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Genetic and productive background of Criollo cattle in Argentina, Mexico, Uruguay and the United States

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ABSTRACT

Cattle were first introduced to the Western Hemisphere in 1493 and by subsequent introductions from the Iberian Peninsula, providing the genetic background of the American Criollo cattle, with influences from Spanish, Portuguese and African breeds. Criollo's high adaptive capacity enabled them to spread and colonize a wide variety of environments. Their ancestry combined with local adaptations created the wide spectrum of American Criollo breeds that we see today, many currently at risk of extinction. We review the existing genetic and production data on the Argentinian, Mexican, Uruguayan and US Creole cattle that form the basis of the current and future research described in this special issue. In these countries, Criollo cattle became the basis of the livestock industry for the supply of meat, hides and animal work, until they were displaced by more specialized European and cebuine type cattle breeds at the end of the 19th century. Since then, Criollo herds remained mostly in marginal regions unsuitable for commercial breeds. Efforts by local producers and research institutions helped to preserve Criollo populations. Several studies have demonstrated that these animals can produce high quality meat and are more resistant to diseases, and emphasize their high fertility, calving ease, longevity and ability to adapt to harsh environments. Mexican Criollos have high genetic diversity but lack strong conservation programs. More detailed genetic characterization within each regional Criollo population is needed to establish appropriate conservation strategies. In US, Texas Longhorn cattle are closely related to Mexican Criollos, while Pineywoods show a stronger relationship with Iberian breeds. Variable levels of genetic diversity were found among all North American Criollos, probably due to crossbreeding. Criollos from Argentina and Uruguay showed clear divergence due to genetic isolation but clustered together, representing the southernmost expansion of bovine cattle in the Americas.

1. Introduction

Cattle were first introduced to the Western Hemisphere in 1493, during the second voyage of Christopher Columbus, and by subsequent introductions from the Iberian Peninsula to the island known as La Española (Haiti and Dominican Republic). Most of these animals came from Andalusia and were representatives of the bovine breeds and types found at that time in Southern Spain. Many came also from the Canary Islands, as these islands were a usual stop for ships traveling from Europe to the New World (Fig. 1). In 1534, the Portuguese also started to introduce their own cattle to the territories of Brazil from Portugal and the islands of Cape Verde (Primo, 1992). These original introductions provided the genetic background of the American Criollo cattle, with influences from Spanish, Portuguese and African breeds. Several studies using different types of genetic markers have revealed this mixed ancestry of the American Criollos, influenced by much later introductions of cebuine breeds, as well as British and other European breeds (Delgado et al., 2012; Ginja et al., 2019; Martínez et al., 2012; McTavish et al., 2013).

Following introduction by early European settlers, cattle expansion

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through the Americas was rapid, and resulted in herds of semi-feral animals in several cases (Primo, 1992). Criollo's high adaptive capacity enabled them to spread and colonize a wide variety of environments, from the arid deserts of southern United States to the glaciers of Patagonia, including mountainous, grassland and tropical landscapes. Their ancestry combined with local adaptations created the wide spectrum of American Criollo breeds that we see today, many that are at risk of extinction due to changes in production systems and goals (Ginja et al., 2019). In spite of the natural divergence found in locally adapted populations, the American Criollo cattle breeds form a unique genetic cluster among other bovine breeds and share common genetic and phenotypic features that make them different from the more popular commercial breeds of today (Delgado et al., 2012; Ginja et al., 2019; Martínez et al., 2012). Our objective is to review the existing genetic and production data on the Argentinian, Mexican, Uruguayan and US Criollo cattle that form the basis of the collaborations and current and future research described in this special issue.

2. Criollo cattle in Argentina

In the 16th century, the current territory of Argentina was part of the vast Virreinato del Río de la Plata and received the first cattle through four different routes: from Potosí (Bolivia) in 1549 when Juan Nuñez de Prado arrived in Tucumán, then in 1551 from Chile via Francisco de Aguirre, in 1554 from Asunción (Paraguay), and also from the south of Brazil. Later, direct trips were made with small groups of animals from the Canary Islands to the Río de la Plata. The spread of cattle before and during that period was a consequence of the foundation of the cities by Spanish colonizers. When Garay founded Santa Fe (1573), he brought from Asuncion a significant number of cattle; later in the second founding of Buenos Aires (1580), approximately 500 animals were brought in from Santa Fe and Asunción. Later, when Corrientes (1588) was founded by Juan Torres de Vera y Aragón, he moved about 1500 cattle from Asunción (Carrazzoni, 1998).

The geographic conditions, moderate climate, abundance of forage and near absence of predators in the central and eastern region of the country (Pampas) led to an expansion of livestock so important that by

Fig. 1. Map of Criollo cattle introduction into the Americas. Adapted from De Alba Martinez (2011) Fig. 1.2 p. 9.

1850, about 20 million bovines were located in that region; cows were important for meat, grease and leather, but more fundamentally as exchange of goods (Martínez, 2021).

In the following decades, the importation of Shorthorn, Hereford and Angus cattle began in order to produce animals with a greater tendency to fatten, which the export market required at that time. The crossbreeding process continued to the extent that the original Criollo cattle of the Pampas region were essentially gone. Criollo cattle were displaced and confined in regions where other breeds could not survive, such as tropical, subtropical, arid and Patagonian areas. In the 1950s, due to the importation of cebuine cattle, the crossbreeding process became more intense in the northeast and northwest regions of Argentina.

