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Elucidating genomic candidate regions for trypanoresistance and body size in cattle of Burkina Faso

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Abbreviations and Acronyms

AAT: African Animal Trypanosomiasis

GHG: GreenHouse Gases

GWAS: Genome-Wide Association Study

LoCaBreed: Characterization and Sustainable Utilization of Local Cattle Breeds project

QTL: Quantitative Trait Loci

Dedication

To GOD the Almighty,

thank you for this grace

To my husband

Compaore Victorin Desiré

To my daughter

Compaore Anissa Manuella Wendpanga

In memory of

My Grand Parents, Yougbaré Ignance and Marie Lonfo

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Abstract

Burkina Faso is a landlocked country in West Africa with an economy primarily based on agriculture and livestock. Livestock production is confronted with enormous difficulties, among which the trypanosomosis, a blood-borne a parasitic disease, is one of the major obstacles. Among the indigenous cattle the taurine Baoulé cattle breed is known to be trypanoresistant. The general objectives of this thesis were to identify candidate genomic regions for trypanoresistance in purebred Baoulé and their crossbreds with Zebu cattle. The specific objectives were to 1) assess the morphometric traits of purebred and crossbred Baoulé cattle; 2) to carry out a genome-wide association study (GWAS) for trypanoresistance and morphometric traits in purebred and crossbred Baoulé cattle and 3) to identify selection in response to trypanosome infection in local cattle breeds and their crossbreds.

The study was carried out in the south-western region of Burkina, including 737 animals genotyped with the Illumina Bovine SNP50 BeadChip from the Bouroum-Bouroum, Kampti and Loropéni departments. Cattle were measured for quantitative and qualitative traits; blood samples have been taken for the diagnosis of positive or negative trypanosome infection by indirect Elisa test and DNA extraction. For the morphometric characterization the quantitative traits were analyzed by fitting the linear model and the chi square test was performed for qualitative traits. The results provided evidence for difference between purebred and crossbred populations, and among crossbreds for all traits. The GWAS and local ancestry analyses found several important genomic regions that can influence morphological parameters and trypanoresistance. Ancestry informative SNPs with highest F_{ST} values were selected to identify hybrids and monitor breeding initiatives in Baoulé cattle. The results of this thesis will serve as basis for further characterization, conservation and improvement strategies for purebred and crossbred Baoulé populations.

Keywords: cattle, Burkina Faso, trypanosomosis, Phenotypic characterization; crossbreeding, GWAS, admixture, selection signature

Zusammenfassung

Burkina Faso ist ein Binnenstaat in Westafrika, dessen Wirtschaft hauptsächlich auf Landwirtschaft und Viehzucht basiert. Die Viehzucht ist mit enormen Herausforderungen konfrontiert, darunter Trypanosomiasis, eine durch Blut übertragene parasitäre Krankheit. Eine heimische Rinderrasse, Taurin-Baoulé, ist gegen Trypanosoma resistent. Hauptziel dieser Studie war die Identifizierung von genomischen Regionen für Trypanoresistenz bei reinrassigen Baoulé und deren Kreuzungen mit Zebu-Rindern. Spezifischen Ziele waren: 1) Bewertung der morphometrischen Merkmale von reinrassigen und gekreuzten Baoulé-Rindern; 2) Durchführung einer genomweiten Assoziationsstudie für Trypanoresistenz und morphometrische Merkmale bei reinrassigen und gekreuzten Baoulé-Rindern und 3) Identifizierung der Selektion als Reaktion auf eine Trypanosomen-Infektion bei lokalen Rinderrassen und deren Kreuzungen. Die Studie umfasste 737 Rinder, welche mit dem Illumina Bovine SNP50 BeadChip genotypisiert und auf quantitative und qualitative Merkmale bewertet wurden. Zur Diagnose einer Trypanosomiasis wurden Blutproben für indirekte Elisa-Tests und DNA-Extraktionen entnommen. Die morphometrische Charakterisierung erfolgte anhand linearer Modellierungen der quantitativen Merkmale. Für die qualitativen Merkmale wurde ein Chi-Quadrat-Test durchgeführt. Die Ergebnisse zeigten für alle Merkmale Hinweise auf Unterschiede zwischen reinrassigen und gekreuzten Populationen, sowie auch zwischen verschiedenen Kreuzungen. Die genomweiten Assoziationsstudien und die Abstammungsanalysen ergaben mehrere wichtige Genomregionen, die die morphologischen Parameter und die Trypanoresistenz beeinflussen können. Die SNPs mit den höchsten FST-Werten wurden ausgewählt, um Hybriden zu identifizieren und Zuchtinitiativen bei Baoulé-Rindern zu überwachen. Die Ergebnisse werden als Grundlage für weitere Charakterisierungs-, Konservierungs- und Verbesserungsstrategien für reinrassige und gekreuzte Baoulé-Populationen dienen.

Schlüsselworte: Rinder, Trypanosomosis, Burkina Faso, Phänotypische Charakterisierung, Kreuzungszucht, GWAS, Hybridisierung, Selktionssignaturen

1. INTRODUCTION

African animal trypanosomiasis (AAT) is a parasitic disease caused by protozoa of the Trypanosoma genus, which develops in the blood and blood tissue, and lymphatic system of mammalian hosts. Trypanosomosis, due to *Trypanosoma congolense (subgenus Nannomonas), T. brucei (subgenus Trypanozoon) and T. vivax (subgenus Duttonella)* (Silbermayr et al., 2013) constitute a major obstacle to the development of livestock breeding in the areas of humid and sub-humid sub-Saharan Africa infested with tsetse flies, which are the biological vectors of these parasites (Hill et al., 2005). Areas infested with tsetse flies (*Glossina sp*) are, however, for the most part those that offer the greatest potential fodder for animal feed and for farming (MacLennan, 1981). The negative consequences of animal trypanosomosis are enormous because they induce significant direct economic losses, due to morbidity and the high mortality they cause in livestock. In addition, they cause delay of growth in young animals, loss of weight, lower milk production, shorter lactations, reduced work strength, infertility, abortions in pregnant cows and death (Hoste et al., 1992; Murray et al., 1990). In susceptible animals, death occurs within a few weeks to a few months after infection. In addition to this, the breeder has increased costs due to trypanocide medications. The costs of direct losses (animal mortality) and indirect losses (drop in production, cost of the prophylaxis and treatment) related to AAT, the main disease parasite of ruminants in tsetse-infested areas, were estimated to about US$ 4 billion annually about 20 years ago (d'Ieteren et al., 1998; Kristjanson et al., 1999).

An effective fight against AAT is a major challenge for the development of animal breeding and agriculture in Sub-Saharan Africa. Current control methods are essentially based on the administration of trypanocides to vertebrate hosts as a cure and on the control of insect vectors as a preventive measure. The use of trypanocidal drugs is, however, expensive, and access to them often difficult. In addition, they tend to lose by efficiency due to the constant increase in trypanosome resistance to the most often used drugs (Delespaux et al., 2008). In addition, the control of the vector populations, using traps, screens or animals impregnated with insecticides, is possible but requires the active and constant participation of all the actors in the production system. This type of control requires significant mobilisation efforts, which are sometimes difficult to achieve. The eradication of vectors is undoubtedly possible in a few specific, geographically small and highly fragmented areas (Bouyer, 2006). The complete eradication does not seem plausible in all the infested areas of the African continent, however, because of

the difficulty of the control, the high costs and the extraordinary time required for the eradication programme, as well as the high probability for re-invasion of the sanitized areas. The effectiveness and sustainability of vector control requires constant effort and monitoring. Finally, the high antigenic variability of trypanosomes currently reduces any hope of developing an effective conventional vaccine in the field (Anene et al., 2001). Traditional control methods are therefore unsatisfactory and an alternative method must be found.

It has long been noted that certain taurine breeds in West and Central Africa have been found to be naturally tolerant of the AAT disease (Murray et al., 1982) than the susceptible Zebu (*Bos indicus*) populations, the main breed of the sahelian regions obliged to graze in the south-western region where natural resources are abundant and can only be maintained in tsetse challenged areas through the use of costly trypanocidal drugs. These tolerant breeds could be divided to 1) "long-horn" taurines, represented by the N'Dama breed, 2) "shorthorn" taurines represented by the so-called "savannah" types (Baoulé and Somba breeds) and 3) the "forest" taurines (Lagunaires and Muturu breeds). These animals are better able to control parasitaemia, i.e., the multiplication of parasites in the blood, and the development of anemia during infection (Murray et al., 1979; Paling et al., 1991). Subsequently, these taurines are affected to a much lesser extent (if at all) by AAT, they develop and grow better, and remain more productive in a tsetse-infested area, compared to zebu breeds or exotic cattle. This capacity has been named trypanotolerance. .

The trypanotolerance is also heritable. Quantitative genetic studies showed that maintenance of hematocrit and productivity under trypanosomal pressure is heritable and that hematocrit control was strongly correlated with productivity (Trail et al., 1990). Thus, the breeding of trypanotolerant cattle could represent an interesting alternative to the very expensive control methods whose effects remain unsustainable. However, current knowledge on trypanotolerance does not allow for efficient selection or crossbreeding schemes. The selection of animals on their own performance (mass selection) proves to be extremely difficult, since the animals would have to be infected and allowed to develop the disease in order to measure their degree of tolerance, which is of course not acceptable for the breeders. The spread of beneficial effect by selection or crossbreeding will therefore be based on the possibility to precisely characterize the trypanotolerant phenotype at the genetic level.

It is therefore essential to be able to characterize the fine chromosomal regions (QTL, quantitative trait loci), or even the genes involved in trypanotolerance. The identification of these regions or genes will enable the design and implementation of selection on trypanotolerance in cross-breeding programs.

Aim of the thesis

The thesis aims to identify candidate genomic regions influencing trypanoresistance in purebred Baoulé and their crossbreds with Zebu cattle.

The specific objectives were to:

1) Carry out morphometric characterization of purebred and crossbred Baoulé cattle in Burkina Faso

2) Carry out a genome-wide association study for trypanoresistance and morphometric traits in purebred and crossbred Baoulé cattle of Burkina Faso

3) Identify selection in response to trypanosome infection in local cattle breeds and their crossbreds in Burkina Faso

The PhD thesis is structured as follows:

First of all, I present a literature review of the current knowledge on trypanotolerance and trypanoresistance traits; then the material used for the study and the methods that have been used to collect the data from the field, and analyze it in the laboratory and *in silico* with various software. Finally, the results and the relevant discussions with general reflections are presented. The concluding remarks at the end highlight the most important findings and show the way forward for these populations.

2. LITERATURE REVIEW

2.1. African animal trypanosomiasis

2.1.1. Definition and differences between trypanotolerance and trypanoresistance

The notion of trypanotolerance and trypanoresistance comes from PARIS' (1906) observation that humpless cattle, or taurines, in West Africa were able to survive in tsetse-infested areas, and that they suffered less than humped cattle, or Zebus, from trypanosomal infection. Since then, different definitions have been proposed to characterize trypanotolerance and trypanoresistance. In parasitology, Bishop and MacKenzie (2003) define "resistance" as the aptitude of an animal to resist infection (invasion of the organism and multiplication of the parasite) or to control the life cycle of the parasite. With the word "tolerance" they define the aptitude of an animal infested by a parasite to resist the pathogenic effects of the infection, i.e. the disease. In the case of West African taurine animals, we speak about trypanotolerance, because trypanosomes only cause a latent infection, without overt clinical signs, accompanied by a production of antibodies. However, there is sometimes a phenomenon of natural elimination of parasites called "self-cure". Thus, trypanotolerant animals are capable of better survival in areas infested with tsetse flies (Murray et al., 1982). Under natural conditions and under presence of a considerable number of tsetse flies, these animals show compared to trypanosensitive animals (such as Zebu type or other exotic breeds):

- Less mortality;
- Lower parasitaemia;
- The capacity to develop a less severe anemia;
- Higher weight gain and reproductive performance.

In West Africa, trypanotolerant cattle are tolerant to both *T. congolense, T. brucei* and *T. vivax*. However, the degree of resistance is higher against *T. vivax* than against *T. congolense* (Mattioli et al., 1999; Murray et al., 1982). It is essential to note that trypanotolerance does not evoke immune tolerance, which is characterized by the absence of an immunological reaction after the introduction of a pathogen into the organism. It is to avoid this possible confusion that some authors preferred in the past the term trypanoresistant (Duvallet, 1987). In this document, we will use the term trypanoresistance to express that it is a tolerance to the effects of the infection, thus to survive and to remain productive in areas infested with tsetse flies.

