Genetic Diversity and Structure of Iberoamerican Livestock Breeds

L. T. Gama[1](✉), A. M. Martinez[2], C. Ginja[3], J. Cañon[4], I. Martin-Burriel[5],
M. A. Revidatti[6], M. N. Ribeiro[7], J. Jordana[8], O. Cortes[4], N. Sevane[4], V. Landi[2],
J. V. Delgado[2], and the BIOBOVIS, BIOPIG, BIOHORSE, BIODONKEY, BIOGOAT and BIOVIS consortia

[1] Animal Genetic Resources Laboratory, Centre for Interdisciplinary Research in Animal Health (CIISA), Faculty of Veterinary Medicine, University of Lisbon, Lisbon, Portugal
`ltgama@fmv.ulisboa.pt`
[2] Departamento de Genética, Universidad de Córdoba, 14071 Córdoba, Spain
[3] Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO-InBIO), Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal
[4] Departamento de Producción Animal, Facultad de Veterinaria, Universidad Complutense de Madrid, 28040 Madrid, Spain
[5] Laboratorio de Genética Bioquímica, Facultad de Veterinaria, Universidad de Zaragoza, Instituto Agroalimentario de Aragón IA2, 50013 Zaragoza, Spain
[6] Departamento de Producción Animal, Facultad de Ciencias Veterinarias, Universidad Nacional del Nordeste, 3400 Corrientes, Argentina
[7] Departamento de Zootecnia, Universidade Federal Rural de Pernambuco, Dois Irmãos 51171900, Recife, PE, Brazil
[8] Departament de Ciència Animal i dels Aliments, Facultat de Veterinària, Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain

Abstract. Creole breeds of the various livestock species mainly derive from animals imported to America from the Iberian Peninsula, starting in the early years of discovery and colonization. Creoles have undergone a long period of selective adaptation to a diverse set of environmental conditions in the Americas, and over the last two centuries some Creole populations were admixed with breeds from other European countries and from India. In spite of various threats, some Creole populations are still maintained nowadays, especially in marginal regions, but they need to be better known, in order to recognize their identity and establish conservation programs. Here, we review the results published over the last years by various Consortia established under the framework of the CONBIAND network, with the goal of studying the genetic diversity, structure and breed relationships in Creole breeds. Overall, Creole breeds reveal high levels of genetic diversity and signatures of Iberian origin, but many breeds also show signs of genetic erosion, due to inbreeding or admixture with exotic breeds. The vast majority of Creoles still maintain their own identity, and these results can be used as a basis for recognition, conservation and genetic improvement of Creoles, which result from over 500 years of selective adaptation.

See consortia membership in http://www.uco.es/conbiand/consorcios.html.

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1 The Origins of Creole Livestock

Domestic livestock species such as cattle, horses, donkeys, pigs, goats, sheep and chicken, did not exist in the American continent when Columbus arrived after his first trip in 1492. The Creole populations of the different species of domestic animals that are currently found in the American continent are the result of animals that were brought over the years, especially in the initial stages of discovery and colonization, beginning with the second voyage of Christopher Columbus, when various domestic animals were taken on board of ships. In the initial period, animals of different species were taken by the navigators, brought from the Iberian Peninsula as well as from the archipelagos of the Canaries and Cape Verde, where the caravels often made a stopover for resupplying. The initial group of animals would multiply rapidly, spreading throughout America, from the Rocky Mountains to Patagonia, adapting to extremely diverse climatic and environmental conditions. These domestic animals taken from the Iberian Peninsula and the islands were a fundamental instrument in the process of territorial expansion, because of their importance as a means of transportation and as a source of labor, food and clothing.

The saga of the arrival and diffusion of animals coming from the Iberian Peninsula to the American continent has been the subject of interest by several authors (Rodero et al. 1992; Primo et al. 2004, de Alba Martinez 2012; Beteta Ortiz et al. 2015), and it is believed that the number of animals that came to America to give rise to the different populations known as Creole was small, particularly in cattle (Rouse 1977). In the first years, the main point of arrival of animals was the island of La Hispaniola, and from there they spread to Mexico and North America, Central America and northern countries of South America (Venezuela, Colombia and Ecuador), migrating thereafter to the south. A few years later, animals from the Iberian Peninsula were brought to the coast of Brazil and to the Rio de la Plata, so that, about 40 years after the arrival of the first group of animals, Creole livestock were found scattered in nearly all the American continent.

Following an undisputable predominance of Creole animal populations in America until the 18th century, the import of animals from Great Britain and continental Europe began. This was followed by the introduction of zebu-type animals from India in the early 20th century, in these now represent a significant fraction of the bovine population in the Americas, particularly in tropical regions. It has also been suggested that the introduction of animals of African origin in the American continent may also have occurred, but there is no consistent historical evidence of this flow of animals.

After an initial phase of adaptation of the animals of Iberian origin to the local conditions of very diverse environments in the Americas, the later arrival of animals of other European origins and zebu resulted, in many cases, in the disordered crossing with the Creole populations that were already installed there. This has resulted in a marked degree of erosion of livestock Creole breeds, many of which have been extinct over the last century. However, some isolated populations of the Creole type still survive, often in marginal regions. At present there is an effort to gain knowledge, rescue and conserve these populations, which are the result of 500 years of adaptation to the diverse set of environmental conditions that were found in the American continent.

Over the last decades of the 20th century, several studies on morphological and demographic characterization of some Creole populations of different species were published, which in certain cases led to their recognition as distinct breeds and definitely contributed to their safeguarding.

At that point, doubts persisted as to whether these populations corresponded to what was historically known as Creole, to what extent they diverged from each other, whether they still had strong Iberian influences or had already been admixed with other breeds (European or Zebu), what degree of identity and differentiation they had, what was their genetic structure, etc.

The answer to these questions was only possible when the use of genetic markers became a current practice, allowing a detailed knowledge of Creole populations, namely their diversity, structure and relationships with other breeds. At the end of the 1990s, uniparental genetic markers were used, especially mitochondrial DNA, which allowed a preliminary assessment of the genetic structure of Creole breeds, despite the limitations of providing information only on genetic contributions of maternal origin.