In 1959, the National Institute of Agricultural Technology - INTA began studies with the first experimental Criollo cattle herd (35 cows and 2 bulls from the NW region) in the Leales unit (currently the Institute for Animal Research of the Semi-arid Chaco [IIACS] in the province of Tucumán). In the first evaluation stage (1959–1970), the Criollo animals were used as controls for comparison with crosses of European breeds and cebuine cattle (Nelore) and later (1971–1988), the characterization of these cattle was continued in an effort to develop a select nucleus (NS) of Criollo cattle with emphasis on defining and adding this breed to the national livestock registry (Holgado and Ortega, 2019). Also at that time, some private breeders that had preserved small Criollo cattle herds started exchanging knowledge, experiences, and animals. In a few years other Criollo cattle herds were established in INTA Units and on private farms. In 1985, by the joint initiative of private breeders and INTA, the current Argentine Association of Criollo Cattle Breeders was established (AACGBC, 2021).

In general, the Argentine Criollo cow is medium-sized (400–450 kg), and has a slightly elongated body shape with a high and advanced tail head that provides a large calving channel; consequently, dystocia problems are almost nonexistent in this breed. Bulls (600–850 kg) have good beef conformation in the conventional sense (Fig. 2). A variety of coat colors occur and although the presence of horns is most common, poll and scur animals do occur. The Association has developed a phenotypic breed standard coded for primary coat colors and combinations.

Since the 1970s, Criollo cattle in Argentina have been studied and characterized for production and reproduction traits, regarding both purebreds and crossbreds in various environments (Corva et al., 1995; Holgado et al., 2017; Rabasa et al., 2005; Rabasa and Holgado, 2000). A comprehensive report on the productive and reproductive behavior research on Criollo cattle and the selection program conducted by INTA in Leales during the period 2006–2016 was published by Holgado and Ortega (2019).

The performance, weight gain and carcass composition at different ages and slaughter weights and for different cuts for the Argentine system were analyzed in an experimental design that included Criollo, Angus, Hereford, Shorthorn, and Beefmaster crossbreds. The organoleptic characteristics of the meat (tenderness, juiciness, flavor, aroma and acceptability) of Criollo cattle and their crosses did not differ significantly from the British breeds or their crosses in that study (Garriz, 2012).

The characterization of the Criollo bovine by means of blood groups and other biochemical polymorphisms also began in the early 1970s (Poli, 1986; Poli and Antonini, 1991). Other studies of genetic diversity conducted using molecular markers at the DNA level such as microsatellite, mitochondrial DNA, and candidate gene polymorphisms generally revealed a high level of polymorphisms (Giovambattista et al., 2001; Lirón et al., 2006). Within the MHC, a new BoLA DRB3.2 allele was described (Poli et al., 2003) and in a comparative study of the mtDNA between Brazilian and Argentine Criollo breeds, seven new haplotypes were found which mirror the mitochondrial lineage distribution among cattle breeds in the Iberian Peninsula from five centuries ago (Miretti et al., 2002).

Anecdotally, producers describe Criollo cattle as more resistant to diseases because they do not observe eye cancer, foot root, or keratoconjunctivitis, among other maladies. Miquel et al. (1994) measured the presence of antibodies to different viral infections as an indicator of viral replication in different genetic groups (taurine, cebuine and crosses) and observed for BHV-1 (Bovine Herpes Virus 1), PI-3 (Parainfluenza 3 Virus) and BVDV (Bovine Viral Diarrhea Virus) that the Criollo × Criollo group contained the lowest percentage. Moreover, no antibodies were present for a-VIA antibody for FMDV (Foot and Mouth Disease Virus), suggesting that in the same conditions as the other breeds, Criollo are more resistant to natural infection by this virus. Also, Guglielmone et al. (1992) showed that under conditions of natural parasitism by *Boophilus microplus* in NW region of Argentina, Criollo cattle were more resistant than Herefords, which were similar to a synthetic crossbred taurine × cebuine, though less resistant than the Nellore breed.

From the numerous studies conducted during the last 50 years, the characteristics that stand out in Criollo cattle are high fertility, calving ease, longevity, the ability to travel, a docile temperament and a great capacity to adapt to different geographical environments ranging from tropical regions in the north to the Antarctic of the south and from grasslands to mountainous terrains.

Currently the Argentine Association of Criollo Cattle Breeders (Asociación Argentina de Criadores de Ganado Bovino Criollo; AACGBC, 2021) promotes the breed by organizing annual technical conferences at national and regional levels and by participating in shows and other events. Five books have been published containing many of the results presented at these conferences. In addition to overseeing the admission and phenotypic inspection of animals, the AACGBC maintains records from private pedigrees and in the Herd Book at the Sociedad Rural Argentina and has over 4500 animals registered in 16 active seed stocks.

3. Criollo cattle in Mexico

Cattle first arrived in México in the 15th century during the Spanish colonization of the Americas through the region that today encompasses

Fig. 2. Argentinian Criollo cow (left) and bull (right) from Palpalá and Cruz de Guerra farms, respectively. Buenos Aires province, Argentina.

the states of Tamaulipas, Veracruz and Tabasco via the Caribbean Islands. These cattle of Iberian origin expanded to the north (including the US), the south, and the Pacific (Fig. 1; See De Alba Martinez, 2011; Rouse, 1977; and Ulloa-Arvizu et al., 2008 for details). This expansion led to a new and flourishing livestock industry for the supply of food, hides, animal work force (e.g. draught) and tallow to manufacture candles and soap. However, by the last quarter of the 19th century, specialized European and cebuine type beef cattle breeds were introduced to produce cattle for exportation (primarily into the US). Consequently, cattle populations of Iberian descent decreased drastically and were relegated to isolated regions, predominantly in the most remote parts of the mountainous areas, in small herds, with no selection for production traits. This natural selection conferred remarkable resilience and an ability to adapt to harsh environmental conditions with scarce forage availability. These small herds remained under the ownership of traditional producers and indigenous communities, and are now the least genetically eroded heritage cattle types. For example, Perezgrovas-Garza (2017) reported a correlation of 0.75 between average altitude and the number of Criollo cows in different regions of Chiapas, Mexico.