In Africa, the trypanotolerant character is also found in wildlife, such as buffaloes, antelopes, warthogs, and others (Grootenhuis et al. (1982) cited by Murray et al., (1990)) and in other

domestic animals such as Djallonke sheep and dwarf goats (Geerts and Raes, 2009; Murray et al., 1982).

2.1. 2. Trypanotolerant and trypanosensitive cattle breeds

2.1.2.1 Origin of the cattle populations in Africa

Today, the African continent is uniquely rich in cattle diversity with around 150 African cattle breeds or populations recognized (Kim et al., 2017; Mwai et al., 2015). These are grouped according to their phenotypes into taurine, zebu, and the ancient stabilized taurine × zebu crossbreed known as Sanga (Hanotte, 2002). Importantly, it is now well established that African cattle carry a taurine maternal ancestry originating from the Near East taurine domestication center(s), while the possible genetic contribution of the now extinct African Auroch (*Bos primigenius opisthonomous*) remains unclear (Bonfiglio et al., 2012; Decker et al., 2014a)

Based on archaeological and molecular studies of African cattle populations (Bradley et al., 1996; Epstein, 1971; Hanotte, 2002; Loftus and Masson, 1994; MacHugh et al., 1997) the *Bos taurus* cattle without the cervico-thoracic hump had been domesticated in Africa and the Fertile Crescent. The first African cattle breeds would be derived from Hamitic cattle (Aurochs, *Bos primigenius primigenius*) that populated northern Africa via Egypt about 7000 years ago. These animals would be the ancestors to the current long-horned taurine, the N'Dama and Kouri. On the other hand, Zebus, or cattle with cervico-thoracic hump (*Bos indicus*), entered the African continent later, via the Horn of Africa (Bradley et al., 1996; Epstein, 1971; Hanotte, 2002; Loftus and Masson, 1994; MacHugh et al., 1997). According to archaeological studies, there was a center of domestication of the Aurochs African, *Bos primigenius opisthonomus*, in the north-oriental region of the African continent at least 9000 years ago (Wendorf and Schild, 1994). Regarding the origin of Zebus, two theories were put forward. The first was that Zebus originate from crossbreeding and selection of *Bos taurus* populations. The second theory proposed that the Zebus were the subject of independent domestication by the first Baluchistan society (in present Pakistan). This last hypothesis is supported by the recent molecular data, denoting the South Asian subspecies of Aurochs (*Bos primigenius namadicus*) as the most probable wild ancestor of Zebu cattle (Meadow, 1993; Bradley et al., 1996; Loftus and Masson, 1994).

When it comes to the spread on the African continent, the taurine populations penetrated the forested, humid and sub-humid areas of West Africa around 4000 BC (Freeman et al., 2004a;

MacDonald and MacDonald, 2000; Marshall and Hildebrand, 2002) while Zebus only began to migrate there around 1000 BC (MacDonald and MacDonald, 2000). Larger-scale migration of Zebus has only occurred from 700 AD, especially during the epidemic of cattle pest disease that decimated the populations taurine cattle at the end of the 19th century (Epstein, 1971; MacHugh et al., 1997). Consequently, the earlier arrival of taurine populations in the savannah and forests of West Africa could explain their better adaptation to subtropical regions infested by tsetse fly (or glossinae) and their tolerance to trypanosomiasis. The introduction of Zebus in these regions was only effective with the help of veterinary prophylaxis and the destruction of tsetse habitats via deforestation (Lhoste, 1991).

Thus, it seems reasonable to assume that the trypanotolerance of West African taurines would be an adaptive trait responding to the selection pressure exerted by trypanosomes from the moment they were introduced to the enzootic zone. More generally, the natural and artificial selection pressure, and the combined effects of the migration and genetic drift have contributed to the development of a wide variety of trypanotolerant cattle populations.

2.1.2.2 African cattle breeds

Morphologically, taurines have a smaller size than Zebus. In addition, there are also populations with different levels of crossbreeding between these two large groups. It should be noted that due to the history of human migrations and animal exchanges, the taurine and Zebu dichotomy is not straightforward in Africa. West African animals have a high proportion of taurine, while in East Africa the Zebus are prevalent (Freeman et al., 2004a, 2006; Hanotte, 2002).

2.1.2.2.1 Trypanotolerant cattle breeds

2.1. 2.2.1.1 Long-horned taurine cattle

The current representatives of the long-horned taurines are the N'Dama and Kouri.

The N'Dama (Figure 1A) is the largest population, with about 4.9 million head representing 49.5% of the 9.8 million trypanotolerant cattle (Hoste et al., 1992). The birthplace of the breed is in the Fouta-Djallon highland in Guinea, but its area of distribution is much larger covering Gambia, western Guinea-Bissau, southern Senegal and Sierra Leone, northeastern Liberia, northeastern Côte d'Ivoire, and Mali (Dayo, 2009a). The N'Dama cattle was also imported into many other countries in West Africa (Benin, Burkina Faso, Ghana, Nigeria, and Togo) and

Central Africa (Cameroon, Congo, Gabon, Central African Republic, and Democratic Republic of Congo).

The Kouri (Figure 1B) represents a special case of African cattle living on and around the border of the islands of Lake Chad (Zafindrajaona et al., 1999). These are morphologically, taurines (they do not have a cervico-thoracic hump), have long horns with a characteristic bulbous form. They have the characteristic submetacentric Y chromosome of taurines, compared to Zebus, which have an acrocentric Y chromosome, but the genetic characterization of Kouri using autosomal genetic markers shows that half of their genome is of Zebu origin (Dayo, 2009a; Freeman et al., 2004b; Zafindrajaona et al., 1999). Furthermore, unlike other West African taurines, the trypanotolerance of Kouri is not clearly established as no serious studies have been conducted on this subject. Their origin also remains obscure and controversial. The Kouri may have originated from crosses between side-horned Zebus and long-horned Hamitic taurine from East Africa, Upper Egypt, and current Ethiopia (Dagris, 2005).

Figure 1A and 1B: Taurins N'Dama (left) and a Kouri cattle (right) ***(Dayo, 2009)***

2.1.2.2.1.2 Short-horned taurine cattle

The short-horned taurine is mainly present in Southwest and Central Africa. Due to the environment in which they are found determines the size of the animals. This group can be subdivided into two types:

- The forest types or small taurine (80 to 90 centimeters height at withers) found in the coastal and forest zones, represented by very small populations (100,000 head or about 1% of the trypanotolerant cattle population) (Hoste et al., 1988; Shaw and Hoste, 1991).

These are the Lagunaires (Figure 2), with a distribution area covering Benin, Côte d'Ivoire, Ghana, Democratic Republic of Congo and Togo; the Muturu (in Nigeria) and the Manjaca breed (in Guinea Bissau). Note that the Manjaca breed is extinct (Dayo, 2009a)..

These different small breeds probably derive from the savannah type with a reduction of body size related to the selection pressures exerted by the rainforest environment where the fodder is poor and the climate is hard (Hoste et al., 1988).

Figure 2: Herd of Lagunaires taurins in Benin (Dayo, 2009)

- The savannah type cattle measures about 90 to 110 centimeters at withers with an estimated population of about 600,000 to 870,000 heads (Rege et al., 1994). They occupy the Guinean or Sudano-Guinean savannas from Côte d'Ivoire to Cameroon. The main breed is the Baoulé cattle (Figure 3).

The Baoulé cattle (also called Lobi cattle) is a rectilinearly shaped breed. The neck is a little short, thicker and carried horizontally in males, but light in the females. The average birth weight of calves is 13 kg (Soro et al., 2015). One of the important characteristics of the Baoulé cattle, living in the south-west of Burkina Faso, is its trypanotolerance. This breed is perfectly adapted to areas infested with tsetse flies, which are vectors of the African Animal Trypanosomosis (AAT), a major parasitic disease in sub-humid and humid zones of sub-Saharan Africa.

Figure 3: Baoulé cattle from Burkina Faso (photo: Yougbaré, 2017)

2.1.2.2.2 Trypanosensitive breeds

On the African continent, the trypanosensitive breeds are represented mainly by the Zebus (Dayo, 2009a). Exotic taurine cattle are also trypanosensitive (d'Ieteren et al., 1998; Murray et al., 1990). The Zebu breeds (Figure 4) are numerous, diverse and distributed mainly in areas lacking glossinae, most often in Sahelian areas, as they are well adapted to warm conditions. Moreover, due to their large size they are more interesting for breeders. During the dry periods of the year, however, the Zebus need to move for several months to more humid areas in search of greener pastures and watering points.

Figure 4: Zebu bull from Burkina Faso (photo: Zoma, 2019)

2.1.2.2.3 Crossbred African Zebu and taurine cattle

The products of crosses between trypanosensitive and trypanotolerant cattle most often have an intermediate behaviour with regard to the pathogenicity of trypanosomes (Murray et al., 1982). Among these populations, some are more or less stabilized crosses, such as the Borgou breed in Benin and Togo, Keteku in Nigeria, Djakoré in Senegal, and Sanga in Ghana.

On the other hand, the situation of the Bambara or Méré in Mali, Côte d'Ivoire and Burkina Faso (Figure 5) and Guinea remains relatively unstable. The size of the crossbred population is estimated at about 2.9 million (Hoste et al., 1988; Shaw and Hoste, 1991).

Figure 5: Crossbred Baoulé-Zébu from Burkina Faso (photo: Soudré, 2019)

In this crossbred population, there is a large individual variability in disease tolerance compared to trypanotolerant taurines, as has been shown in the Borgou cattle breed in Benin (Doko et al., 1997) .

2.1.3 Changes in population size for taurine and zebu cattle

There are approximately 33 million heads of cattle in West Africa. Of them, about 23 million heads correspond to humped Zebu animals while the rest include a number of hump-less taurine populations (Traoré et al., 2015). In 1985, trypanotolerant cattle populations were estimated at 9.8 million head in 19 countries in West and Central Africa (Hoste et al., 1988). An FAO report on the numbers of trypanotolerant breeds, dating back to 1998, reported 11.7 million cattle (Agyemang, 2005). However, this report did not detail the share of the different groups (long-horned and short-horned taurines) in the total number of trypanotolerant cattle. Trypanotolerant breeds account for about 5% of the cattle population, i.e. about 8 million of the 147 million cattle recorded in these countries (Murray et al., 1990).

The numbers of pure taurine breeds are in decline, which could be explained by two factors. On the one hand, there is an overall decline in the areas inhabited by tsetse flies corresponding to the decline in isohyets (Courtin et al., 2008) as well as a deterioration of their habitat caused by anthropic and climatic factors (Bouyer, 2006). For example, the clearing of savannahs and the degradation of the cordons cause local reduction or disappearance of glossins (Bouyer et al., 2007) Thus, Zebu populations enter humid areas or, more radically, Zebu breeders become established in humid areas where they replace taurine breeds, as for example in Nigeria between Muturu taurins and Fulani White Zebus (Jabbar and Diedhiou, 2003). Also, the owners of trypanotolerant breeds often cross their cattle with larger Zebus to obtain larger animals, which also leads to the decrease of purebred taurine populations. A complete replacement with trypanosensitive breeds is also being done, even if the breeders are obliged to regularly use trypanocidal drugs as a consequence. Indeed, taurines are generally small animals, from low productivity and whose trypanotolerance is limited at the local level (related to the local trypanosome strains). Targeted breeding and selection practices also in trypanoresistant taurine breeds, however, could yield a greater benefit and increased productivity. Studies conducted in 19 countries in the most humid parts of West Africa and of Central Africa have shown that even in a low-risk trypanosomal area, the productivity of N'Dama and West African short-horned taurines was equivalent to that of trypanosensitive Zebus (Murray et al., 1990). In addition, trypanotolerance might not be limited at the local

level, as shown by the taurine Lagunaires and N'Dama successfully imported and established in 1920 in Zaire (current Democratic Republic of Congo), far from the cradle of the breed (Dargie et al., 1979). However, a study carried out to determine perceptions and assess the characteristics of cattle in the peri-urban dairy farms of Bobo-Dioulasso (Burkina Faso) has shown that with the improvement of production conditions, taurines were often excluded from the herds despite their great adaptability to the environment of the subhumid zones (Hamadou and Kamuanga, 2004). The study also revealed that only F1 crosses between taurines and Zebus fulfilled the criteria of the breeders, like large size and high productivity, which could explain the strong degree of crossbreeding of breeds in peri-urban farms.