At the beginning of the 21st century, the XII-H network of the CYTED program (which was subsequently followed by the CONBIAND network) brought together the activities of a large number of research groups working on the characterization and conservation of Animal Genetic Resources throughout Iberoamerica. With the foundations and exchange platform provided by these networks, the opportunity materialized to systematically address the study of the genetic diversity of Creole populations of different species. In the strategy defined by this group in the beginning of the 21st century, microsatellites were adopted as the genetic markers of choice to be used to assess genetic diversity in Creole populations, as these are neutral autosomal markers that were recommended by FAO for this purpose and have been widely used in all species of domestic animals.

As a result of the activities of the CYTED and CONBIAND networks, various consortia were established to study the genetic diversity of livestock species. From the activity of these consortia, a series of research projects and publications were generated, which represent a fundamental contribution for an in-depth knowledge of the diversity and structure of Creole breeds, and their relationships with other breeds.

In this chapter, we put together a brief review of the research work on genetic characterization of Creole breeds carried out by these consortia, covering the bovine, swine, caprine, equine and asinine species, and it is expected that, in the near future, similar research activities will be expanded to other species.

2 Cattle

Over the last few years, a number of studies have been carried out in the framework of the CYTED XII-H and CONBIAND networks on Creole cattle genetic diversity, and several research groups were organized within the Biobovis consortium. This broad-range research work included DNA samples from the American continent, the Iberian Peninsula, the Atlantic Islands (Azores and Canary Archipelagos), the European continent and the British Isles, covering a total of 3333 animals representing 81 breeds from 12 countries.

In an initial stage, Ginja et al. (2010) studied the genetic diversity of mitochondrial and Y chromosome DNA in Iberoamerican cattle populations. The Creole breeds revealed mt-DNA haplogroups of European, African, Iberian and Atlantic origin, while Y chromosome markers indicate an influence of the same groups of breeds, as well as a strong influence of zebu. It seems, therefore, that an unquestionable African influence existed in the development of the Creole breeds, which may, however, have also been mediated by Iberian breeds.

Martin-Burriel et al. (2011) studied 51 Iberian bovine breeds using 21 microsatellite markers. The expected heterozygosity was 0.685 and the mean number of alleles/locus was 7.6. There were signs of an ancient African influence in Iberian breeds, and a reduced number of breeds showed influence of exotic germplasm (i.e. commercial transboundary breeds). The proportion of the total genetic diversity justified by differences between breeds was 8.6%, and some breeds showed a deficit of heterozygosity, indicating the existence of inbreeding or substructure. The authors concluded that the relationship between the breeds studied depended more on their geographical proximity than on their morphotype.

Cañon et al. (2011) analyzed the establishment of conservation priorities in Iberian cattle breeds based on genetic criteria, using the same database as Martin Burriel et al. (2011). Depending on the weight given to the intra- or inter-racial components contributed by each breed to total genetic diversity, the conservation priorities were completely different. For example, when more emphasis is placed on inter-racial diversity, the more isolated and differentiated breeds (which are also breeds with higher levels of inbreeding) are given priority. On the other hand, if priority is given to intra-racial variability, breeds with the highest level of heterozygosity would be chosen, but there is a risk of prioritizing breeds whose higher variability results from a more extensive influence of exotic breeds. Some alternative methods were tested in which different weights were given to the intra- and inter-racial components of genetic diversity, and these resulted in quite different conservation priorities.

Delgado et al. (2012) studied 26 Creole cattle breeds using 19 microsatellites. The expected heterozygosity was 0.738, with an average number of 6.9 alleles/locus. Differences among breeds accounted for 8.4% of total genetic diversity, and several breeds showed heterozygosity deficit, but in some breeds there was an excess (possibly due to crossbreeding). The Creole breeds are generally well differentiated, so that a number of ancestral populations of $K = 21$ were estimated to have originated the 25 Creole breeds studied, which indicates an important degree of isolation between them. The genetic distances between breeds estimated in this study indicate the existence of five clusters, namely: breeds of Mexico and the Texas Longhorn; breeds of Panama and some Colombians; Caracú from Brazil and Creole breeds of Argentina and Uruguay; Romosinuano, Costeño con Cuernos, Sanmartinero and Casanareño breeds, all from Colombia; and a group of widely dispersed breeds, presumably with zebu influence.

Martinez et al. (2012) analyzed 27 Creole, 39 Iberian, 9 European and 6 Zebu breeds, using microsatellites to investigate the influence of different breeds on the genetic composition of Creole cattle. The Creole breeds presented greater genetic diversity than any of the other groups, with a higher expected heterozygosity and number of alleles/locus than any of the other breed groups (Table 1). Most Creole populations have a closer