Although animals with at least some influence of heritage cattle genetics exist all across México, there are a few distinguished regional groups of Criollo types with little influence of crossbreeding that have been differentiated in size, weight and conformation according to local environmental conditions (McIntosh et al., 2020) and identified in some anecdotal and scientific literature as breeds. However, these ‘breeds’ should be more accurately referred to as biotypes (Quezada-Casasola et al., 2014), given their common origin and genetic constitution (Ginja et al., 2019) without a deliberate selection towards a breed standard defined by a breeder organization. In the 2002 Mexican report presented to FAO by the National Department of Agriculture (SAGARPA, 2002) regarding livestock genetic resources in México, five Criollo cattle biotypes were listed, along with the production system, ecological region and their population status (Table 1). Other biotypes (Criollo from the Tzotzil-Tzeltal highlands of Chiapas; Criollo Mixteco in Oaxaca, Guerrero and Puebla, also reported in the literature as Criollo Poblano; and Criollo Nunkini in Campeche (and probably Yucatán) have been reported in compendiums of Criollo cattle (De Alba Martinez, 2011; Perezgrovas-Garza, 2017) and scientific literature (Ginja et al., 2019; Martínez et al., 2012; Delgado et al., 2012; Ulloa-Arvizu et al., 2008).

Except in the case of the dairy breed Criollo Lechero Tropical de México (Rosendo-Ponce and Becerril-Pérez, 2015), there are no well-organized programs for genetic improvement or conservation of Criollo cattle in México, whereas in other countries from North, Central and South America, well-defined Criollo breeds have been established. Also, research and characterization studies are quite limited in México. The population sizes reported for some of the Criollo biotypes listed above are quite variable, because in some cases the estimates include only animals with no apparent signs of crossbreeding influence while in others crossbreds and “purebreds” are combined. This disparity may partially explain differences in reports on the divergence among Mexican regional Criollo cattle types when analyzed within country and region (Russell et al., 2000; Ulloa-Arvizu et al., 2008) compared to studies that include several countries (Delgado et al., 2012; Ginja et al., 2019; Martínez et al., 2012). Another reason for this discrepancy could be differences in sample sizes, the number and type of molecular markers used, and/or the statistical approaches for analyzing data.

The best characterized and most thoroughly studied Criollo cattle types in México are those from Nayarit, Chihuahua, Baja California and Chiapas. Those are also the most isolated and best conserved populations, especially those owned by indigenous communities in the case of Nayarit, Chihuahua and Chiapas. Because of frequent contact with the families who care for the cattle or by management during the milking process or use as work animals, these cattle are typically docile; thus, their temperament is commonly described as calm. As for phenotypic characteristics, coat color variation is an important and common characteristic of these cattle, including the different colors observed for original Spanish breeds in Spain and all their combinations. There are also remarkable similarities for other morphological characteristics for animals without apparent crossbreeding; for instance, typical horns are well set in a fairly wide poll, not too long, slanting slightly forward from the base, parallel to the ground, or sloping upward gradually, beginning to curve forward, or forward and upward, approximately at the ear tips (Fig. 3). The ears are small and hairy, which indicates no influence of *B. indicus* genetics. The dewlap is short and not very pronounced, the rump narrow and raised, highlighting the iliac (hip) bones. The preputial sheath in the bull and navel in cows are short and close to the stomach. The testes are of regular size and the udders well set. The insertion of the tail is high and long, with the tassel abundant and long as well. Variations around these most typical characteristics are well illustrated by McIntosh et al. (2020).

The Mexican Criollo Cattle Breeders Association (ASOCRIOLLO) developed guidelines for phenotypic requirements for registration of Criollo cattle in the breed Herd Book, based on desirable traits that were defined during a characterization study of Criollos from Chihuahua (Hernández, 2001). Later (Hernández Sandoval and Chihuahua, 2012), when breed registration was intended to be expanded to other Criollo populations in México, the guidelines were validated with data from Criollo Chinampo cattle from Baja California Sur, Criollo Mixteco from Puebla, Guerrero and Oaxaca, and Criollo Coreño from Nayarit. The conclusion was that the guidelines developed with Criollo Rarámuri were adequate for the other type of Criollos, given their high phenotypic similarities.

Typical weights for Criollo cattle of México depend on feed availability during growth. For example, Criollo Rarámuri of the same age raised in the lower part of the Copper Canyon tend to weigh more than those raised in higher altitudes of the Copper Canyon. In general, across regions, under the typical harsh conditions of the geographic borders of

Table 1
Cattle Criollo biotypes present in Mexico (Adapted from SAGARPA, 2002).

Region	Common Names	Main States	Production System[a]	Climate	Observations
• The Gulf	• Del Golfo	• Tamaulipas • Veracruz	F/E	Dry Tropical	At risk
• Sierra Madre Occidental	• Coreño • Del Nayar	• Nayarit • Jalisco • Durango	F/E	Tropical/Temperate	Rare without crossbreeding
• Northern Mountains	• De Rodeo • Raramuri • Frijolillo (Sonora)	• Chihuahua • Durango • Sonora	F/E	Arid/Semi-arid/Temperate	Marketed for rodeo in USA
• Baja California Desert	• Chinampo	• Baja California	F/E	Arid	Rare
• The Gulf	• Lechero Tropical de México	• Veracruz • Tamaulipas	E	Dry Tropical	Small herds

[a] Production system: F = Family; E = Extensive in small herds.