2.1.4 Genetic background of trypanotolerance – early detection methods

Studies have shown that trypanotolerance is a quantitative and multigenic trait (Dolan et al., 1994). The disease resistance of first generation (F1), resulting from the crossing between the zebu Boran and the taurine N'Dama, is intermediate between those of the parents (Leak et al., 1993). The maintenance of hematocrit and productivity under parasitic pressure had a good heritability and that hematocrit was highly correlated with productivity. Indeed, a study conducted on N'Dama taurines in Gabon showed that the heritability of growth, mean hematocrit and minimum hematocrit were 0.39 ± 0.31 standard deviation (SD), 0.64 ± 0.33 SD and 0.50 ± 0.32 SD, respectively (Trail et al., 1990). In F2 cattle from the N'Dama taurine and Boran Zebus crossing, van der Waaij et al. (2003) evaluated the heritability of the mean hematocrit at 0.31 ± 0.19 SD while the mean and log parasitaemia weights were 0.11 ± 0.11 SD and 0.18 ± 0.15 SD respectively. The extremely negative impact of bovine trypanosomiasis on the farm, the limitations of control methods and the existence of a genetic component of trypanotolerance have led to a significant increase in the incidence of the disease, and has pushed the various African and European research structures to take an early interest in the identification of markers associated with this trait. However, the first research projects were oriented to research on breed markers (Belemsaga et al., 2005; Quéval and Bambara, 1984). Molecular genetics research related to trypanotolerance has benefited from the development of the tools available during the 1990s (bovine genetic and physical maps, experimental devices, numerous polymorphic markers, computer tools and statistics). Various approaches were used to research trypanotolerance in African taurine breeds:

- the genetic mapping (or linkage analysis) approach, which was consistent with the research of QTL (Quantitative Trait Loci) on an experimental population of type F2, obtained from the

crossing of F0 individuals from trypanotolerant populations (N'Dama) and trypanosensitive (Zebu Boran). The objective was to identify chromosomal regions that were involved in the variability of tolerance and/or sensitivity to trypanosomiasis. This was assessed after experimental infection of animals (Hanotte et al, 2003) ;

- the transcriptomic approach, which aimed to identify over- or under-expressed genes during the infection and which could explain the tolerance and/or susceptibility (Berthier et al., 2008, 2003; Hill et al., 2005; O'Gorman et al., 2009);
- the metabolic pathway-based method, which combined the previous two types of information (Fisher et al., 2007; Rennie et al., 2008).

2.2. Genome wide association studies

The *Bos taurus* genome was sequenced and initially published in 2009, within the Bovine genome project (Eck et al., 2009), with the most recent update of the ARS-UCD1.2 assembly from 2018. With the advent of high throughput genotyping technologies, the discovery of cattle SNPs and the development of commercial cattle SNP-chips with tens and hundreds of thousands polymorphic markers, the analysis of the genome has become possible. SNP-chips can be used for genome wide association studies (GWAS) to find SNPs that are in linkage disequilibrium (LD) with a quantitative trait locus (QTL) with a trait of interest. The main purpose of a GWAS is to identify chromosome regions that harbor the gene(s) that contribute to the phenotypic variation of a trait, which then could serve as putative regions of QTL for further studies (Sahana et al., 2010). Moreover, because of the high density of SNPs in GWAS, it is better suited for fine-mapping of QTLs compared to traditional linkage analysis which usually estimates QTLs within very large chromosome intervals (Goddard and Hayes, 2009). Hence, GWAS can be expected to have higher power than linkage studies to detect QTLs behind quantitative traits that are influenced by many genes of small effects (Cordell and Clayton, 2005; Sahana et al., 2010).

GWAS can be categorized into SNP-based and haplotype-based analyses. A haplotype-based analysis is generally regarded as a powerful approach to detect rare causative variants. Nevertheless, statistical analyses in current GWAS mostly focus on SNP-based analyses because of problems with unclear solutions generally occurred in haplotype-based analyses, for example, the loss of power due to many degrees of freedom, an uncertainty to define haplotype phases or unsuitable assumptions commonly used to impute missing phases (Balding, 2006; Meng and Fingerlin, 2008; Wason and Dudbridge, 2010).

A number of genome-wide association studies have targeted African cattle for the investigation of selection signatures (Bahbahani et al., 2018; Kim et al., 2017; Taye et al., 2017). These studies have also applied different selection scan approaches and have utilized genome wide SNP data ranging from low density SNP data (50K chip) to full genome sequences. The focus of these studies has largely been to identify selection signatures related to tropical environmental adaptation (disease resistance, tick resistance, and heat tolerance), production traits (milk and meat production) and morphological traits (coat color and growth traits).

Several studies have reported results in the West African longhorn N'Dama cattle from Guinea and Gambia using low to high density SNPs data (Barendse et al., 2009; Dayo et al., 2009; Gautier et al., 2009) and full genome sequence data (Kim et al., 2017; Taye et al., 2017). The reason being that N'Dama cattle is the most popular among West African breeds might be that it is often referred to as the trypanotolerant breed of reference.

Unravelling the genetic basis of trypanotolerance has been the major drive for the genome wide studies in N'Dama cattle. Candidate genes such as *ARHGAP15, TICAM1, INHBA, SLC40A25* and *HCRTR1* which are of relevant to trypanotolerance traits including the control of parasitemia, anaemia and feeding behaviour have been reported. The validation of these findings in other trypanotolerant cattle breeds will be a worthwhile pursuit.

2.3. Genetic structure of crossbred populations

The genome of crossbred (admixed) individual is a mosaic of ancestral haplotypes formed by recombination occurring at every generation (Price and Stephenson, 2009; Sankararaman et al., 2008). In a recently admixed population, ancestral populations have been mixing for a relatively small number of generations, resulting in a new population with different proportions of the original populations. Due to recombination events, the genome of admixed individuals is fragmented into shorter genome regions of different ancestries (Figure 6).

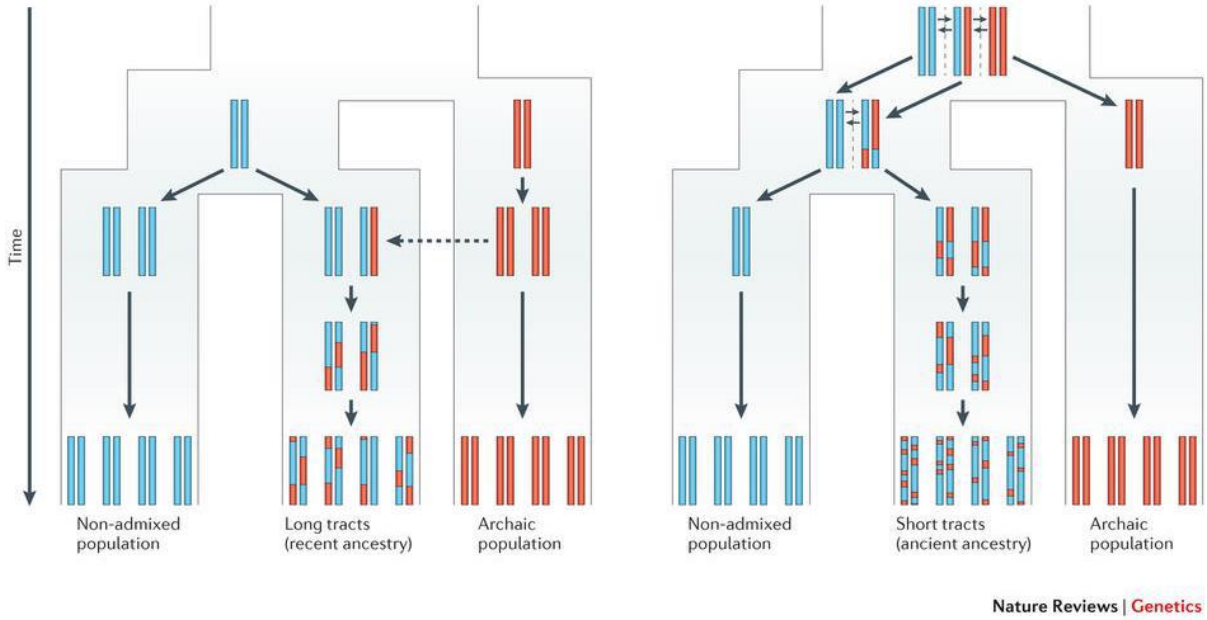

Figure 6: Expected lengths of ancestral segments in a recent admixed population (left panel) and in an ancient admixed population (right panel) (Racimo et al., 2015)

Estimation of the proportional contributions of ancestral populations in admixed (crossbred) individuals is important to clarify the population structure, historical background and pattern of admixture along the genome of admixed individuals. Recent advance in high-throughput genotype sequencing technology have provided unprecedented opportunities to learn about the evolutionary history of admixed populations at both global and local levels.

- Global genetic ancestry establishes ancestral proportions averaged across the genome of an individual
- Local genetic ancestry is the identification of the ancestral origin of distinct chromosomal segments within an individual genome

There is a growing concern in association studies about confounding effects, due to considerable discrepancy between the allele frequencies in the cases and the controls. An accurate inference of locus-specific ancestry in admixed populations has improved the genetic disease (Parkinson, Diabetic disease, Alzheimer and other diseases) association studies in human genetics (Hu et al., 2013; Rosenberg et al., 2010; Sankararaman et al., 2008; Seldin et al., 2011).

2.4. Selection signatures

In contrast to demographic processes of mutation, genetic drift and gene flow, which influence the entire genome, natural selection influences specific functionally important parts of genome (Bamshad and Wooding, 2003; Oleksyk et al., 2010). Selection tends to cause specific changes in the patterns of variation among selected and also in neutral linked loci, leaving its footprints in the adjacent chromosomal regions. There footprints are known as selection signatures (Gouveia et al., 2014; Kreitman, 2000; Moradi and Abedini, 2012). The recent availability of high density single nucleotide polymorphism (SNP) markers and the development of analytical approaches offer the opportunity to screen the genome for evidence of selection. Analysis of F_{ST} (Weir and Cockerham, 1984), as the measure of genetic distance, was one of the first approaches to screen genome to detect the loci which exhibited high variation in allele frequency between populations. An alternative strategy is based on increased linkage disequilibrium (LD) and search for homozygous regions along the genome, where their frequency is more than expected (Tang et al., 2007; Voight et al., 2006). This approach is called extended haplotype homozygosity (EHH) which is defined as the probability that two randomly chosen chromosomes carrying the core haplotype which are identical by decent (Sabeti et al., 2002).

In addition, the genome-wide distribution of ancestral segments in admixed individuals can be examined to detect a selection signature that occurred after admixture (Tang et al., 2007). Using admixed populations to study selection has a considerable history in human genetics, particularly analyzing African, Native American and Caucasian ancestries (Khayatzadeh et al., 2016) .

A limited number of selection signature studies involving African Zebu have only recently been published, involving Zebu breeds from South Africa (Makina et al., 2015) and East Africa (Bahbahani et al., 2018; Kim et al., 2017; Msalya et al., 2017; Taye et al., 2017). Only two of these studies (Kim et al., 2017; Taye et al., 2017) have utilized full genome sequencing. These two studies include three Zebu breeds (Kenana, Ogaden, Boran) and one Sanga breed (Ankole). Kim et al. (2017) compared the genome of African cattle to cattle living in temperate regions (European and Asian taurine) with the aim to detect genes involved in adaptation to the tropics. In regards to heat tolerance, they identified a long-range haplotype across African cattle within one of the heat tolerance QTLs on BTA 22 and also identified one heat shock protein of 70 kDa (heat shock protein 4, HSPA4). The degree of haplotype sharing at these two regions was observed to be more extensive in the African Zebu than African taurine, this is in concordance with previous report regarding Zebu superior ability to regulate body temperature during

exposure to heat stress (Hansen, 2004). They also reported positive selection signals in genome regions including two genes, SOD2 and PRLH, and they suggest their possible roles in heat stress response in Africa Zebu.

In contrast to the non-African cattle breeds, non-synonymous mutations near fixation in the Zebu cattle were identified in these genes. In particular, the suggestive role of PRLH gene in thermotolerance is based on its regulatory function on the expression of prolactin (PRL), a gene which has been reported to impact hair morphology and thermoregulation in cattle with the slick coat phenotype (Kim et al., 2017; Littlejohn et al., 2014). Other genes in African cattle within candidate genome regions under selection were the BOLA gene, reported to be involved in tick resistance and the coat colour genes, KIT and MC1R were identified when Ankole cattle was compared to other African cattle (Kim et al., 2017).