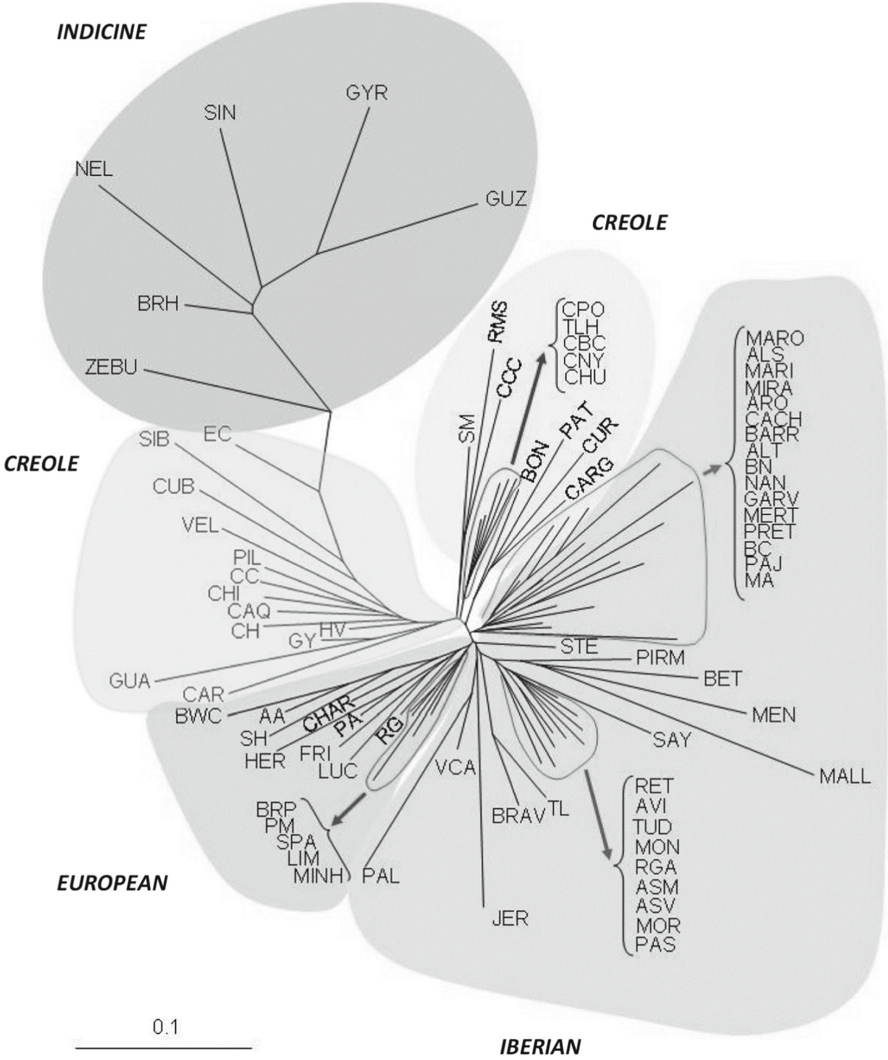

Fig. 1. Dendrogram constructed from D_A genetic distances among 81 cattle breeds from the Iberian Peninsula, Continental Europe, British islands, American Creole and Indicine cattle (adapted from Martinez et al. 2012). See Table 2 for definition of breed acronyms.

relationship with Iberian breeds (especially breeds from the south of the Iberian Peninsula), but some are influenced by British breeds and an important group reveals clear indications of crossbreeding with zebu. This could be more clearly identified in the tree summarizing genetic distances between breeds (Fig. 1), where it was clear that while some Creole breeds were close to Iberian cattle, others showed stronger influence of zebu or of British breeds. For the whole group of Creole breeds analyzed, the estimated contribution of the various ancestral populations to the Creole genetic pool was 63% from

Iberian breeds, 17% from Zebu, 10% from British and 10% from Continental European breeds. However, there were important differences between Creole groups in the relative importance of the contributions of the various ancestral groups. Overall, the results of this research indicate that the various Creole breeds have their own identity, as they differ greatly from each other, both in genetic structure and in the influences that they have received from other breeds. The erosion suffered by some Creole breeds in recent years, mainly as a result of crossbreeding with European and Zebu breeds, could compromise the results of several centuries of adaptation to a wide range of environmental conditions.

Table 1. Indicators of genetic diversity in Creole breeds of various livestock species, in comparison with Iberian and commercial breeds.

	Group	Sample used		Genetic diversity indicators[a]		
		No. breeds	No. animals	Na	Ae	He
Cattle[b]	*Creole*	*27*	*907*	*14.2*	*4.1*	*0.81*
	Spanish	26	1199	12.5	3.9	0.78
	Portuguese	13	675	10.7	3.6	0.75
	British	5	200	8.9	3.3	0.75
	Cont. European	4	184	9.9	4.0	0.76
	Zebu	6	168	11.3	3.3	0.74
Pig	*Creole*[c]	*17*	*613*	*6.3*	*3.3*	*0.62*
	Iberian[d]	17	731	5.1	2.6	0.53
Goat[e]	*Creole*	*23*	*786*	*5.7*	*2.7*	*0.63*
	Iberian	24	775	6.4	2.9	0.65
	Canarian	5	200	5.6	2.8	0.64
	African	13	441	6.6	3.0	0.67
Horse[f]	*Creole*	*27*	*1414*	*7.8*	*4.1*	*0.76*
	Celtic-type	13	478	7.5	4.1	0.76
	Iberian-type	7	320	6.8	3.7	0.73
	Cosmopolitan	2	120	6.0	3.4	0.71
Donkey[g]	*Creole*	*13*	*350*	*4.4*	*2.2*	*0.54*

[a] Na = mean number of alleles; Ae = effective number of alleles; He = expected heterozygosity.
[b] Adapted from Martinez et al. (2012).
[c] Adapted from Revidatti et al. (2014).
[d] Adapted from Gama et al. (2013).
[e] Adapted from Sevane et al. (2018).
[f] Adapted from Cortés et al. (2016).
[g] Adapted from Jordana et al. (2016).

Table 2. Breed acronyms for Figs. 1 to 6.