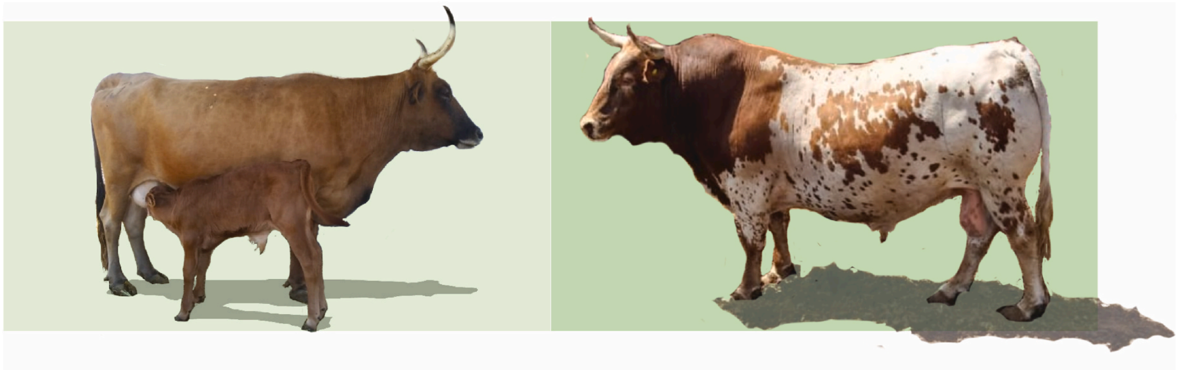

Fig. 3. Mexican Criollo cow and calf (left) and bull (right) from Mesa de las Borregas farm and UACH Teseachi Experimental Station in Guerrero and Namiquipa municipalities, respectively. Chihuahua, México.

indigenous communities in the states of Chihuahua (Hernández, 2001) and Nayarit (Martínez Velázquez, 2005), cows weigh between 230 and 300 kg, while bulls reach 280–400 kg. However, the same Criollo Rarámuri cows raised under more productive rangelands in the Central Valleys of Chihuahua can reach 350–400 kg. Although Criollo Chinampo calves in Baja California have been reported to be heavier at young ages than Rarámuri and Coreño calves, adult cows and bulls tend to weigh less (Villavicencio et al., 2009). Adult cow weights reported by Perez-grovas-Garza (2017) for Criollo cows in Chiapas range between 300 and 450 kg.

As mentioned previously, the Mexican Criollo has been relegated to very harsh environments and low-income communities, which have contributed to the acquisition of adaptation mechanisms to survive and reproduce. Performance observed under those poor conditions could suggest these animals are unproductive. According to data collected in 2010 through a survey of 187 Criollo Rarámuri producers in the Sierra Madre Occidental in the state of Chihuahua (José Ríos, personal communication), the mean ± standard deviation for some performance variables were: first calving age, 3.5 ± 0.29 yr; calving rate, 53 ± 19.8%; calving interval, 20.2 ± 0.37 mo; weaning age, 9.8 ± 1.17 mo; number of calves weaned per cow during life time, 5.3 ± 0.68. However, recent controlled trials at the Universidad Autónoma de Chihuahua showed that growth efficiency and reproductive performance of Criollo improve considerably when food availability and other environmental factors improve. According to Vargas-Cázares et al., *In Preparation*), average daily gain with a mixed ration individually fed for 56 d, after a 14 d preconditioning period, was lower (0.77 ± 0.03 vs 1.33 ± 0.04 kg*d^{-1}) for female Criollo calves than for Hereford × Angus female calves of same age (8 ± 1.2 mo), and the same was true for mean daily dry matter intake (4.86 ± 0.2 vs 8.15 ± 0.3 kg*d^{-1}), there were no differences in feed to gain ratio (7.6 ± 0.3 vs 7.0 ± 0.4) or residual feed intake (RFI; 0.04 ± 0.1 vs 0.05 ± 0.1 kg). The differences in feed intake corresponded to the differences in mean initial body weight (121.6 ± 9.2 *vs* 195.2 ± 10.2 kg). In another two-year study, with the first year under low input rangeland conditions and the second under a winter irrigated pasture, Criollo Rarámuri and Hereford × Angus heifers reached puberty at the same age on both forages, as indicated by serum P_4 concentrations; however, average age at puberty was earlier under irrigated winter pasture conditions than under rangeland conditions. The weight at puberty was the same under both conditions within breed; however, Criollo weighed 76 kg less than Hereford × Angus heifers (Vargas-Cázares et al., *In Preparation*).

Crossbreeding studies (Martínez Velázquez et al., 2006, 2008) conducted at the research station “El Verdineño” of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP) located in Nayarit, Mexico, in a two breed diallel design with Criollo Coreño (CC) and Guzerat (G), a *B. indicus* breed, and crossbreeding of the resulting cows to Angus bulls by artificial insemination in a second stage of the project, respectively, revealed the maternal potential of the Criollo cow for producing feeder calves under a crossbreeding scheme, with improved fertility, maternal ability and growth and survivability of the calf to weaning. The mean kilograms of weaned calf per cow exposed were 98.4 ± 8.4, 143.5 ± 24.1, 116.15 ± 10.9 and 83.97 ± 7.9 kg for G, G x CC, CC x G and CC cows, respectively.

Ongoing research at the Universidad Autónoma de Chihuahua (Vargas-Cázares et al., *In Preparation*) seeking to understand the mechanisms by which cows with Criollo genetic influence are able to reproduce well even with low nutrient availability during late gestation and lactation has shown that second and third gestation F1 Hereford × Angus (HA) cows mobilize more body energy reserves than F1 Angus × Criollo (AC) cows. A four to eleven-fold increase in β-hydroxybutyrate serum concentrations during late gestation and lactation from late March to early July (before the rainy season) was observed for HA vs AC cows in a two-year study. The average body weights of the two groups of cows in the final gestation period were 461 vs 380 kg, respectively. A longer postpartum interval to the beginning of follicular activity and first ovulation was detected for HA vs AC and purebred Criollo cows.

Criollo bulls have been described as highly fertile with a remarkable libido and the capability to reproduce in environmental conditions in which other breeds are not able. In a four-year study, Quezada-Casasola et al. (2016) reported that in the Chihuahuan Desert, semen characteristics of Criollo from Chihuahua were not affected by season, and values obtained for traits such as motility, live sperm percentage and testosterone concentration were higher in Criollo bulls than in European-breed bulls in the hottest season.