Under neutral evolution we expect each admixed individual's genome to represent an ensemble of ancestry blocks randomly sampled with a probability similar to genome wide average. However, ancestral contributions in the genome of recently admixed individuals vary at locus levels due to sampling error of the existing population, random evolutionary error of genetic drift and systematic biases of natural selection (Long, 1991; Oleksyk et al., 2010; Tang et al., 2007).

2.5. Methodologies for local ancestry estimates

The genome of an admixed individual comprises a mosaic of ancestral haplotypes formed by recombination occurring at every generation. The boundaries and origin of each ancestral segment can be reconstructed along each chromosome by statistical methods which can estimate ancestral allele and haplotype frequencies and their distribution in the admixed populations (Hu et al., 2013). Extreme fluctuations in ancestry differences (Δ ancestry), which are calculated by subtraction of the genome wide ancestry from locus-specific ancestry for each ancestry component, are unlikely to have occurred by chance and can exhibit a selection signature in admixed individuals (Tang et al., 2007).

Generally, the software tools for genetic ancestry estimates rely on multivariate statistical methods, using hidden Markov Models (HMM) and use the ancestral information as reference panel.

The approaches for local ancestry inference rely either on Li and Stephens (Li and Stephens, 2003) framework, using an approximation to the coalescent with recombination, or on model-based clustering algorithms with no need to information on parametric population genetic model. Examples of algorithm using Li and Stephens (2003) include HAPMIX (Price and

Stephenson, 2009), LAMP-LD (Baran et al., 2012) and MULTIMIX (Churchhouse and Marchini, 2013). The other method for local ancestry deconvolution is based on smaller genome segments (windows) and then clustering relative to the reference panels, as applied in LAMP (Sankararaman et al., 2008) and PCAdmix (Brisbin et al., 2012).

2.6. Heterosis and the benefits of crossbreeding

Crossbred or admixed animals result from interbreeding, where sire and dam originate from different breeds or lines (Balding, 2006). An optimized crossbreeding program exploits the complementarity of the involved purebred parental populations based on breed additive genetic effects, termed "specific combining abilities" and makes use of the additional economic benefits of heterosis (Freyer and Lewis, 2008).

Heterosis or hybrid vigor refers to the superiority in performance of the crossbreds compared to the average of their parents (Hill and Mackay, 2004). Heterosis is most pronounced for fitness traits; fertility and longevity, all with relatively low heritability (Mäki-Tanila, 2007). Heterosis effects are intermediate for milk production, weight gain, feed efficiency, and body size; and lowest in carcass traits. Reproduction and maternal traits have low heritability and the traditional response to selection in breeding program will generally be slower compared to high heritability traits. However, significant improvement can be made through crossbreeding programs that maximize heterosis. For growth and milk traits with moderate heritability, genetic improvement can be achieved by applying both selection and crossbreeding programs. The amount of general heterosis for production traits in dairy cattle is reported 3 to 4 percent, while higher levels of heterosis are observed for functional and reproductive traits (Freyer and Lewis, 2008).

According to quantitative genetic theory, heterosis of a crossbred animal depends on genetic distance between its parents (Hill and Mackay, 2004). Here, genetic distance refers to the squared difference in allele frequencies between parents, taking into account all quantitative trait loci (QTL) contributing to heterosis, i.e., heterotic loci (Jiang et al., 2017). Heterosis can be explained by overdominant gene effects, where heterozygosity at individual loci leads to superior performance relative to that of either homozygous class (Lippman and Zamir, 2007). In the presence of partial to complete dominance, heterosis can arise because of the joint effects of multiple loci (Lippman and Zamir, 2007). According to Boeven et al., (2020) if heterosis is caused by positive (over) dominance effects, breeders should strive to increase the genetic

distance between parental populations to maximize heterosis. Even if dominance effects are absent, epistatic interactions between loci can contribute to heterosis (Boeven et al., 2020; Lippman and Zamir, 2007). If heterosis results primarily from epistatic interactions, the optimum design of hybrid breeding programs is elusive. Even more so as Moll et al. (Moll et al., 1965) proposed that parents should not exceed an optimum genetic distance to avoid a reduction in grain-yield heterosis due to detrimental epistatic effects. The concept of a maximized fitness of individuals under an optimal genetic distance between parents has recently also been suggested by analyses in model organisms (Wei and Zhang, 2018). To use heterosis most efficiently in breeding, it is critical to understand the contribution of (over)dominance and epistatic effects and the dependency on the genetic distance between parents (Boeven et al., 2020).

The increased performance in crossbred animals is due to changes in non-additive genetic effects of dominance and epistasis components of heterosis. Dominance component of heterosis are caused by gene interaction within loci. The degree of heterosis for a specific breed combination, expressed in a crossbred animal, is equal to the chance that the animal, at a specific locus, has one gene from each of two breeds (Sorensen et al., 2008).

Epistatic effects are caused by gene interaction between loci and epistatic loss is considered as unfavorable gene effect in crossbred offspring due to breakdown of parental epistatic complex (Khayatzadeh et al., 2016).

Under both natural and artificial selection, co-adapted positive gene complexes accumulate. However, favorable gene combinations established in the parental breeds may be lost by crossbreeding for traits that have been under selection. Different models for estimating effects of recombination caused by additive × additive (A×A) interaction have been proposed (Kinghorn, 1983).

Kinghorn (1983) modeled dominance and two-locus interaction, using epistatic term to describe effects of breakdown of parental combination. He considered heterozygosity as synonymous with dominance and epistatic loss is proportional to the probability that two non-allelic genes randomly chosen in diploid individual are of different breed origin.

The observed heterosis in first-generation crosses (F1) is the sum of the dominance component of heterosis (normally positive) and the epistatic loss effects (normally negative). In a two-breed crossbreeding program heterosis drops to 50% in the second-generation crosses (F2) and continuing crosses between 2 breeds, 67% of the F1 heterosis will, on average, be expressed. Including more parental breeds causes the more heterosis maintained after F1 generations, while it causes the cross to be diluted for desired traits.

Amount of heterosis depends on degree of dominance and its direction, differences in allele frequencies of genetic variants contributed in heterosis between parents (genetic distance between parental populations), number of involved parental populations and type of crossbreeding (Khayatzadeh et al., 2016).

2.7. Consequences of crossbreeding for locally adapted breeds

In Africa, and to a lesser extent in Asia, the general increase in the overall livestock population over the past 20 years has compensated for the decreasing proportion of locally adapted animals within species, allowing sizes of local populations to remain relatively stable. On the other hand, the population sizes of a majority of local and regional breeds have decreased in Latin America, while the overall livestock population has increased less in size than in Africa (Leroy et al., 2020).

The increased presence of exotic and crossbred animals does not necessarily mean replacement of local populations, especially if the new animals are not raised in the same production environments (for instance, if new, peri-urban farms are developed). However, even if the importation of exotic animals is not intended to directly replace locally adapted breeds, they may nevertheless remain a threat as they enter in competition with traditional breeds and herds for resources and market share. Erosion of the diversity of local animal genetic resources is especially problematic given the phenotypes of interest that are possessed by those breeds (Leroy et al., 2016) and the ecosystem services they and their production systems provide (Leroy et al., 2018). In relation to their capacity to withstand endemic diseases and harsh climate conditions, survive on low-quality diets and walk long distances to access food and water, locally adapted ruminant breeds are especially well suited for the valorization and maintenance of pastoral rangelands, which constitute a large share of the global agricultural area (2 billion ha, of which 1.3 billion ha is not convertible to cropland according to Mottet et al., (2017) and therefore of critical importance for food security and livelihoods. More generally, the increased number of crossbred and exotic animals is indicative of a shift in production systems toward greater intensification and specialization.

This process may impact negatively on landscapes and use of resources, as illustrated by Magnani et al., (2019). They showed that the sedentarisation of pastoralists and promotion of exotic breeds over local ones resulted in land fragmentation of the middle valley of the Senegal River. Also, considering the specific adaptive potential and robustness of locally adapted

breeds, breed replacement may reduce the resilience of livestock production systems. The use of mixed herds and modifying herd composition to favour more resistant species or breeds are components of a classical strategy of herders facing long-term droughts (Blench and Marriage, 1999) and the use of locally adapted breeds has been suggested as an option to cope with constraints (drought, feed shortage, disease) induced by climate change (Bettridge et al., 2018; Musemwa et al., 2012). Considering the short and long term impact that the COVID 19 pandemic will have on food and agriculture in general and livestock in particular (e.g. shortage of labor and animal feed, (Zhang et al., 2020)), both the adaptability of local breeds to less-intensive and/or short supply chains, and their general resistance to zoonotic diseases (Marshall et al., 2019) give them potential competitive advantages relative to exotic ones. Considering the specific issue of mitigation of climate change, locally adapted breeds tend to perform poorly relative to exotic breeds with regard to intensity of greenhouse gases (GHG) emissions, due to their inferior production. However, standard measures of intensity are somewhat biased, as they typically consider only the ratio of GHG emissions to yield of a single commodity, ignoring other ecosystem services usually associated with locally adapted breeds and their production systems. Single-commodity measures of GHG intensity also fail to account for the differences among breeds in their ability to survive while consuming poor quality forage and converting it into human-edible food (Hoffmann, 2010).

3. MATERIALS AND METHODS

3.1. Description of the study environment

The study was conducted in the southwestern region of Burkina Faso as part of the Characterization and Sustainable Utilization of Local Cattle Breeds (LoCaBreed) project. The southwestern region is located around 10° 19´ 00´´ N latitude and 3° 10´ 00´´ W longitude. This area is the original habitat of Baoulé cattle. The climate is of the Sudanese type with two distinct seasons: a rainy season from June to October and a dry season from November to May. In 2018 the total amount of rainfall was 1399 mm. The annual average minimum temperature was 22 °C and the annual average maximum was 34 °C. The lowest monthly average minimum temperature was registered in January (16 °C) and the highest monthly average maximum in April (37 °C). In this area, people produce crops, keep livestock and also perform agroforestry. Production systems are mixed crop-livestock, with the Lobi ethnic group concentrating on subsistence crop production and the migrant Fulani ethnic group tending to keep their lifestyle of pastoral livestock production (Zoma-Traoré et al., 2020). The cattle population in this region is estimated about 343,000 heads, representing about 4% of the estimated national stock of 9 million (MRA, 2014).

3.2. Description of farms

Data was collected in 27 villages from the Loropéni, Kampti and Bouroum-Bouroum departments in the south-western region of Burkina Faso (Figure 7). Three sites were selected depending on the availability of Baoulé and crossbreds (Baoulé with Zebu): in the Bouroum-Bouroum department we worked with sedentary farmers with Baoulé cattle, in the Kampti department with Fulani transhumant and Mossi farmers herding crossbreds and in the Loropeni department sedentary farmers with crossbreds. A total of 88 farms: 55 in Bouroum-Bouroum, 15 in Loropéni and 18 in Kampti were chosen according to the willingness of the farmers to participate in the breeding program of the LoCaBreed project.

In Bouroum-Bouroum, the ethnic group of Lobi people own and keep purebred Baoulé animals. In Kampti, there are crossbreds with Zebu as well as Baoulé x Zebu cattle kept by the ethnic group of nomadic Fulani and Mossi ethnic group, who are often owners or keepers of these animals. Finally, in Loropéni mainly crossbred animals kept by Lobi and Djan breeders, who are the owners of these animals, were included in this study. The livestock system is extensive

in all studied departments, with 7 to 100 cattle per breeder. The animals are on pasture all day and are irregularly supplemented with agricultural by-products like rice, maize and cottonseed cake. In some places, daily management of animals might be entrusted to an employee from the Fulani ethnic group, who are perceived as experts in cattle herding and breeding. The sanitary management of farms is maintained by private veterinarians and/or extensions workers, employed by the Ministry of Livestock, with limited treatments against ticks, eczema and other ectoparasites, internal deworming and trypanocide treatments.