Cattle (Fig. 1)	SPANISH. Betizu (BET), Toro de Lidia (TL), Menorquina (MEN), Alistana (ALS), Sayaguesa (SAY), Tudanca (TUD), Asturiana de los Valles (ASV), Asturiana de las Montañas (ASM), Retinta (RET), Morucha (MOR), Avileña (AVI), Pirenaica (PIRM), Rubia Gallega (RGA), Mallorquina (MALL), Monchina (MON), Serrana de Teruel (STE), Parda de Montaña (PM), Bruna de los Pirineos (BRP), Pasiega (PAS), Berrenda en Colorado (BC), Berrenda en Negro (BN), Marismeña (MAR), Pajuna (PAJ), Negra Andaluza (NAN), Vaca Canaria (VCA), Vaca Palmera (PAL); PORTUGUESE. Alentejana (ALT), Arouquesa (ARO), Barrosã (BARR), Brava de Lide (BRAV), Cachena (CACH), Garvonesa (GARV), Marinhoa (MARI), Maronesa (MARO), Mertolenga (MERT), Minhota (MINH), Mirandesa (MIRA), Preta (PRET), Ramo Grande (RG); CREOLE. Guabalá (GUA), Guaymi (GY), Texas Longhorn (TLH), Criollo Poblano (CPO), Criollo de Baja California (CBC), Criollo de Chihuahua (CHU), Criollo de Nayarit (CNY), Criollo de Chiapas (CHI), Blanco Orejinegro (BON), Caqueteño (CAQ), Sanmartinero (SM), Romosinuano (RMS), Costeño con Cuernos (CCC), Chino Santandereano (CH), Velasquez (VEL), Lucerna (LUC), Hartón del Valle (HV), Criollo Casanareño (CC), Criollo Ecuatoriano (EC), Criollo Uruguayo (CUR), Pampa Chaqueño (PA), Criollo Pilcomayo (PIL), Criollo Argentino (CARG), Criollo Patagónico (PAT), Caracú (CAR), Cubano (CUB), Siboney (SIB); ZEBU: Gyr (GYR), Brahman (BRH), Sindi (SIN), Guzerat (GUZ), Nelore (NEL), Zebu Cubano (CUZ); Other EUROPEAN. Friesian (FRI), Hereford (HER), Brown Swiss (BSW), Aberdeen Angus (AA), British White (BWC), Charolais (CHAR), Jersey (JER), Limousin (LIM), Shorthorn (SH)
Iberian Pigs (Fig. 2)	Alentejano (ALE), Bísaro (BIS), Malhado de Alcobaça (MAL), Celta (CEL), Chato Murciano (CHM), Entrepelado (ENT), Euskal Txerria (ETX), Lampiño (LAM), Manchado de Jabugo (MJA), Negro Canario (NCA), Negro de Formentera (NFO), Negro de los Pedroches (NPE), Negro Mallorquín (NMA), Retinto (RET), Torbiscal (TOR), Spanish Wild Boar (SWB), Portuguese Wild Boar (PWB)
Creole Pigs (Fig. 3)	Mulefoot (MF), Red Wattle Hog (RWG), Guinea Hog (GH), Pelón Mexicano (PEL), Baja California (BCA), Criollo El Salvador (SAL), Criollo Cubano (CUB), Crioolo Guadeloupe (GUA) Criollo Venezolano (VEN), Zungo (ZUN), San Pedreño (SPE), Criollo del Pacifico (PAC), Criollo Ecuatoriano (ECU), Criollo Boliviano (BOL), Pampa Rocha (PRO), Criollo Argentina Northeast Wet Region (ANW), Criollo Argentina Northeast Dry Region, (AND)
Goats (Fig. 4)	Iberian Peninsula - Pirenaica (PIR); Moncaína (MON); Azpi Gorri (AZ); Blanca de Rasquera (RAS); Guadarrama (GUAD); Retinta (RET); Verata (VERA); Blanca Andaluza (BLANCA); Celtibérica (CELTIB); Blanca Celtibérica (BC); Malagueña (MALAG); Murciano-Granadina (MG); Florida (FLO); Payoya (PAY); Negra Serrana (SER); Formentera (FOR); Pitiusa (IB); Mallorquina (MALL); Bravia (BR); Serpentina (SP); Algarvia (AL); Charnequeira (CH); Serrana (SR); Preta de Montesinho (PM); Canary Islands -; Ajuí (AJ); Majorera (MFV); Palmera (PAL); Tenerife Norte (TFN); Tenerife Sur (TFS); Africa - Cape Verde (CVERDE); Barki (BARKI); Baladi (BALADI); Saidi (SAIDI); Morocco Goat (MOR); Tunisian Local Goat (TU); Bushguinder (BU); Maradi (MARADI); West African Dwarf (WAD); Sahel (SAHEL); Gwembe Dwarf Goat (ZAM); Kalahari Goat (KAL); Boer (BOER); Outgroup - Rawhiti (RW); Arapawa Goat (ARAPA); Golden Guernsey (GG); Saanen (SAAN); Alpine (ALP); Anglo-Nubian (ANG); Creole - Spanish Goat (SPA); Myotonic (MYO); San Clemente Island (SCL); Criolla Cubana (CUB); Criolla Colombiana (COL); Criolla Venezolana (VEN); Criolla del Ecuador (ECU); Galapagos Goat (GAG); Criolla Peruana (PER); Azul (SAZ); Moxotó (MOX); Marota (MRT); Canindé (CND); Repartida (REP); Graúna (GRN); Sem Padrao Racial (SRD); Criolla Boliviana (BOL); Criolla Paraguaya (PGY); Criolla del Nordeste (NEA); Neuquina (NUQ); Chilluda (CHI); Pampeana Colorada (PCA); Angora (TAN)

(*continued*)

Table 2. (*continued*)

Horses (Fig. 5)	Cr. Argentino (CAR), Mangalarga (MGB), Marajoara (MJB), Pantaneiro (PNT), Puruca (PUR), Chilote (CHI), Isla de Pascua (ISP), Cr. Colombiano Vaqueria (CVC), Paso Fino Colombiano (CPF), Trocha Pura Colombiana (CTC), Trocha y Galope Colombiano (CTP), Trote y Galope Colombiano (CTG), Cr. Cubano (CUB), Cr. Ecuatoriano (CEC), Cr. Salvadore ~ no (CSA), Cr. Panameño (PAN), Cr. Paraguayo (CPA), Peruano de Paso (PEP), Cr. Uruguayo (CUR), Appaloosa (APA), Morgan (MOR), Quarter Horse (QHO), Rocky Mountain (RMU), Saddlebred (SDB), Spanish Mustang (SMU), Tennessee Walking (TWH), Mount Taylor Mustang (MTM), Arabian (ARA), Asturcon (AST), Burguete (BUR), Cabalo do Monte Galego (GAL), Hispano-Breton (BRT), Hispano-Arabe (HIA), Jaca Navarra (JNV), Losino (LOS), Mallorquin (MAL), Menorquin (MEN), Marismeño (MAR), Monchino (MON), Pirinenc Catala (PIC), Potoka (POT), Pura Raza Español (PRE), Thoroughbred (PSI), Retuertas (RET), Trotador Español (TRO), Garrano (GAR), Lusitano (LUS), Sorraia (SOR), Merens Pirineo Frances (MER), Barb (BER)
Donkeys (Fig. 6)	Creole: Argentina (ARG); Bolivia (BOL); Brazil (BRA); Chile (CHI); Colombia (COL); Cuba (CUB); Ecuador (ECU); Guatemala (GUA); Mexico (MEX); Paraguay (PAR); Peru (PER); Uruguay (URU); Venezuela (VEN); European: Mirandesa (MIR); Andaluza (AND); Balear (BAL); Catalana (CAT); Encartaciones (ENC); Majorera (MAJ); Zamorano-Leonesa (ZAM); Pantesco (PAN); Grigio Siciliano (SIC); Ragusano (RAG); Greek (GRE)

Ginja et al. (2013) studied conservation priorities in 67 Iberoamerican cattle breeds, based on genetic diversity criteria. Overall, Creole breeds have higher levels of genetic diversity, particularly those breeds that show signs of crossing with zebu. Of course, these are the breeds considered to be prioritized for conservation when the sole criterion of choice is the contribution of intra-racial variability to the total genetic diversity. However, when priority is given to inter-racial diversity, priority is given to the most differentiated breeds (Guabalá, Romosinuano, Criollo Patagonico, Siboney and Caracú). In approaches that combine the within- and between-breed components of genetic diversity, the priority depended on the weight assigned to each of them. Overall, the Creole breeds had a higher conservation priority than Iberian breeds.

