this centric fusion on the basis of its worldwide distribution and its monocentric condition [23,28], the 1/29 translocation could have been introduced into the Americas five centuries ago when the Spanish and Portuguese conquerors brought the first cattle into the continent. This is a clear example of how the spreading of centric fusion can result from the introduction of carrier animals.

The incidence of the 1/29 translocation within four Bolivian Creole cattle breeds was evaluated taking into account parameters like the management type (including dairy and meat production, and level of isolation), geographical region, historical origin, sex and rate of Zebu introgression. Comparison between the observed frequencies in males and females within populations, and in the whole sample, did not show significant differences. These results are in agreement with data reported in several cattle breeds [9,33].

When the incidence of 1/29 translocation among studied Creole cattle breeds was compared through Fisher's exact and $F_{\rm ST}$ tests, significant differences were found. The genetic differentiation in the incidence of 1/29 translocation between Creole populations could be a consequence of factors like founder group, genetic drift, gene introgression, natural and artificial selection, and husbandry type. In addition, the failure to find evidence of 1/29 translocation carriers in the Creole-like cattle sample studied suggests that these breeds probably differ from the analyzed Creole cattle breeds.

The first factor considered here is gene introgression. The Zebu origin of the acrocentric Y chromosome in Bolivian Creole cattle was confirmed through molecular analysis by Giovambattista et al. [22]. Taking into account that Zebu breeds did not show the 1/29 translocation, it was expected that introgression of Zebu gene into the Creole cattle population could result in a dilution of the frequency of centric fusion. The genetic dilution could be stronger as the rate of mixing increased. However, our results did not support this hypothesis because an inverse relation between variables was not found. For example, the Chaqueño breed exhibited the highest frequency for the 1/29 translocation and Y acrocentric chromosome.

The observed genetic differentiation could be produced by other factors like management and artificial and natural selection. Surprisingly, the estimated pairwise $F_{\rm ST}$ values showed that only the Saavedreño population exhibited significant differences, while Yacumeño, Chaqueño and Altiplano populations did not show significant gene differentiation. The Saavedreño population has been bred under an intensive system and has, for more than 30 years, been selected to become a double-purpose tropical breed for both milk

yield and fertility traits. In addition, pedigree data are registered and artificial insemination is usually used in this breed. In contrast, Yacumeño, Chaqueño and Altiplano populations are bred for beef production using extensive management, and a group of bulls is mated in natural service with relatively large groups of cows. Carrier animals are phenotypically normal, and no physical traits, except fertility reduction of approximately $\approx 4\%$ [13], have yet been associated with the 1/29 translocation. However, identification of this reduction would be difficult or impossible for breeders. For this reason, breeders cannot select animals according to their fertility.

Despite the fact that carrier animals exhibit a fertility reduction, this abnormality is present in high frequency in many breeds, including three of the four studied Bolivian Creole cattle breeds. Rangel-Figueiredo and Iannuzzi [9] postulated that it is reasonable to suppose that this centric fusion is maintained in populations because carrier animals are phenotypically superior to karyologically normal ones. Unfortunately, there is no data that evaluates the fertility rate, production and fitness performance of carriers in relation to normal animals in the populations studied.

The eight studied populations, (four Bolivian Creole cattle breeds and the Creole-like cattle from four farms), are of small size and exhibit a high degree of geographical isolation. For this reason, we cannot eliminate the effect of founder groups, genetic drift and inbreeding as factors influencing the incidence of the 1/29 translocation. In support of this, reports from several countries indicate that spreading of centric fusion can result from the introduction of carrier animals [34–36]. Moreover, several authors proposed that the high incidence of 1/29 translocation in some breeds could be accounted for the high inbreeding coefficient originating from a reduced effective population size [9].

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