The inferred natural selection in Mexican Criollo cattle through almost 500 years of low or no human intervention likely contributed to the development of mechanisms to resist diseases and parasites, although to our knowledge, this has not been studied. Characterization of the genetic variation in northern Mexican Criollo regional populations was conducted using PCR-RFLPs analyses and sequencing on the BoLA-DRB3.2 gene. The PCR-RFLPS showed 52 alleles, 24 of which were new and 10 of these new alleles were sequenced to full characterization (Félix et al., 2006). Since the bovine major histocompatibility complex (bovine leucocyte antigen, BoLA) is associated with the susceptibility or resistance to diseases, the high polymorphism found in the BoLA-DRB3.2 gene in Mexican Criollo could be related to the adaptation of these animals and their capacity to respond to a wider range of pathogen antigens. A more recent study (Fernández et al., 2015) demonstrated that this high genetic diversity in the BoLA-DRB3.2 locus is present in Criollo populations from the state of Baja California and other locations in the state of Chihuahua as well.

A production strategy implemented by the Universidad Autónoma de Chihuahua and some producers in a pilot study sought to incorporate the adaptability and maternal productivity traits of Criollo in a traditional cow-calf production system and crossbreed with specialized beef production breeds (Quintana-Gallegos et al., *In Preparation*). The male offspring of cows Angus x Criollo (A × C) sired by Angus, Hereford and Piedmontese [A × (A × C), H × (A × C), P × (A × C), respectively] were compared with the male offspring of Angus cows sired by Hereford (H × A). No differences were found in the feeding trial performance or carcass yield among crossbred groups finished in a feedlot, although they were on average 177 ± 20 kg above the mean body weight of the purebred Criollo steers (370 ± 17 kg). The mean birth weight was lower for P × (A × C) crossbred calves (30.3 ± 3.4 kg) although it was not statistically different. This result is important because even though the animals were carriers of the myostatin variant gene involved in the "double muscle" phenotype of Piedmontese, dystocia was absent. P × (A × C) calves had higher weight at weaning (147.3 ± 10.5 kg; $p < 0.05$) than H × A (127.4 ± 5.8 kg), H × (A × C) (112.5 ± 8.2 kg) and A × (A × C) (97.6 ± 8.2 kg). For other carcass and meat traits such as texture ($p = 0.14$), rib eye area ($p = 0.10$) and round ($p = 0.03$) and loin ($p = 0.10$) primary cuts weight, the P × (A × C) animals tended to have the best values; while the opposite was true for marbling. These results show that using Criollo as maternal breed in crossbreeding systems for beef production under arid and semiarid climates in northern Mexico could be an alternative to the traditional H × A cross and warrants further research.

4. Criollo cattle in Uruguay

Cattle were first introduced in the region that today belongs to Uruguay in 1611, from the Jesuit Missions of Alto Uruguay (currently Paraguay) and some years later also from southern Brazil (Primo, 1992). These ancestral populations thrived on the natural grasslands of the region and soon spread throughout the country, becoming the basis of beef production in colonial times, and later on, of the hide and dried meat export industry during early independence. The introduction of British breeds and Holstein animals in the 1870s signaled the beginning of the decline of Criollo populations, which were regarded as semi-wild and less productive than their recently introduced counterparts. The mild climate and high availability of pastures imposed few restrictions to the development of these new commercial breeds, leading to intermingling with Criollo populations. By 1930's there were very few pure Criollo herds remaining in the country (Armstrong and Postiglioni, 2010).

Currently there are only two known pure herds of Uruguayan Criollo cattle (UCC). The largest herd is located at the UCC reserve in San Miguel National Park in southeastern Uruguay. It comprises around 600 purebred individuals managed by public institutions and is not used for commercial purposes. Another small population of around 60 animals (plus several dozen crossbred individuals) in northeastern Uruguay is managed by private owners and used for beef production. At present, there is no gene flow between these two populations. However, plans for research collaborations are underway, including the creation of a semen bank. In 2019, UCC was finally recognized as a breed and entered the registries of the national herdbook association (Asociación Rural del Uruguay), and is currently considered a conservation priority (Armstrong et al., 2021).

Uruguayan Criollo cattle display the typical Criollo morphology and body conformation described in earlier sections, with high sexual dimorphism and lyre-shaped horns (Fig. 4). They exhibit dark eyelids and nose pigmentation and a wide variety of coat colors and patterns (Armstrong and Postiglioni, 2010).

Most genetic studies conducted to date were on the UCC reserve herd. Cytogenetic studies revealed that the Robertsonian translocation rob.1/29 is present at a low frequency in this population (Armstrong and Postiglioni, 2010), although no obvious reproductive problems have been detected relating to this condition. Microsatellite marker analyses revealed a relatively high genetic diversity (expected mean heterozygosity = 0.664) and low inbreeding coefficient (F_{IS} index = 0.037) (Armstrong et al., 2013). Mitochondrial DNA analysis identified three different haplotypes in this population, all belonging to the European consensus, and one exclusive to Uruguay in South America, previously found in Portuguese breeds (Armstrong et al., 2013). Milk gene polymorphism analyses revealed very similar A and B allele frequencies for κ-casein and β-lactoglobulin genes, while the αs1-casein and α-lactoalbumin gene B alleles appeared in much higher frequencies. There was a very high frequency of the *DGAT1* allele associated with low milk fat content and high milk yield (Rincón et al., 2006). Three molecular markers associated with meat marbling (diacyl-glycerol acyl transferase, *DGAT1*; thyroglobulin, *TG*; and leptin, *LEP*) were analyzed in both UCC populations. The reserve herd showed higher frequencies of alleles and genotypes associated with low marbling scores in all markers, while the crossbred herd exhibited a tendency for higher frequencies of alleles associated with greater marbling, probably due to indirect selection for higher live weights (Armstrong et al., 2011).