At present, the research groups involved in the various consortia are undertaking additional studies, including breeds of different origins and combining various types of genetic markers, to investigate in greater detail the origin and genetic structure of the Creole bovine breeds.

3 Pigs

The BIOPIG Consortium has been studying the diversity and genetic structure of swine breeds in the Iberian Peninsula and the American continent.

In this context, Gama et al. (2013) used a panel of 24 microsatellites in a sample of 844 pigs representative of the major 17 native breeds in Portugal and Spain, and some groups of wild boars from these countries. Genetic diversity was high in the breeds studied, with an expected heterozygosity of 0.53 and an average of 5.1 alleles/locus (Table 1). The breeds with reduced census presented signs of genetic bottleneck (expressed as lower allelic diversity), while the more numerous breeds sometimes showed substructure. Between-breed diversity represented about 20% of the total genetic diversity, and was mainly explained by differences between the Celtic, Mediterranean and Basque groups, rather than differences between domestic and wild pigs. The different varieties of the Iberian Pig had a close relationship but were genetically distinct from each other and well-structured (Fig. 2). Significant genetic proximity with wild pigs was detected in the breeds of the Iberian branch, but not in Celtic breeds, which probably reflects admixture due to accidental crossbreeding with wild relatives in the Mediterranean group. The geographical distribution of genetic diversity essentially reflected differences in herd size and production systems between the north and south of the Iberian Peninsula, such that the spreading of the Iberian genetic influence across the territory almost exactly mirrored the distribution of the "dehesa-montado" system in which these pigs are traditionally raised. Hence, an interdependence between animal and agroforest resources clearly occurred, which underscores the important role played by native pig breeds towards environmental sustainability.

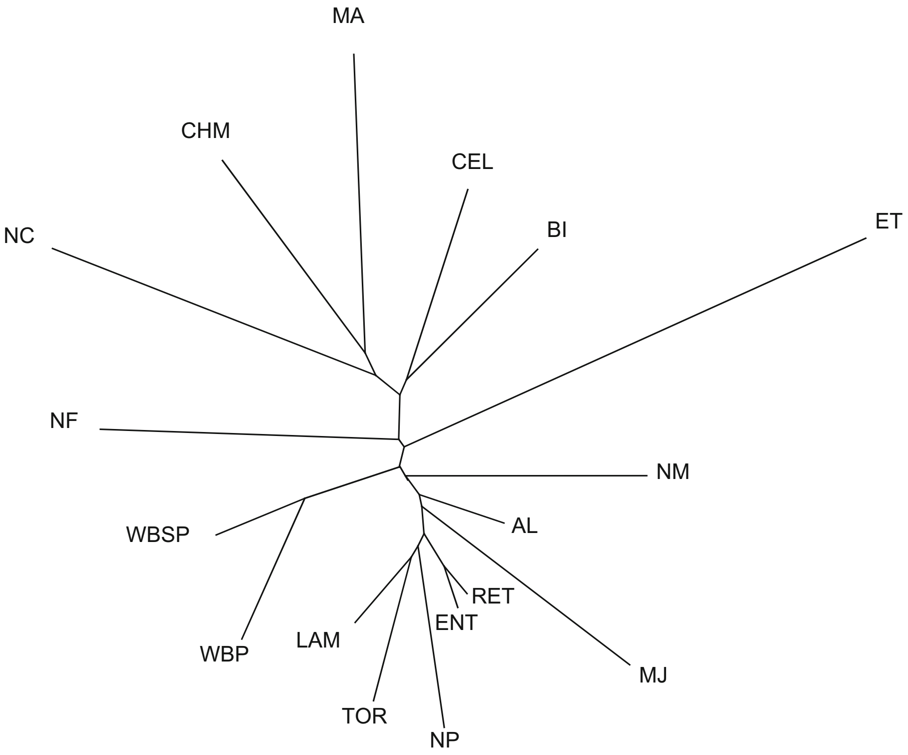

Fig. 2. Neighbour-joining tree summarizing the Nei D_A genetic distances among 17 native pig breeds from Spain and Portugal, and wild-boar pigs sampled in the two countries (Adapted from Gama et al. 2013). See Table 2 for definition of breed acronyms.

Revidatti et al. (2014) studied the diversity and genetic relationships in 17 Creole breeds from 11 countries of the American continent with 24 microsatellite markers. The expected heterozygosity was 0.62, with a mean of 6.25 alleles/locus (Table 1). The