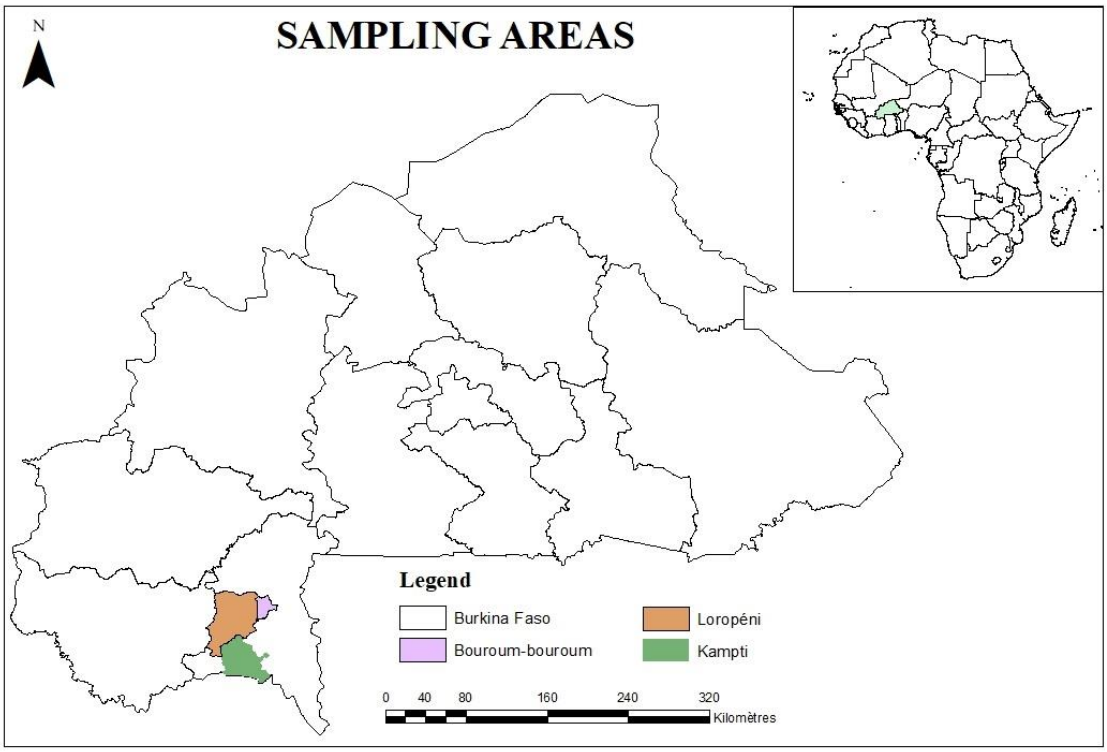

Figure 7: The location of the study area within Burkina Faso

3.3. Description of available phenotype and genotype data

3.3.1. Phenotype data

The study population was assessed for 24 quantitative body measurements (Table 1) and 20 qualitative traits (Table 2) following the FAO, (2012) guidelines, and including several additional traits such as discolored abdomen, speckle, blackness, brindle color, and white spots to account for possible additional variation within the target area.

Table 1: List of quantitative traits measured according to FAO (2012) Guidelines on phenotypic characterization of animal genetic resources

Head and horn measurements (11)	**Body measurements (13)**
cranial length, head width, head length, cranial width, facial length, facial width, muzzle circumference, distance between horn tips, distance between horn bases, horn length, earn length	height at withers, thoracic perimeter, height at sacrum, body length, length of scapula ischium, hip width, ischium width, tail length, chest depth, shoulder width, chest width, teat length, weight

Table 2: List of characterized qualitative traits with their respective levels

Traits (20)	**Level**
Color of muzzle	2 levels: Pigment/No pigment
Head spotting	2 levels: Spot/No spot-on forehead
Eyelid pigmentation	2 levels: Black/White
Color of the hoof	2 levels Pigment/No pigment
Stripe mullet	2 levels: Dark/Inverse
Lower legs color	2 levels: Charred/Faded
Color of chignon	2 levels: No/Yes
Discolored abdomen	2 levels: No/Yes
Speckle	2 levels: No/Yes
Coat pattern	4 levels: Pied/ Speckled /Uniform/ Red pied
Coat color	7 levels: Black/ Black pied/ Fawn/ Grey/ Roan/ Sand/White
Blackness	3 levels: Strongly/ Medium/ Slightly
Color of horn	5 levels: Black/ Brown/ Grey/ Two-color mixed/ White
Dewlap size	2 levels: Well-developed/ Poor developed
Hump position	2 levels: No hump/ Thoracic
Presence of horn	2 levels: No/Yes
Backline	3 levels: Concave/Convex/ Straight
Horn shape	5 levels: No/Crescent/Crown/ Cup/Wheel
White spots	5 levels: No/Irregular/ Lateral/White head
Brindle color	3 levels: Absent/ Slightly brindle/ Strongly brindle

Body measurements were carried out by two technicians, who were trained by the same person (Figure 8). The training took place before the start of the collection of morphological data. The measurements were done using a Lydthin stick, a tape measure and vernier calliper scale. Brindle color and white spotting were considered as parts of the comprehensive morphological characterization and therefore included in addition to coat color.

Figure 8: Measurements of the animals during the field work (Yougbaré, 2017)

The farmers were asked to indicate if the animal was purebred or crossbred. Before the reports were completed the crossbred status was vetted also by the recording technician.

After morphological measurements blood sample were taken from the animals. Blood was collected with needle from jugular vein (Figure 9) in EDTA tubes.

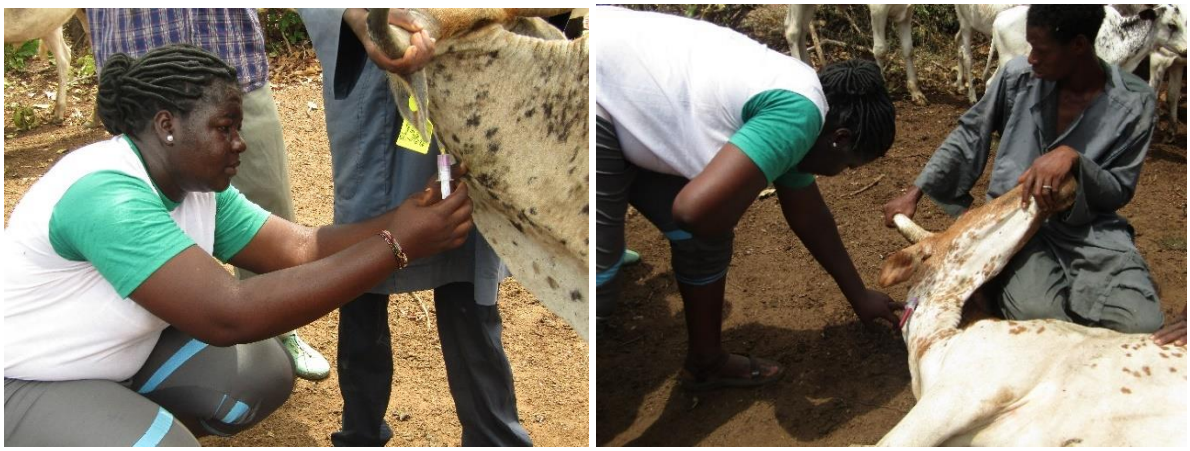

Figure 9: Blood samples are being taken from the animals (Ouédraogo, 2017)

Blood samples from a total of 2000 animals including 1000 purebred Baoulé and 1000 cross-breds were collected.

DNA extraction from EDTA blood samples was performed with the MasterPureTM DNA Purification Kit for Blood Version II (Biozym Scientific, Oldendorf, Germany) following the manufacturer's protocol (Figure 10).

Figure 10: DNA extraction from EDTA blood samples (Michelle, 2018)

The indirect Elisa has been used for the diagnosis of positive or negative trypanosomosis infection from blood samples (Desquesnes et al., 2003).

3.3.2. Genomic data and quality control

The genotype data from the Illumina Bovine SNP50 BeadChip were available for 737 animals including 387 Baoulé from Bouroum-Bouroum and 350 crossbreeds from Kampti and Loropeni (Table 3)

Table 3: The list of genotyped animals with their trypanosomosis status

Regions	**Negative animals**	**Positive animals**	**Total**
Bouroum -Bouroum	204	183	387
Kampti	87	89	176
Loropéni	69	105	174
Total	360	377	737

The number of SNPs at the beginning was 47,843 variants. Quality control of the data was performed with PLINK 1.9 (Chang et al., 2015). The dataset was cleaned using standard quality control to exclude non-autosomal SNPs as well as SNPs with minor allele frequency lower than 0.01, those with a call rate of < 95% and those that deviated from Hardy Weinberg

equilibrium with Fisher's exact test with P-value < 10E-6. Animals with a call rate < 90% were excluded. After applying quality control:

- 38,322 SNPs and 619 animals including 340 purebred Baoulé and 279 crossbreds Baoulé and Zebu were used for the GWAS analyses.
- 31,612 SNPs and 802 animals were left for the global admixture analysis and local ancestry estimation. We assigned 30 purebred Baoulé (global admixture levels ≥ 0.999 Baoulé) and 30 purebred Zebu (global admixture levels ≥ 0.987) as reference populations to investigate local admixture levels in 716 animals that were considered as potential crossbreds based on the sampling information. Animals found to be purebred after first screening were removed from the pool of crossbreds. It should be noted that in this part additional 65 animals containing 30 purebred Zebus and 35 crossbreds genotyped with the Bovine SNP50 BeadChip data from Pérez O'Brien et al., (2014) were included in the analysis.

3.4. Morphometrics data collection and analysis

A total of 421 animals (111 males and 310 females) were included in the study; 155 adult Baoulé from Bouroum-Bouroum from 55 farms, and a total of 266 crossbreds: 136 from Kampti from 18 farms and 130 from Loropeni from 15 farms. Only cattle between 4 years and older were included. Age was inferred by denting, allowing separation of young animals in various age categories and adult animals, 5 years or older. We did not rely on age in years reported by farmers. The animals were categorized into two groups according to their ages and weight; cattle that were 4 or 4.5 years of age weighed 189.59 ± 62.16 kg and cattle that were 5 years or older and weighed 219.54 ± 54.65 kg. The weight was assessed using weigh-band that determines weight based on its strong correlation with the chest circumference. To limit relatedness between sampled individuals, farmers were asked about the origin and relationships of animals. Sampling was thus, limited to between 5 and 10 individuals per herd.

- Quantitative Traits

Quantitative traits were analyzed by fitting the following linear model:

$y = \mu + \text{genotype-location} + \text{sex} + \text{age} + \text{genotype-location}*\text{age} + \text{genotype-location}*\text{sex} + \text{age}*\text{sex} + e$

Where μ is the overall mean for each trait, y is the vector of measurements and e is the residual variance for each measurement. The fixed effects were:

- Genotype-location: it is the combination between the genotype of the animal: purebred Baoulé or crossbred, and the study area: Bouroum-Bouroum, Kampti and Loropeni. Therefore, three levels were defined for genotype-location: sedentary purebred for Bouroum-Bouroum, sedentary crossbred for Loropeni and transhumant crossbred for Kampti
- Sex: sex of the measured animal: male or female
- Age: approximate age of the animal at the time of measurement, with two levels: up to 5 years old and 5 years old and older
- Two-way interactions between fixed effects (genotype-location*age, genotype-location*sex and age*sex) were also included

The linear models for different traits were fitted using lm function in R (The R Development Core Team, 2008). The Shapiro test and Q-Q normality plots were used to examine the distribution of quantitative data. The distribution was normal for all traits. We used the ANOVA function from the car package (Fox et al, 2019) to find the significance of each fixed effect in the model. The Least Square Means (LS-Means) for different levels of genotype-location were calculated. The Tukey test was used for pair-wise comparison and values were considered to be significant with p-value < 0.05, using the lsmeans package (Lenth, 2018).

To compare LS-means for the effect of main interest, genotype-location, models were run, including only significant effects and interactions.

- Qualitative Traits

The chi square tests for qualitative traits were performed with R. The multiple pairwise comparisons for sedentary purebred of Bouroum-Bouroum, sedentary crossbred of Loropeni and transhumant crossbred of Kampti were corrected using the Bonferroni approach in the stat package in R (Bolar, 2019).

3.5. GWAS analysis of trypanosome prevalence and morphometric traits

The trypanosomosis status and a wide set of morphological traits was recorded for 646 animals including 360 purebred Baoulé and 286 crossbred Zebu x Baoulé cattle from the Southwest of Burkina Faso. For the association study a univariate linear mixed model for marker association tests was fitted with a single phenotype as:

$y = \mu + X\beta + sex + age + \varepsilon$

Where y was the vector of phenotypes; μ was the intercept; X was a vector of SNP genotypes; β was the effect size of the SNP; and ε is a vector of errors. In addition, the sex of the individual (male, female) and the continuous variable of age were considered as covariates.