Recently, research was conducted to evaluate UCC beef production potential (Armstrong et al., 2021). In comparison with Hereford steers raised in the same conditions, purebred Criollo steers attained almost the same slaughter weight at a similar age, suffered less weight loss during the winter season, and had larger rib eye areas ($P = 0.014$) and subcutaneous fat depth ($p = 0.045$). Although Criollo steers weighed less at slaughter, no significant differences were detected compared with Hereford steers regarding carcass weight and carcass attributes ($p > 0.050$). Criollo steers yielded higher muscle percentage ($p = 0.002$), lower intermuscular fat percentage ($p = 0.049$) and lower bone percentage ($p = 0.023$) than Hereford. Regarding meat quality, no significant differences were detected between breeds regarding shear force, color, or cooking loss measurements ($p > 0.05$), and Criollo steers tended to have more intramuscular fat ($p = 0.058$). A sensory panel trial revealed no differences between breeds in tenderness, flavor or general acceptance of cooked meat ($p > 0.05$). In conclusion, our research

Fig. 4. Uruguayan Criollo cow (left) and bull (right) from San Miguel National Park, Rocha, Uruguay.

suggests that the Criollo cattle from Uruguay may be comparable to a highly selected British breed for beef production purposes (Armstrong et al., 2021).

5. Criollo cattle in US

Cattle of Spanish origin were first introduced into what is present day New Mexico, US around 1539, with reports indicating that Coronado introduced ~500 head there, slightly later, during his travels from México between 1540 and 1542 (Anderson et al., 2015; Bowling, 1942; Rouse, 1973). Limited information regarding the fate of those cattle exists, therefore Criollo (also referred to as Creole) introduction into New Mexico by way of México is speculated to have occurred circa 1598 when Don Juan de Oñate brought a herd of 2500–7000 head (Fig. 1; Rouse, 1973; Anderson et al., 2015).

Criollo cattle were introduced into Florida by way of the West Indies as early as 1566–7 and additional introductions of Iberian-descended cattle are reported between 1608 and 1640 to American colonies including Virginia, Delaware, New Jersey, and Massachusetts. Following the development of Santa Fe, NM, as a cattle business town in 1609, Iberian cattle were moved into California by Serra and Portola in 1769. The majority of the first cattle brought to the early US were used for oxen and production of hides and tallow; few records of these animals being used in large numbers for beef or dairy purposes exist (Bowling, 1942).

Until the 1800s, Criollo cattle were allowed to roam freely on pristine rangeland as far east as Florida, as far north as Oregon and Montana, and west beyond California to Hawaii where they were called “Hawaiian Wild Cattle” (Rouse, 1977; Sponenberg and Olson, 1992). Very little artificial selection besides some castration of bulls for oxen was practiced, allowing natural selection to drive group evolution for nearly 400 years (McTavish et al., 2013; Rouse, 1977). These feral herds were progenitors of American Criollo-landraces including an extinct California strain, and extant Texas Longhorn, Florida Cracker, Pineywoods, and Corriente breeds (McTavish et al., 2013; Sponenberg, D.P., Olson, 1992; Sponenberg et al., 2019). United States-Criollo cattle reached a peak in population in the 1870s, when over 15 million head roamed the nation. Criollo cattle at that time, occupying nearly all corners of the western frontier, may be credited with American's self-identifying, and romanticized ‘cowboy’ culture and spirit (Rouse, 1977; Specht, 2016). Upon introduction of a number of European and cebuine cattle in the mid-late 1800s, the populations of Criollo landrace breeds were severely threatened due to supplantation, crossbreeding, or being banned because of their disease resistance to bovine babesiosis which they carried and transmitted to other newly introduced European stock. At that time, intervention by a few concerned ranchers helped to maintain small populations of those cattle to preserve them from ‘incursions’ of genetics from non-Criollo biotypes (Sponenberg and Olson, 1992).

Numerous early sources refer to Criollo cattle of what is now the United States as thrifty, intelligent, and well suited to the harsh south and southwestern climates. These traits induced a select group of ranchers to promote the renaissance of these biotypes and was also the reason that the University of Texas adopted ‘Bevo’ (a longhorn steer) as their mascot in 1920. Bevo's ‘ranginess’ unfortunately lead to his demise when the football team ate him for Thanksgiving that same year (Specht, 2016). As the result of a well-articulated *New York Times* article by famed Texas historian J. Frank Dobie, one of the first government organized efforts to preserve the Texas Longhorn also occurred in 1920, when US Forest Service members established a small herd to be raised on the Wichita Mountains Wildlife Refuge in Oklahoma, which is still in existence today (Specht, 2016). Still, there is no governmental oversight of Corriente, Florida Cracker, or Pineywoods cattle conservation and widespread efforts to preserve them did not occur until the 1980s when breeders throughout the southeastern and western states began to operate cooperatively (NACA, 2020; Sponenberg and Olson, 1992). North American breed associations for Texas Longhorn, Pineywoods, Florida Cracker, and Corriente cattle were not founded until 1986, 1999, 1988, and 1982, respectively (e.g. NACA, 2020).

Single nucleotide polymorphism (SNP) data from Texas Longhorn and Florida Cracker cows indicate they have ~81 and 60% Iberian influence, 6 and 36% commercial *B. taurus* influence, 5 and 1% African *B. taurus* influence, and 8 and 3% *B. indicus* influence, respectively (Pitt et al., 2019). Results that show such marked levels of commercial influence on landrace breeds (e.g. Florida Crackers) suggests that more deliberate work is needed to limit further genetic introgression and perhaps that coordinated genetic breeding efforts of the purest animals of each biotype could conserve the unique phenotypic and genetic qualities that these animals possess to ensure genetic variation as well as provide specific production goals such as that of sustained beef production in the southwestern US (Sponenberg et al., 2019).