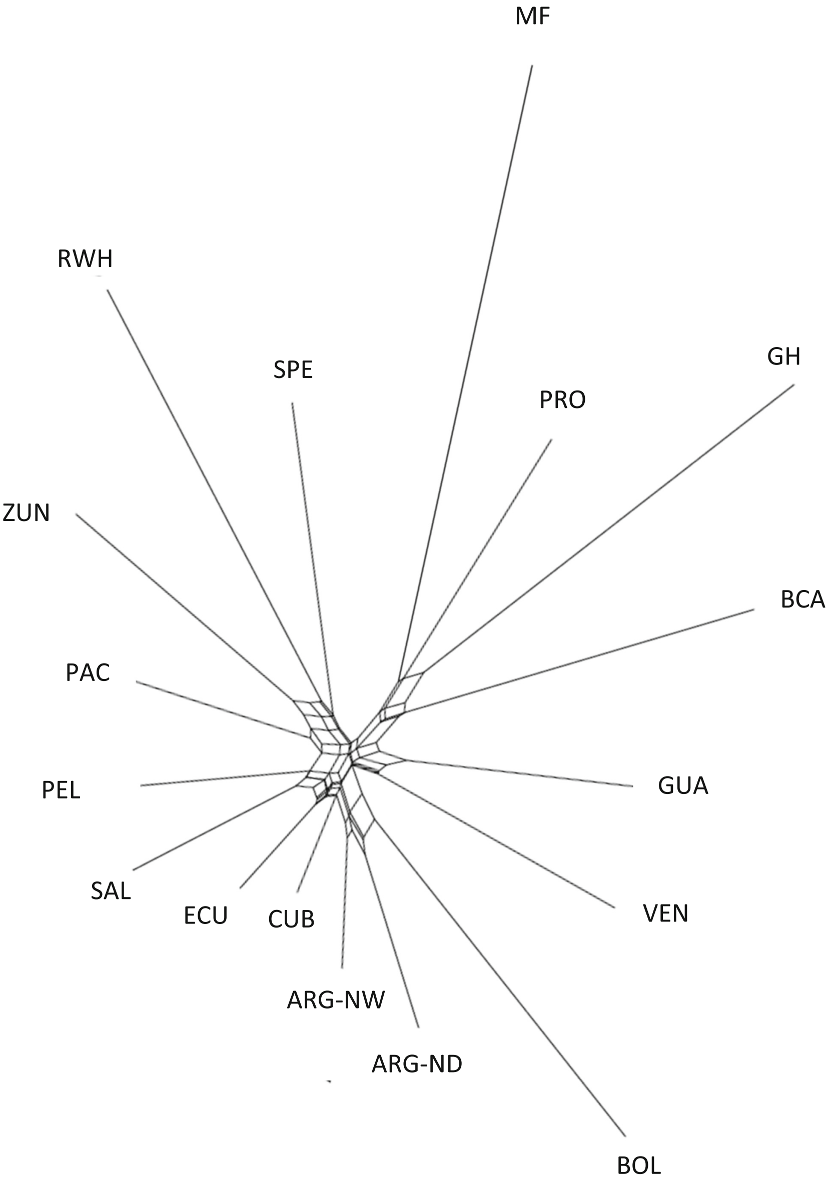

Fig. 3. Neighbournet dendrogram summarizing the Nei D_A genetic distances among 17 Creole native pig breeds (Adapted from Revidatti et al. 2014). See Table 2 for definition of breed acronyms.

proportion of genetic diversity represented by differences between breeds was 0.11 (indicating an important within-breed diversity), and nearly all breeds had a heterozygosity deficit. The Mulefoot and Guinea hog breeds from the United States formed a cluster with the Mexican from Baja California and the Uruguayan Pampa Rocha, while Colombian breeds clustered with the American Red Wattle breed (Fig. 3). The fact that some breeds with distant geographic distribution showed signs of genetic proximity between them may reflect a common origin in the initial phase of colonization.

Cortes et al. (2016) studied conservation priorities in 45 Iberoamerican and commercial swine breeds, corroborating that the priority given to each breed depends on the relative importance attributed to its contribution to inter- and intra-racial genetic diversity. When the major goal was the partial contribution to total heterozygosity, a high priority was given to Creole pig breeds, whereas Weitzman procedures prioritized breeds from the Iberian Peninsula. With the combined within- and between-breed approaches, different conservation priorities were achieved. The Core Set Kinship-based methodologies highly prioritized Creole pig breeds (in particular from Cuba, Colombia, Bolivia and Guadeloupe) while weighing the between- and within-breed components with F_{ST} and 1-F_{ST}, respectively, resulted in higher contributions of Iberian breeds. Of course, other factors in addition to the contribution to genetic diversity must be taken into account when setting conservation priorities.

4 Goats

The diversity and genetic structure of the Iberian Peninsula goat breeds were studied by Martinez et al. (2015), using 20 microsatellite markers in a sample of 975 representative animals of 25 officially recognized breeds in Portugal and Spain and 4 populations not yet recognized. The level of genetic diversity was high, with means of 0.65 for expected heterozygosity and 6.24 for the number of alleles/locus. Overall, breed differentiation accounted for about 7% of total diversity, and about half of the breeds had a heterozygosity deficit. Nevertheless, genetic differentiation between the breeds studied was generally small, with the exception of the breeds from the Canary Islands, which were quite distant from the continental breeds, possibly because of their isolation as well as the influence they received from African breeds in the past.

Ginja et al. (2017) used microsatellites to study a group of 910 animals, recruited in 24 Creole goat populations sampled in the American continent, and 112 animals from 3 cosmopolitan breeds. The genetic diversity found in Creole breeds translated into an expected heterozygosity of 0.64 and an average number of 5.82 alleles/locus, and the breeds from isolated islands (Galápagos and San Clemente) showed lower levels of genetic variability. The diversity found between the set of 27 studied breeds represented 13% of the total diversity. The breeds from Brazil were clearly differentiated relative to the others, and an additional cluster could be identified, corresponding to the Creole goat breeds from Argentina, Peru, Venezuela, Bolivia and Cuba. A small number of Creole breeds revealed the influence of commercial transboundary breeds.

A preliminary comparison of goat breeds from Portugal and Brazil was reported by Ribeiro et al. (2012), who studied in detail the 12 breeds recognized in both countries. The mean F_{ST} distances were 0.03 among Portuguese breeds, 0.07 among Brazilian