Single-SNP associations based on the genome-wide efficient mixed model association algorithm were performed using GEMMA (Zhou and Stephens, 2012). The genomic relationship matrix was used to account for population structure. The two significance thresholds used in the evaluation of the results were an arbitrary indicative threshold of $-\log10(p) = 5$, and the threshold based on the Bonferroni correction with a base of $p = 0.05$ and 38,322 SNPs independent tests (SNPs left after quality control), at $-\log10(p) = 5.86$. The regions within ±0.5 Mb of the most significant SNPs above the Bonferroni threshold were declared as significant, and were searched for any associated genes. The significant regions were checked for genes based on the ARS UCD1.2 Bos Taurus Genome Assembly on the NCBI database.

3.6. Global admixture analysis

Unsupervised global ancestry estimation was performed with the full SNP set using ADMIXTURE software (Alexander et al., 2009) with the number of ancestral populations (Baoulé and Zebu) fixed at two (K =2). The admixture barplots were created in R with the *barplot* function (The R Development Core Team, 2020). We calculated the frequencies of the admixture levels for all animals in Excel and plotted them in categories of 0.1 steps.

3.7. Local Ancestry Estimation in admixed populations

LAMP (Local Ancestry in adMixed Populations) is a program for estimating locus-specific ancestries in admixed individuals, using allele frequencies of the reference populations (Sankararaman et al., 2008). We used LAMP in LAMPANC mode and provided the estimated allele frequencies files for Baoulé and Zebu as the purebred ancestral populations. The following parameters were set: admixture proportions (alpha) = 0.8 for Baoulé and = 0.2 for Zebu based on the global ancestry estimation using ADMIXTURE program, number of generations since admixture (g) = 07 and recombination rate (r) = 10^{-8}. We estimated the local ancestry proportion, as well as the 'delta ancestry' with R in trypanosome positive and negative trypanosomosis animals following Khayatzadeh et al. (2016). The 'delta ancestry' reflects the extreme fluctuations in ancestry differences across the genome, which are calculated by subtraction of the genome wide ancestry from locus-specific ancestry for each ancestry component, are unlikely to have occurred by random evolutionary error of genetic drift and can potentially exhibit a selection signature in admixed individual (Tang et al., 2007). To identify significant deviations from the genome-wide average ancestry, we performed permutation tests (Doerge and Churchill, 1996) of the local ancestry proportions over the whole genome of admixed animals (Tang et al. 2007), separating animals with positive and negative trypanosomosis status. For each animal, we concatenated the local ancestry estimations of all 29 autosomes and then permuted the circularized genome by cutting at a random location and rearranging the two resulting pieces of the genome for each individual independently. This type of permutation preserves the extent of Linkage Disequilibrium (LD), assuming that it is homogeneously distributed over the whole genome. We implemented 1000 permutations. The distributions of maximum and minimum over all permutations were then used to define the 5% and 10% genome-wide thresholds levels that indicated significant deviation of the observed local ancestries from the genome-wide average ancestry (Gautier and Naves, 2011;

Khayatzadeh et al., 2016;Tang et al., 2007). Finally, we used a parametric Welch t test implemented in R using the t.test function to test significant differences in the admixture rates of positive and negative Baoulé x Zebu crosses.

3.8. F_{ST} outlier analysis

We applied BayeScan 2.1 (Foll and Gaggiotti, 2008) to identify F_{ST} outlier loci putatively under selection between the trypanosome positive (n = 244) and negative (n = 266) crossbreds animals using a cut-off at $p < 0.05$ corrected for a false discovery rate (FDR; Benjamini and Hochberg, 1995). The regions within ± 0.5 Mb of the most significant SNPs were searched for any potential associated genes based on the ARS UCD1.2 Bos Taurus Genome Assembly on the NCBI database.

3.9. Identification of ancestry informative SNPs for effective hybrid detection

We aimed to identify SNPs with the highest F_{ST} differentiation. We re-filtered the original dataset for MAF < 10%, individual and genotype missingness. The F_{ST} values were calculated according to WEIR and COCKERHAM implemented in PLINK for 60 animals (30 pure Baoulé and 30 pure Zebu). With these we were able to provide a set of top 200 F_{ST} markers, which were then used as a starting point to manually remove the ones less than 5 Mb to each other - preference given to higher F_{ST} markers. Based on this, we selected the top 15, 25, 50 and 100 SNPs, and extracted these for the crossbred animals and repeated the global admixture analysis (K = 2). We used the *cor* function in R to calculate the Pearson correlation coefficient (Pearson's *r*) for determining the linear association between admixture levels estimated based on the different sets of ancestry informative SNPs (all 31,612 SNPs

versus the top 100, 50, 25, 15 SNPs). Significance of the Pearson's *r* was assessed with the P Value from Pearson (R) Calculator (Social Science Statistics, 2021)..

4. **RESULTS AND DISCUSSION**

4.1 The morphometric differences between purebred Baoulé and their crossbreds.

4.1.1. Quantitative Traits

All of the examined 24 traits were significant at $p < 0.05$ (Table 4). The differences were significant for genotype-location for all traits, except teat length. The genotype-location effect was further explored, in significant interaction with the fixed effects of age and sex. The effect of age was significant for 18 traits and sex was significant for 12 traits.

Table 4: Linear model parameters for quantitative traits (all full models were significant)

Traits	*R-squared*	Adjusted R-squared	DF	F-statistics	Genotype – location F value	Age F value	Sex F value	Genotype-location* Age F value	Genotype-location * Sex F value	Sex * Age F value
Head length	0.58	0.57	9/367	56.10	97.83***	5.96*	ns	ns	ns	ns
Cranial	0.34	0.32	9/367	21.07	31.04***	7.00**	9.60**	3.40*	4.23*	ns
Head width	0.22	0.21	9/367	11.78	10.39***	21.33***	45.82***	ns	0.41***	ns
Cranial width	0.12	0.10	9/367	5.81	3.51*	9.02**	18.16***	ns	ns	ns
Facial length	0.19	0.15	9/365	9.48	21.70***	ns	ns	ns	ns	ns
Facial width	0.07	0.05	9/366	3.22	3.06*	5.59**	ns	ns	ns	ns
Muzzle circumference	0.13	0.11	9/367	5.96	5.94**	17.32***	19.72***	ns	3.78*	3.68*
Horn length	0.58	0.57	9/365	57.01	54.39***	14.14***	11.78***	3.49*	4.97**	ns
Distance between horn	0.29	0.27	9/357	16.14	22.26***	ns	31.34***	ns	ns	5.32*
Distance between horn base	0.06	0.04	9/366	2.79	3.54*	ns	ns	ns	ns	ns
Ear length	0.30	0.28	9/365	17.14	28.02***	ns	ns	ns	ns	3.05*
Height at withers	0.52	0.51	9/367	43.86	87.66***	5.48*	5.11*	ns	ns	ns
Thoracic perimeter	0.37	0.36	9/366	24.34	29.94***	25.38***	8.64**	3.95*	4.52**	ns
Height at sacrum	0.64	0.64	9/367	74.06	135.62***	ns	ns	ns	ns	ns
Body length	0.44	0.42	9/367	31.69	41.16***	8.83**	ns	ns	3.54*	ns

Length of scapula ischium	0.37	0.35	9/367	23.63	30.24***	12.93***	ns	ns	5.05**	ns
Hip width	0.24	0.23	9/366	13.19	17.23***	4.32*	3.92*	ns	ns	5.14**
Ischium width	0.28	0.26	9/367	15.55	18.23***	5.70*	4.96*	ns	ns	ns
Tail length	0.25	0.23	9/366	13.28	18.10***	4.19*	ns	ns	ns	ns
Chest depth	0.33	0.32	9/366	20.36	33.24***	7.35**	ns	ns	ns	ns
Shoulder width	0.26	0.24	9/367	14.41	22.56***	4.93*	5.52*	ns	5.88**	ns
Chest width	0.08	0.06	9/366	3.58	3.16*	5.45*	ns	7.32**	ns	ns
Teat length	0.10	0.09	5/283	5.35	ns	ns	-	ns	-	ns
Weight	0.34	0.32	9/359	20.65	24.70***	22.14***	9.51**	4.30**	6.13**	ns

Notation: * for $p < 0.05$; ** for $p < 0.01$; *** for $p < 0.001$ and ns for non-significant

Special attention was given to assess differences within the genotype-location effect via LS-Means comparison, to find out if the significance in the overall model was driven by differences between Baoulé and crossbreds, and among the two crossbred groups (Table 5).

The difference was significant between each of the three groups (Table 5) for fourteen traits: head length, cranial length, thoracic perimeter, height at sacrum, body length, length of scapula ischium, hip width, horn length, distance between horn bases, height at withers, tail length, chest depth, shoulder width and weight. Five traits differed between the purebred Baoulé and both crossbred populations: facial length, distance between horn tips, ear length, cranial width and chest width.

Table 5: Least square means for the quantitative traits

Traits	Bouroum-Bouroum (Baoulé, sedendary)	Kampti (crossbred, transhumant)	Loropeni (Crossbred, sedentary)
Head length	39.7[a]	46.5[b]	44.2[c]
Cranial length	19.3[a]	22.3[b]	20.3[ab]
Head width	16.1 [a]	17.2[b]	16.0[a]
Cranial width	14.9 [a]	16.6[b]	16.1[b]
Facial length	20.2[a]	23.6[b]	23.2[b]
Facial width	20.2[a]	23.6[a]	23.2[a]
Muzzle circumference	36.5	37.4[a]	35.7[b]
Horn length	13.6[a]	27.8[b]	24.8[c]
Distance between horn tips	31.0[a]	43.2[b]	39.6[b]
Distance between horn base	13.3a	14.2[b]	12.4[c]
Ear length	15.6[a]	19.3[b]	18.7[b]
Height at withers	93.5[a]	111.7[b]	106.6[c]
Thoracic perimeter	129[a]	141[b]	135[c]
Height at sacrum	95[a]	119[b]	112[c]
Body length	75.9[a]	89.1[b]	84.1[c]
Length of scapula ischium	109[a]	122[b]	116[c]
Hip width	28.1[a]	32.1[b]	30.9[c]
Ischium width	11.1[a]	13.4[b]	11.4[a]
Tail length	86.5[a]	105.3[b]	91.5[c]
Chest depth	48.0[a]	53.7[b]	52.5[c]
Shoulder width	25.1[a]	28.1[b]	25.6 [c]
Chest width	10.9[a]	14.4[b]	12.1[b]
Teat length	2.63[a]	2.96[b]	2.36[a]
Weight	174[a]	241[b]	210[c]

The significant level was considered to be p-values < 0.05

The indices (a, b and c) indicated significant difference in pair-wise comparison of genotype-location, derived from Tukey test. Different indices indicate significant difference and the same indices show no difference in pairwise comparison

In addition, four traits differed significantly among the crossbred populations: the muzzle circumference, head width, ischium width and teat length (Table 4). Our results showed an increased body size of crossbred animals from Kampti and Loropéni compared to the purebred Baoulé cattle from Bouroum - Bouroum. Comparing the two crossbred populations from Kampti and Loropéni, the results showed that the crossbred animals from Kampti appear to be larger than crossbreds from Loropéni.

The significant differences were found for 24 quantitative trait measurements, confirming the notable differences in size between purebred and crossbred Baoulé. These results were in agreement with those of Traoré et al., (2015), who showed clear differences for most body measurements in cattle in West Africa. Among qualitative traits, some traits such as coat color and horn shape showed large variation within cattle breeds. This likely is due to local livestock keepers' preferences rather than the breed identity (Desta et al., 2011; Traoré et al., 2015). This might be due to a lack of specific breed identity agreements on phenotypic traits. Even if any informal agreement on breed identity was in place, this would cover a larger variation than we see for the main commercial breeds in Europe.

In order to establish an agreement on the breed identity Houessou et al., (2019) confirmed the necessity of combining molecular analyses, phenotypic characterization and herders' knowledge for a more accurate differentiation of the breeds and subtypes of cattle raised in extensive African livestock production systems for their effective management and preservation. The observed variation, such as the one in coat color, might be a consequence of adaptation mechanisms to the local environment in Burkina Faso, as reported by Saleem et al., (2013) in cattle breeds and Khan et al., (2007) for buffaloes in Pakistan, Katongole et al., (1994) for sheep in Botswana, Mani et al., (2014) for goats in Niger, and Lauvergne, (1985) for African livestock in general. Our study, similarly to Traoré et al., (2016), our study also confirms that qualitative traits does not seem to be utilized in the definition of cattle breeds or cattle groups in West Africa. The observed variation in qualitative traits for individuals belonging to the same breed is markedly different to the more consistent breed definitions in Europe. While in the European breeds the qualitative traits are of particular importance to include animals into

the herd book, in the West African populations in general, and for the Baoulé cattle in particular these conditions were more relaxed.