Today's Texas Longhorn, Pineywoods, Cracker, and Corriente cattle are somewhat similar in conformation and closely resemble other North American Criollo biotypes which are characterized by square frames, narrow hips, broad heads, wide-set upward facing horns, and athletically suited muscles (Perezgrovas- Garza, 2017) as well as smaller frame sizes (300–400 kg) compared to beef breed counterparts (Fig. 5; McIntosh et al., 2020). Like other Criollos, these four breeds possess increased levels of thermotolerance and parasitic resistance (Figueroa et al., 1992). General body weights range from 363 kg (Corriente cows) to over 816 kg (among mature Longhorn steers; Halloran, 1966; NACA, 2020). Texas Longhorns notably have long horns (hence their namesake) which are likely the result of natural selection that favored animals best equipped to fend off large predators like wolves and which can exceed 185 cm in span (Halloran, 1966). Corriente cattle have been intentionally bred for their fast athletic abilities and curved horns which makes them ideally suited for rodeo bulldogging and roping sports (Anderson et al., 2015).

A pilot study evaluating 30-mo old steers grown and finished on Chihuahuan Desert grasslands showed that Criollo steers reached marketable weights (363–454 kg) and yielded extremely tender meat when samples between the 12th and 13th rib were tested in a Warner-Bratzler shear device (Anderson et al., 2015). A follow-up study that evaluated Rarámuri Criollo, Mexican Criollo, and Criollo × beef crossbreds developed on Chihuahuan Desert rangeland found similar results, with all biotypes finishing between 346 and 482 kg (McIntosh et al., 2021). Yield grade and marbling score were not different between biotypes, though crossbreds grew to heavier weights; quality grade for those desert grass-finished steers was between Standard + and Prime. These results indicate that Criollo steers developed on grassland may be a viable alternative to conventional beef production supply-chains (McIntosh et al., 2021). A study comparing Texas Longhorn steers to conventional breeds in a feedlot system found that Longhorn animals were smaller than their beef-breed counterparts, but still produced as much muscle (on a percentage basis), and beef that was deemed palatable and met the specifications of USDA quality grades and yields (Adams et al., 1982). These results also support the use of Criollo-type cattle in more conventional systems.

A number of producers across the country are now working to preserve and maintain American-landrace Criollo breeds (and biotypes; Sponenberg and Olson, 1992). Information regarding foundational herd stock, current status, and breed trajectories for Texas Longhorn, Pineywoods, and Florida Cracker cattle is provided by Sponenberg and Olson (1992) and Sponenberg et al. (2019). Lineage of the American-Corriente foundational stock is somewhat more difficult to elucidate, though the North American Corriente Association and Rouse (1977) both suggest that Corriente were nearly eliminated from North America by the late 1800s, therefore reintroduction from small isolated herds in remote regions of Mexico and Central America was necessary. The North American Corriente Association suggests that the term “Corriente” is often used indiscriminately with regard to small Criollo cattle and became the default name for the breed because it was a common trade-term between northern Mexican and Southwestern US ranchers when the US began importing such cattle for rodeo in the mid-1900s.

Fig. 5. Raramuri Criollo cow (left) and bull (right) from USDA-ARS Jornada Experimental Range herd in Las Cruces, NM, USA.

Genetic analyses of Mexican Criollo cattle have shown, as in the US, geographic-dependent genetic isolation of several biotypes (Ulloa-Arvizu et al., 2008); one such group of genetically isolated Criollo is being preserved and studied by the USDA-ARS Jornada Experimental Range in New Mexico, US (Anderson et al., 2015). The Rarámuri Criollo, whose namesake honors their ancestral caretakers, the Tarahumara who called themselves Rarámuri and came from the Rio Oteros region of the Sierra Tarahumara, Mexico, have been the subject of a number of behavior studies. Scientists have sought to characterize and compare their grazing behavior with more conventional beef breeds to identify novel management strategies for ranchers in arid environments (see: McIntosh et al., 2021; Nyamuryekung'e et al., 2021; Peinetti et al., 2011; Spiegal et al., 2019 and articles in this issue).

6. Genetic relationships between the populations under study

Studies by Delgado et al. (2012), Martínez et al. (2012) and Ginja et al. (2019) regarding genetic characterization, genetic footprints and genetic ancestry of American Criollo cattle breeds, respectively, included five Criollo types from México, three from the US, two from Argentina and one from Uruguay. Mexican Criollos from Chihuahua, Baja California, Nayarit and Puebla clustered together with the Texas Longhorn breed of the US. Only the Méxican Criollo of Chiapas diverged and clustered with Criollo breeds from Ecuador, Paraguay and Colombia. Ginja et al. (2019) reported that the Criollo from Chiapas had the greatest influence of *Bos indicus* within the Mexican Criollos studied, the Criollo from Chihuahua had the most pronounced conservation of Iberian genetics and the Portuguese influence was most noticeable in Criollos from Chihuahua and Nayarit. Compared to many South American Criollo breeds, which show strong individuality, Mexican Criollos have greater genetic diversity. This may be due to the lack of strong conservation programs. In the case of the Criollo Poblano, significant levels of inbreeding were observed (Delgado et al., 2012). Likely because they tend to be raised in several closed and independent herds, compared to other Criollos in Mexico which are typically raised in communal villages.

When analyzed in the multi-country studies mentioned above, the Mexican Criollo types show high genetic similarities. However, when analyzing genetic divergence among geographically isolated populations of Criollo from Chihuahua (Russell et al., 2000) and Nayarit (Cozzi et al., 2019) it was determined some of those groups may genetically differ from others. Thus, more detailed genetic characterization within each regional Criollo population warrants further attention in order to establish appropriate conservation strategies.