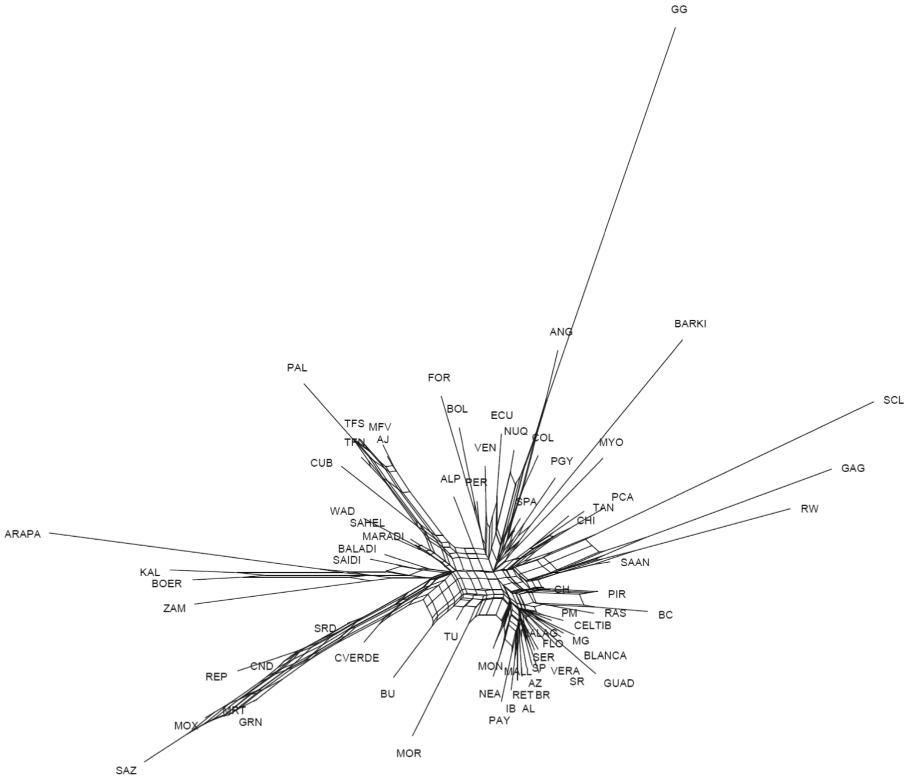

Fig. 4. Neighbournet dendrogram constructed from the Reynolds genetic distances among 71 goat populations (Adapted from Sevane et al. 2018). See Table 2 for definition of breed acronyms.

breeds and 0.15 between breeds from Portugal and Brazil. The breeds of each of the analyzed countries were in well-individualized clusters, approximately equidistant to the Alpine breed, which was used as an outgroup. However, some Brazilian breeds (Graúna and Canindé) showed signs of a possible link to the Portuguese breeds, albeit weak.

Sevane et al. (2018) studied the genetic diversity in 71 goat breeds, including 29 breeds from Spain and Portugal, 23 Creole breeds from the Americas, 13 breeds from Africa and 6 cosmopolitan plus New Zealand breeds using microsatellite markers. The major goal was to provide a comprehensive perspective on the genetic diversity in American goat populations and to assess their origins and evolutionary trajectories. The existing genetic diversity was highest in African breeds, followed by Iberian and Creole breeds (Table 1). The dendrogram representing breed genetic distances (Fig. 4) indicates the existence of three major groups, i.e., Iberian, Canary Islands and Brazilian breeds, such that most Creole populations grouped around Iberian breeds, consistent with a close genetic relationship among all these goats. The major exceptions to this pattern were the Brazilian, Colombian, and Cuban breeds, such that the Cuban breed shared their position with West African populations (Canary Islands, Bushguider from the Saharawi Camps, and Nigerian) while the Brazilian breeds grouped in one separate cluster, together with

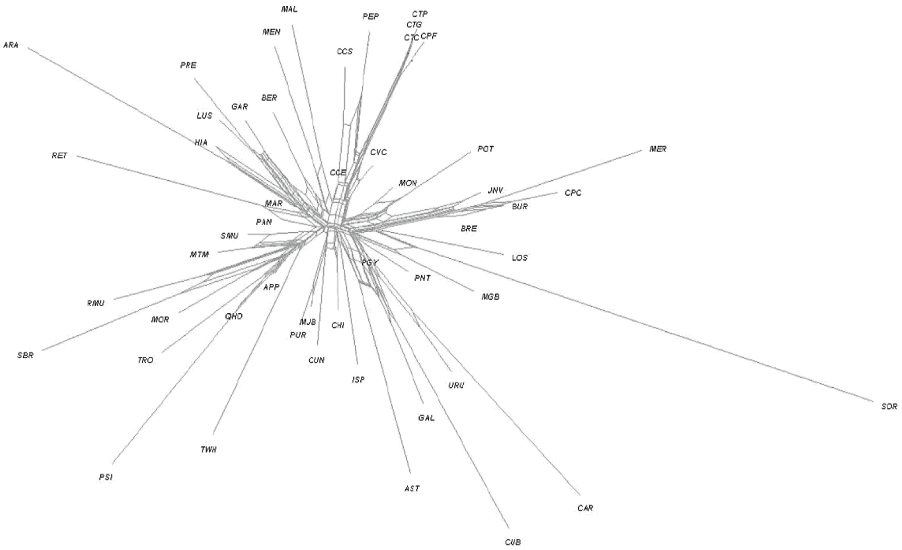

Fig. 5. Neighbournet dendrogram summarizing Reynolds genetic distances among 51 horse breeds (Adapted from Cortés et al. 2016). See Table 2 for definition of breed acronyms.

the goats from Cape Verde. Taken together, these results indicate a lack of geographical patterns in the distribution of goat genetic diversity in the Americas, with a wide differentiation among the various Creole breeds. Important Iberian signatures could be detected in nearly all Creole populations, with an important contribution of African populations to many Creole breeds. Some degree of genetic isolation was detected in Brazilian breeds, which had nevertheless some influence from Cape Verde goats.

5 Horses

The Biohorse consortium, established within the CYTED XII-H and CONBIAND Networks, gathered the efforts of various research groups working on Creole-type and related horse breeds throughout Iberoamerica.

Cortes et al. (2016) analyzed 25 microsatellite markers in 27 Creole breeds of horses sampled in the Americas, 19 breeds from the Iberian Peninsula, one breed from Morocco and one from France, and two cosmopolitan breeds (Thoroughbred and Arabian). Genetic diversity, assessed by the number of alleles/locus and expected heterozygosity, were highest in Creole horse breeds (Table 1). In the analysis of genetic relationships for the set of 50 breeds studied (Fig. 5) five clusters were identified, corresponding to: Celtic group; Iberian group; American breeds with Thoroughbred influence; majority of Colombian breeds; other Creole breeds. The last group was the one that presented greater proximity to the Iberian breeds. For the group of Creole breeds analyzed, the genetic contribution of the various founder clusters was approximately 50, 30 and 20% for the Celtic, Iberian and Arabian-Thoroughbred groups, respectively. Although they share a common origin, the Creole breeds of horses have their own identity and in most cases lack appropriate recognition and adoption of conservation programs.