The differences on some quantitative traits like facial length, distance between horn tips, ear length and chest width and some qualitative traits as color of muzzle, head spot and horn shape between the purebred and crossbred populations can be explained to some degree by crossbreeding. Crossbreeding is an attractive approach to effectively combine breed and type characteristics (Gregory and Trail, 1981). The goal is to combine the adaptive potential and trypanotolerance of local Baoulé with the bigger body size of the zebu, which is an unstructured population at the body measurements level (Moussa et al., 2017). This crossbred population is comparable to Sanga cattle with intermediate body size measurements between zebu and West African taurine cattle (Traoré et al., 2016).

4.1.2. Qualitative Traits

Each of the 20 traits was analyzed with a chi square independent test on the effect of the genotype-location and 12 of which were significant with a p-value < 0.05 (Table 6).

Significant differences via pairwise chi square test between purebred Baoulé and the crossbreds were found for 10 traits: color of muzzle, head spotting, stripe mullet, lower legs color, speckle, coat color, blackness, color of horn, horn shape and white spotting. Significant differences between Bouroum-Bouroum (Baoulé, sedentary), Kampti (crossbred, transhumant) and Loropéni (crossbred, sedentary) were found for hump position, lower legs, coat color and white spotting, respectively. For color of muzzle, head spot and horn shape we have found significant differences between purebred Baoulé and both crossbred populations (Table 6).

Table 6: Chi square independent test for genotype-location effect for qualitative traits

Traits	Bouroum-Bouroum (Baoulé, sedentary) (140)	Kampti (crossbred, transhumant) (118)	Loropéni (crossbre, sedentary) (119)	p-value
Color of muzzle	**A**	**ab**	**b**	0.013
No pigmented	**7**	**7**	**17**	
Pigmented	133	111	102	
Head spot	**A**	**b**	**b**	< 0.001
No spot	78	98	104	
Spot	62	20	15	
Hump position	**A**	**b**	**c**	< 0.001
No hump	140	24	63	
Thoracic	0	94	56	
Stripe mullet	**A**	**a**	**b**	< 0.001
Dark	140	118	104	
Inverse	0	0	15	
Lower legs	**A**	**b**	**c**	< 0.001
Charred	125	71	57	
Faded	15	47	62	
Discolored abdomen a		**a**	**a**	0.048
No	107	77	93	
Yes	33	41	26	
Speckle	**A**	**ab**	**b**	< 0.001
No	109	105	113	
Yes	31	13	6	
Color of horn	**A**	**a**	**b**	0.009
Black	57	38	57	
Brown	3	0	0	
Grey	3	4	1	
Two-color mixed	74	72	51	
White	3	4	10	
Blackness	**A**	**b**	**ab**	0.035
Strongly	133	106	102	
Medium	4	6	11	
Slightly	3	6	6	

White spot	**A**	**b**	**c**	< 0.001
No	88	100	110	
Irregular	51	16	8	
Lateral	0	2	1	
White head	1	0	0	
Horn shape	**A**	**b**	**b**	< 0.001
No	0	1	0	
Crescent	19	53	48	
Crown	3	8	10	
Cup	94	44	44	
Wheel	22	11	17	
Coat color	**A**	**b**	**c**	< 0.001
Black	88	25	35	
Black pied	24	10	14	
Fawn	6	21	10	
Grey	4	2	5	
Red pied	0	1	0	
Roan	16	7	9	
Sand	0	9	5	
White	2	37	41	

The overall assessment of the qualitative traits for the three locations revealed a diverse population with no strict breed identity in terms of phenotype structure. The Baoulé animals were different from the crossbreds with some traits like color of muzzle, head spot and horn shape. The color variation of body parts was significantly higher in the Baoulé x Zebu crossbreds. Although a large proportion of the crossbreds was darkly colored similar to Baoulé, the body color variation was more evenly distributed from black to white colors.

Interestingly, the occurrence of the hump significantly differed between the transhumant and the sedentary breeders of the crossbred cattle. The distribution of phenotypes showed a higher proportion of zebu admixture levels in the transhumant populations, which characterizes their breeding system.

The differences for quantitative traits like the muzzle circumference, head width, ischium width teat length and weight, observed between the crossbred populations could be due to the ethnic

differences, differences in the composition of the herd and differences in the livestock husbandry system in the transhumant Kampti and sedentary Loropéni breeders. In Kampti, the animals were held mostly by the Fulani who come from the Sahelian zone of Burkina Faso and who have a large number of Zebus in their herd. The Fulani move from place to place depending on the availability of food and give importance to the animal often more than to themselves. In Loropéni the crossbred herds are owned by the Lobi and Djan people who raise predominantly purebred Baoulé cattle mostly for social events like funerals and weddings, and do not practice transhumance.

Differences in body shape between the purebred and crossbred Baoulé analysed in the current study were due to major differences in origin (Chen et al., 2010; Pérez- Pardal et al., 2010a, 2010a). In fact, the crossbreeding with Zebu increases body size, which is considered as an improvement by the breeders. The reason for this preference was the use of crossbred animals for ploughing, as well as their greater economic value. The economic value was also highlighted by Batz, (1999) and R. Roschinsky et al, (2014) who identified profitability as an important factor in crossbreeding adoption. In order to maintain the crossbreeding, however, the Baoulé cattle with small body size must be conserved, which might cause an economic loss to individual breeders. On the other hand, the use of this trypanotolerant breed reduces the use of chemicals to control the disease, contributing to a balanced ecosystem health.

This significant size difference between the small, purebred Baoulé and their larger crossbreds with zebu also reflects the difference in rearing system between different areas. Variation between the interaction of genotype-location and age categories can also be explained by small size and the lower growth rate of Baoulé cattle compared to crossbreds (Soudre, 2011). In addition to the growth rate, the herding practices might be influential. The crossbreds were mainly held by Fulani, who are renowned by their excellence in herd management. They supplement the animals' feed with the residues of agricultural products such as cereals and legumes and take care of animal health (Ouédraogo et al., 2020). The purebred Baoulé cattle were largely held by Lobi livestock keepers, who usually do not devote such attention to their herd. The feeding of the animals relies on pasture alone, without a health monitoring system in place. These differences in rearing systems as shown in our results were comparable to those of Boettcher et al, (2003) in Canada and Kearney et al, (2004a) comparing pasture systems with conventional systems in the US.

Interaction of genotype-location and age categories (Table 5) can be explained by differences in availability of feed between the study sites, which is affecting growth rates, thus the differences in quantitative characteristics. The abundance of fodder varies according to seasons, with limited availability in the dry season and abundance in the rain season. It is also noted that there is much more fodder in Kampti and Loropéni compared to Bouroum-Bouroum due to their more favorable environmental conditions because of the increased rainfall. The abundance of fodder in Kampti and Loropeni increases the size differences in addition to Zebu and Baoulé crossbreeding. These results were similar to those of Berry et al, (2003), who found genotype - environment interactions related to the silage quality and abundance in Ireland.

The results for interaction of genotype-location and sex show the differences considering the three study locations. In general, Bouroum-Bouroum and Loropéni breeders give more importance to males because they are used for ploughing in agriculture, whereas in Kampti the Fulani breeders gave more importance to females used for breeding and dairy production.

In all three sites there was a preferential treatment of animals for feeding and health care depending on the importance that the breeder gives the preferred sex. These results are similar to those of Burrow, (2012) who affirms that sex and environment interactions may provide new opportunities for selection to improve performance by simultaneously taking into consideration sex and the environment. The interaction of genotype-location and sex were also explained by the effect of the crossbreeding which alters the morphometric parameters of the offspring from the crossing between Zebu and Baoulé cattle. These results were in agreement with Bourdon, (2000) who affirm that crossbreeding uses breed or 'sire x dam' complementarity which is defined as: 'an improvement in the overall performance of offspring resulting from mating individuals with different, but complementary, breeding values. Considering the sex difference, sexual dimorphism can be phenotypically expressed as differences in skeletal size and/or body mass. Differences reported for the conformation traits of males compared to females were in agreement with earlier reports on cattle (Mammo et al., 2017; Polák and Frynta, 2010). The influence of sex on morphometric traits in this study were likely connected with the usual between-sex hormonal action which leads to differential growth rates. Isaac, (2005) reported that sexual dimorphism in body size was clearly widespread among many mammalian taxa, with male-biased dimorphism being the more common, but certainly not the exclusive pattern. Yakubu et al., (2009) reported that the morphological traits of male and female goats were similar.

4.2 Genome-wide association study for morphological traits

From the wide range of measured traits, we intend to focus on those that describe the potential morphological differences between taurine and zebu cattle. From the qualitative traits these were ear shape and dewlap size, both typical and easily recognizable characteristics of the zebu cattle. From the quantitative traits these were the general body size measurements, such as height at withers, body length, chest width, depth and girth. The differences in head size were analysed via the head length and width, cranial length and width, as well as the length of the ear. Furthermore, we searched for genomic regions with a possible influence on trypanosomiasis tolerance. By associating the results of indirect Elisa for trypanosomosis infection and genotypes of purebred Baoulé cattle, as well as their crosses we identified genomic regions with significant SNPs and their underlying genes**.**

4.2.1. Qualitative traits

The GWAS analysis of qualitative traits with the fixed effects of sex and age allowed identifying regions in a number of chromosomes responsible for these traits (Table 7).

Table 7: Chromosomes with significant effects for qualitative traits

Traits	Chromosome number	Number of analyzed individuals
Ears position	1,2,3,5,8,9,10,11,12,14,16,17,18,21,22,24,25,27,28	198
Dewlap size	2, 3, 4, 12, 18,19	198

Both, the elongated floppy ears as well as the increased navel and dewlap size in zebu are a consequence of increased thermoregulatory mechanisms via excess skin.

For dewlap size, there were multiple indicative, but just two significant SNPs above the Bonferroni threshold (Figure 11).

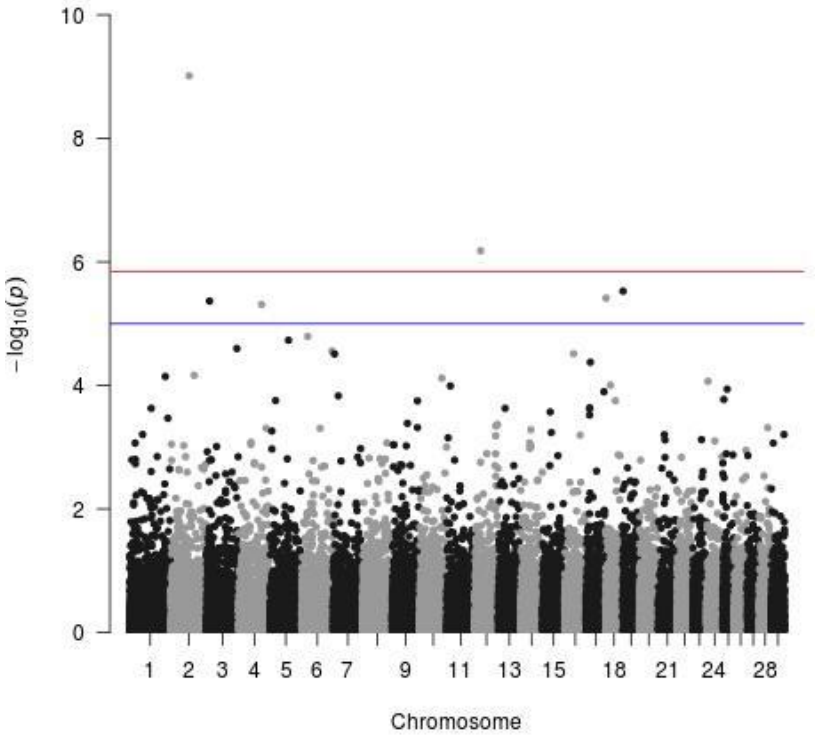

Figure 11: Significant SNPs for the dewlap size trait (blue line = indicative threshold – log10(p) = 5; red line = Bonferroni threshold –log10(p) = 5.86)

One was located on CHR 2 at 70.14Mb, with the surrounding genes CCDC93, INSIG2 and EN1, and the second on CHR 12 at 22.48Mb, with the surrounding genes LHFPL6, COG6 and FOXO1. As a possible candidate of an increased navel size, the HMGA2 gene on CHR 5 at 47.9Mb was identified in the Brasilian Nelore cattle (Aguiar et al., 2018). For our trait dewlap size, we did not identify any significant SNP in the region. Interestingly, for the ear position we found a significant SNP at 46.12 Mb in the immediate vicinity of HMGA2. In general, for the ear position there were 30 significant SNPs (Figure 12) above the Bonferroni threshold (Table 8), but none of them with a clear overlap with previously described ear morphology related genes (Adhikari et al., 2015).