According to Ginja et al. (2010), Miretti et al. (2002) were the first to analyze mitochondrial DNA (mtDNA) in Criollo cattle (see Argentine section for more information), and Giovambattista et al. (2000) were the first to evaluate North American Criollo lineages (albeit seeking male-mediated *Bos indicus* introgressions). These authors sought to evaluate mtDNA among North and South American Criollo and breeds from Europe, Africa, and Asia, to determine genetic contributions of Criollo from breeds originating in Eastern hemispheric continents. Ginja et al. (2010) found that haplotype 209 (Hap209) was most common among Criollo tested (which included Texas Longhorns, Pineywoods, and Florida Crackers), and that they shared the most haplotypes, a group of genes inherited together from a single parent, in descending order with: Iberian Peninsula, British Islands, Atlantic Islands, and cebuine, confirming, as hypothesized, that Criollo had descended primarily from Southern Spain with some African indicine influences. Haplotypes Hap054, Hap243, and Hap274 were found to be exclusive to Criollo, Iberian, and Atlantic breeds tested. Of 78 haplotypes tested among breeds in this study, 48 that were unique to Criollo and African matrilines (T1, T1a, or AA) were present in all Criollo populations (Ginja et al., 2010).

McTavish et al. (2013) improved upon previous studies by analyzing nuclear SNPs rather than mtDNA and Y chromosome markers as was done by Ginja et al. (2010). This analysis allowed a more complete assessment of genome introgressions and admixtures because "the 47, 506 nuclear loci … can reflect independent coalescent histories due to recombination and assortment" (McTavish et al., 2013, p. E1398). These authors reported 28% heterozygosity among three Criollo cattle types: Texas Longhorn (US), Corriente (MX), and Romosinuano (CO). McTavish et al. (2013) also found evidence of indicine and African taurine introgression among the Criollo types tested. African taurine ancestry is likely the result of historical livestock trading across the strait of Gibraltar and the introduction of cattle to the New World through the Canary Islands. According to these authors, indicine introgression was already present in southern European breeds, though data suggest that more recent introgressions are likely to have occurred in the US.

Ginja et al. (2019) report uniparental and autosomal genetic markers (microsatellites) in DNA from 114 world-wide cattle breeds, including three US-derived Criollo: Texas Longhorns, Pineywoods, and Florida Crackers. These authors increased mtDNA and Y-chromosome haplotypes by greater than half of their earlier (2010) study. They found that Texas Longhorn cattle were closely related to most Mexican Criollos, and that Pineywoods were more closely related to Iberian breeds. Generally though, as in previous studies, these authors found variable levels of genetic diversity among all North American Criollo (eg., Florida Crackers) which they attributed to dilution by crossbreeding (Ginja et al., 2019). These authors reported similar haplogroups, genetic populations that share a common ancestor, among US-derived Criollo. They also reported similar haplotype diversity among all three breeds (0.84–0.88; haplotypes for Texas Longhorn, Pineywoods, and Florida Crackers included: T1: 6, 2, 1; T3 10, 16, 12; and N: 16, 18, 13; with total haplotypes: 7, 11, 10, respectively). The T1c lineages among US and other Criollos which is rare in Iberian cattle but ubiquitous in African cattle, again, point to an Ibero-African influence on Criollo cattle genetics (Ginja et al., 2019).

Criollos from Argentina and Uruguay showed clear divergence due to the genetic isolation of the populations, but clustered together, representing the southernmost expansion of bovine cattle in the Americas (Delgado et al., 2012; Martínez et al., 2012; Ginja et al., 2019).

According to Delgado et al. (2012), both Criollo types from Argentina (Argentinian Criollo and Patagonian Criollo) together with the Uruguayan Criollo and the Caracu breed from the South of Brazil, form a very distinctive cluster that diverges from all other Criollo breeds and show rather low genetic diversity, as expected from populations that represent the extreme of dispersion of historical routes. No influence of cebuine breeds was found in Argentinian or Uruguayan Criollos, although a relationship with British breeds was detected, likely due to the introduction of British breeds in the late 19th century to the River Plate (Martínez et al., 2012). Argentinian and Uruguayan Criollos were among the breeds that exhibited the strongest individuality and uniqueness (Ginja et al., 2019). Argentinian Criollos displayed a predominance of T3 haplogroup of mitochondrial DNA, common to most Criollos and Iberian breeds, while Uruguayan Criollos showed a predominance of Q haplogroup, which is also present in a few Criollo breeds and in Portuguese breeds. Both Criollo breeds had Y haplotypes present in other Criollos and Iberian breeds, as well as one haplogroup present mainly in British breeds (H49; Ginja et al., 2019).

In conclusion, the genetic studies and their results illustrate the historical background of the Criollo breeds from different geographical regions, and highlight the importance of five centuries of selective adaptation to different environmental conditions, from the arid landscapes of the southern US and Mexico, to the grasslands of the Pampas region of South America.

7. Conclusions

American Criollo biotypes form a defined genetic cluster with influences primarily from Spanish, Portuguese and African lineages, and by much later introductions of cebuine and British breeds. Actions to characterize and preserve the unique genetic and phenotypic features of American Criollo breeds are needed, especially considering that their local adaptations are valuable for production purposes. Criollo breeds, pure or crossbred, could valuably contribute to production systems because of improved fertility, maternal ability, calving ease, longevity, disease resistance, thermotolerance and adaptation to harsh environments traits, as well as high quality meat production. Breeders associations are very important for the development and conservation of these and other local/heritage breeds. Criollo breeds constitute viable resources for sustainable beef production.

CRediT authorship contribution statement

Armstrong E.: conceptualization, original draft preparation, writing, reviewing and editing; Rodriguez Almeida FA: conceptualization, original draft preparation, writing, reviewing and editing; McIntosh M.M.: writing, reviewing and editing, figure preparation; Poli M.: writing, reviewing; Cibils A.F.: conceptualization, reviewing; Martínez-Quintana JA.: writing; Félix- Portillo M.: writing; Estell R.E.: conceptualization, reviewing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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