6 Donkey

Donkeys played a very important role in the colonization of the American continent, both directly as working animals, but also as producers of mules, which were very important as animals used for transportation and draught. Jordana et al. (Jordana et al. 2016) used a panel of 14 microsatellites to study the genetic diversity, breed structure and relationships in a sample of 350 donkeys from 13 countries of the American continent, in comparison with samples from 476 animals from 11 asinine breeds from Italy, Greece, Portugal and Spain. The expected heterozygosity in the American breeds was 0.54, with an average of 4.4 alleles/locus (Table 1), which is much lower than the genetic diversity found in other livestock species in America. In the analysis of genetic relationships between breeds (Fig. 6), two well-identified clusters were detected in the American asinine population, including the breeds from Argentina, Bolivia, Chile, Ecuador, Paraguay, Peru and Uruguay, and in the second, the breeds from Cuba, Guatemala, Mexico and Venezuela.

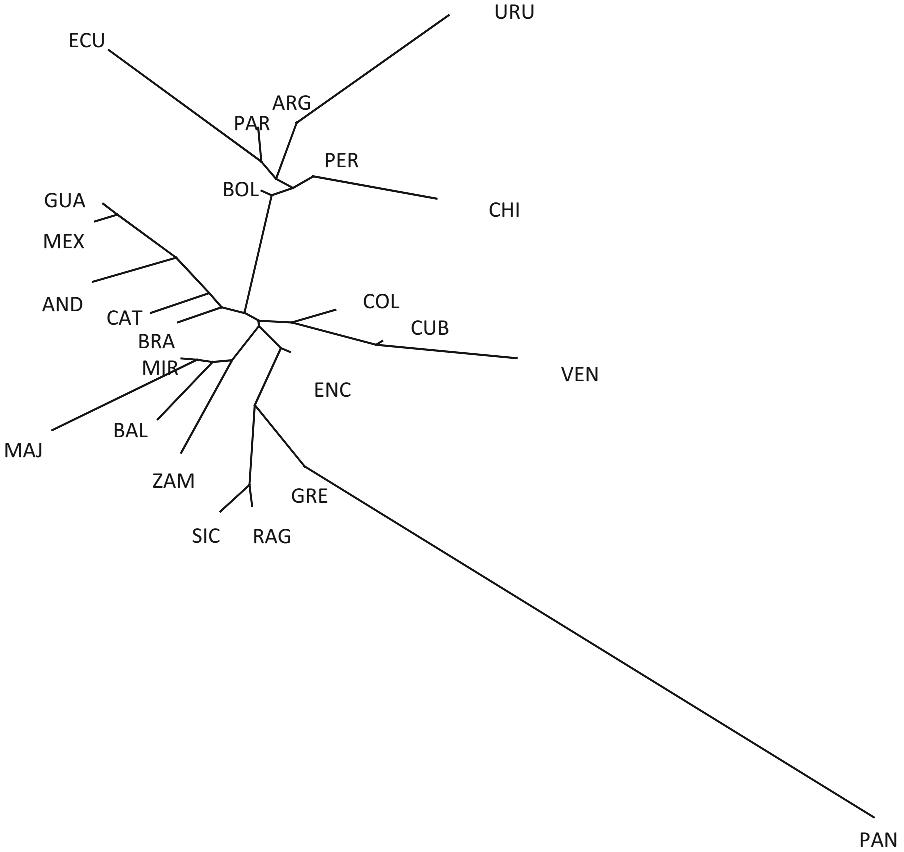

Fig. 6. Unrooted tree of Reynolds genetic distances for 24 American and European donkey populations obtained with the neighbour-joining algorithm (Adapted from Jordana et al. 2016). See Table 2 for definition of breed acronyms.

On the other hand, the breeds from Brazil and Colombia had mixed contributions from those two clusters. The breeds in the first cluster were close to each other, but away from the Iberian breeds, while the donkeys from Mexico and Guatemala showed influence of the donkeys from Andalusia and the donkeys from Brazil were close to those of Catalonia.

7 Conclusions

The Creole populations that currently exist in many countries of the American continent are the result of the introduction of Iberian breeds since the 15th century, possibly with additional influences from African breeds. More recently, Creoles have also been influenced by other breeds, especially in the last century.

In the last 10 years, a systematic research work has been carried out on the diversity and genetic structure of these Creole populations, accomplished by various research groups structured in consortia established in the framework of the CYTED XII-H and CONBIAND networks.

These studies allow us to conclude that, in all the species evaluated, the Creole breeds have high levels of genetic diversity, a unique identity and clear signatures of their origin in the breeds from the Iberian Peninsula. However, many of the Creole breeds are not adequately recognized or protected, and many show signs of genetic erosion either as a result of accumulated inbreeding due to their small census, or because of uncontrolled crossbreeding with exotic breeds.

The work carried out so far demonstrates the unique identity of the Creole breeds, their structure and genetic relationships, and therefore constitutes a fundamental basis for the adoption of measures aimed at the recognition, conservation and genetic improvement of these breeds, which result from more than 500 years of selective adaptation.

8 Future Perspectives

Research work similar to those described above is currently underway for the sheep species within the BIOVIS consortium, covering more than 70 sheep breeds, and the first results are expected to be available shortly. In recent years, other species have been incorporated into the research carried out by different CONBIAND groups working on the biodiversity of domestic animals, including chicken, turkey, guinea pigs, etc.

The development of panels of high-density genetic markers allows us to foresee new challenges, namely the possibility of investigating with non-neutral markers the diversity of Iberoamerican livestock populations. Indeed, the influence that Iberian breeds had in the development of Creole breeds, and the ability that they revealed to adapt to extremely diverse environmental conditions over the centuries, opens up excellent possibilities for investigating genetic markers associated with the unique adaptive mechanisms that these breeds have developed under very diversified environmental conditions. There is still much to be done and the synergies that have been established among the various research groups that have collaborated in the CONBIAND Network consortia are a guarantee that the fruitful cooperation that was established will continue and be strengthened, thus raising awareness, providing better knowledge and promoting the Creole breeds of Iberoamerica.

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