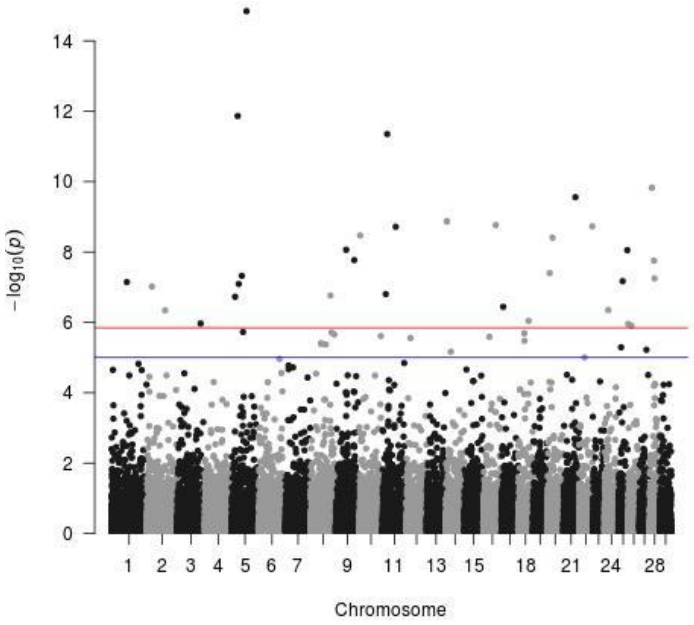

Figure 12: Significant SNPs for the ear position trait (blue line = indicative threshold – log10(p) = 5; red line = Bonferroni threshold –log10(p) = 5.86)

Table 8: Significant SNP positions and genes detected for ear position

CHR	Position (Mb)	p-value	Gene name
5	67.17	1.427976e-15	STAB2, NT5DC3, LOC505479, C5H12orf42, PAH
5	27.82	1.370694e-12	ACVR1B, FIGNL2, SCN8A, NR4A1, ATG101, KRT80, KRT7, KRT89, GRASP, ANKRD33
11	21.01	4.453821e-12	EPYC, DCN, LUM, KERA
28	10.24	1.501148e-10	RYR2
21	55.10	2.762805e-10	TP53BP1, ZSCAN29, MIS18BP1, TGM5, TOGARAM1, FRMD5, TUBGCP4, ADAL, PRPF39, FANCM, PPIP5K1
14	6.42	1.330248e-09	KHDRBS3
14	6.39	1.362059e-09	KHDRBS3
16	55.88	1.728063e-09	RABGAP1L, GPR52, TNN
22	59.30	1.869962e-09	EEFSEC, MGLL, KBTBD12, RUVBL1, GATA2, RAB7A, KIAA1257, IQSEC1, MGLL, GATA2, HMCES, RAB43, KIAA1257, EFCC1, IQSEC1
11	59.11	1.926522e-09	LRRTM4
10	3.51	3.379697e-09	KCNN2
20	24.24	3.920169e-09	LOC530348, SNX18, CDC20B, MTREX, DHX29, GZMK, LOC101908144
9	46.67	8.665168e-09	-
25	40.02	8.929194e-09	SDK1
9	82.80	1.701806e-08	EPM2A, SHPRH, FBXO30
28	20.63	1.770388e-08	-
20	11.47	3.997985e-08	PIK3R1, LOC101902212
5	46.12	4.76024e-08	DYRK2, CAND1
28	22.63	5.653865e-08	CTNNA3
25	19.17	6.763742e-08	LOC524391, LOC786628, CRYM, TMEM159, DNAH3, ANKS4B
1	69.10	7.167943e-08	KALRN, UMPS, ITGB5, MUC13, HEG1, SLC12A8
5	32.48	8.144792e-08	VDR, SENP1, PFKM, COL2A1, TMEM106C, RPAP3, RAPGEF3, HDAC7
2	22.77	9.539847e-08	CIR1, SP3, OLA1, GPR155, SCRN3, SP9,
11	14.39	1.576455e-07	MEMO1,SRD5A2, XDH, TGFA, SLC30A6, SPAST
8	89.04	8 1.72265e-07	SHC3, S1PR3
5	15.94	1.874109e-07	MGAT4C, RASSF9, NTS
17	7.83	3.639279e-07	DCLK2, IQCM
24	17.02	4.486478e-07	TRNAK-UUU
2	81.80	4.574848e-07	-

18	46.67	9.079853e-07	ZNF146, WDR62, NPHS1, NFKBID, ZNF382, KMT2B, ARHGAP33, APLP1, PROSER3, ATP4A, TBCB, ZNF461, ZNF529, ZNF565

4.2.2. Quantitative traits

The overview of the GWAS results for the quantitative traits is shown in Table 9. From these traits, height at withers and body length were measured for a higher number of individuals, as these were part of a general screening, with the more detailed measurements done on a smaller set.

Table 9: Genome wide significant SNPs effects for quantitative traits

Traits	Number of chromosomes	Number of analyzed individuals
Height at withers	3, 8, 14	598
Body length	19	599
Chest width	1,2,5,8,9,11,4,16,18,20,21,22,2,25,26,28,29	198
Chest depth	1,3,5,6,7,8,9,11,14,15,16,17,18,22,29	198
Chest girth	2,3,4,6,9,11,14,15,16,17,19,21,25,27,28,	197
Head length	1,3,5,6,8,9,11,14,17,18,20,21,22,25,27,28	192
Cranial length	1, 3, 5, 7, 8, 9, 13, 16, 23,25	192
Head width	1,2,5,8,9,10,11,14,16,17,19,20,21,22,24,25,27,28,29	197
Cranial width	7, 8,15	197
Earn length	1,2,3,5,6,8,9,10,11,14,15,16,21,22,24,25,26,27,28	194

The quantitative traits are by definition influenced by a large number of genes of small effect. Large scale GWAS analyses in humans uncovered hundreds of genes, which together explained about 20% of the variation in human height (Wood and Carden, 2014). In our data set, even with the highest number of phenotypes we were not able to detect a large number of genes with plausible effects on height or size related traits.

The results were summarized in Table 10, showing overlaps between significant regions the between single trait analyses.

Table 10: Overlapping significant regions for quantitative trait GWAS analyses

Chromosome	Position	Traits
5	27.823	Chest girth, head length, head width, ear length
	67.166	Chest width, head length, head width, chest girth
	109.513	Chest depth, cranial length
7	0.428	Cranial width, cranial length
	49.277	Chest depth, cranial length
8	89.046	Chest width, head width
9	46.669	Chest width, chest girth, head length, head width
	82.801	Chest width, head length
11	21.011	Earn length, chest width, head length, head width, chest girth
	21.146	Cranial length, chest depth
	59.110	Chest girth, chest depth, head length, head width, earn length
14	6.393	Head width, head length, chest girth, chest width
	6.416	Head width, head length, chest girth, chest width
16	55.882	Chest width, head length, head width
20	11.474	Head width, chest girth, chest width
21	55.096	Chest width, chest girth, head length, head width
22	59.306	Head length, earn length, head width
23	15.346	Chest depth, cranial length
25	19.174	Head width, chest width
26	14.934	Chest width, head width
28	10.241	Earn length, head width, head length

The significant region on CHR5 at 27.8 Mb contained a large number of genes, many related to keratin development, involved in the formation of hair (Heid et al., 1986), horns and wound repair (K and Pa, 1998) In addition, ACVRL1 in the same genomic region was a growth factor, related to endothelia and blood vessel formation (Shao, 2009). The relation of this genomic region to the traits, chest girth, head length, head width and ear length is not clear.

Another region on CHR5 at 67.166Mb harbored the most significant SNP nearby an unidentified pseudogene LOC112446821. Further nearby genes were STAB2, with a proven involvement in the bovine oviduct formation (Ulbrich et al., 2004).

The region on CHR5 at 109.5 contained multiple genes of interest, the first one being the TRIOBP gene that was found to influence hearing impairment (Wesdorp et al., 2017). This gene could be of relevance to the cranial traits, although the proven effect seems to influence hair cell stereiocilia that is essential for hearing (Kitajiri et al., 2010), rather than the cranial cavities. Another interesting gene in the same region was the ANKRD1 gene, influencing height at withers in horses (Al Abri et al., 2018) .

The very beginning of CHR7 at around 0.5Mb contained a genomic region of interest, with two genes almost on the top of the most significant SNP. The FLT4 gene was involved in the proliferation and growth in cattle (Keogh et al., 2019; Seabury et al., 2017). Interestingly, it was also an endothelial and vascular growth factor similarly to the genes found on CHR5, and involved in the bovine oviduct formation (Garcia et al., 2019) .

The region on CHR7 at 49.3Mb harbored a fairly large number of genes. Among the relevant ones for the quantitative traits belongs the SPOCK1 gene, a growth factor (Miao et al., 2013), which appears to have influence on proteoglycans. Proteoglycans are a critical part of the extracellular structure, that act as a filler substance between the cells of the organism, but also act in a complex way to trap soluble growth factors in the hematopoietic cells and supportive tissues of the organism (Kaneko et al., 2008). Another gene of great interest in the same region is EGR1 gene, a transcription factor with important roles in various cell types in response to different stimuli, in particular when it comes to the influence on bovine skeletal muscle via regulation of the MyoG gene expression (Zhang et al., 2018).

The genomic region that was found as significant on CHR8 at 89.0 Mb did not contain any genes. The closest gene to this location was the MEF2C at 88.2 to 88.4 Mb with high relevance to growth. This gene, also known as Myocyte Enhancer Factor 2 plays a pivotal role in morphogenesis and myogenesis of skeletal, cardiac, and smooth muscle cells (Juszczuk-Kubiak et al., 2011). It was also shown to influence the growth of bovine muscle development in various stages of life in both Holstein and Limousin cattle (Juszczuk-Kubiak et al., 2014). An extremely interesting point is also the connection of the MEF2C gene to the development of the cardiovascular system (Xu et al., 2012). Although, Xu et al. (2012) highlights the importance of MEF2C in relation to retinal vessel loss, which is not closely related to the

quantitative traits studied in this paper. This is the second occurrence along with the FLT4 gene on CHR7 when genes appear to have a pleiotropic effect related to development of the cardiovascular system and muscle growth. These findings put also the previously identified ACVRL1 gene on CHR5 into a new perspective. Although it was previously characterized only related to the cardiovascular system, we could hypothesize about its additional pleiotropic effects for growth following the same logic as for MEF2C and FLT4.

There were no genes of any kind located in the significant region at 46.7Mb on CHR9. The other region at CHR9 at 82.8Mb contained several genes such as UTRN, EPM2A, FBXO30, SHPRH and GRM1, but none of them with an apparent effect on quantitative size traits.

On CHR 11 the region around 21.2 Mb was found significant for a number of traits. This region harbors the GALM gene involved in glycol-metabolism and meat quality traits in cattle (Zhang et al., 2018). This genomic region was also identified to harbor a selection signature for body weight in Korean breeds (Edea et al., 2020). The gene TMEM178A was found to be suggestively associated with loin muscularity in multiple beef cattle breeds (Doyle et al., 2020). In the same region was the MAP4K3 gene, involved in the Trypanosome resistance of the N'Dama cattle (O'Gorman et al., 2009).

The region on CHR11at 59.1Mb contained only LRRTM4, a single gene spanning about 1Mb in length. This gene was previously found to be associated with milk yield traits and mastitis resistance (Cai et al., 2020), as well as yearling weight in Hanwoo cattle (Li et al., 2017).

The most significant SNP on CHR14 was directly on the top of the KHDRBS3 gene, found to be associated to fat deposition in cattle (Nayeri and Stothard, 2016; Seabury et al., 2017), as well as cell growth and proliferation in a study of Brazilian Nelore cattle (Mudadu et al., 2016).

On CHR16 the most significant SNP at 55.8Mb was the nearest to the gene GPR52 with no apparent connection to size or growth traits, but it is involved in feed efficiency in *Bos indicus* beef cattle (Alexandre et al.,2018). The CACYBP gene in the same region was related to skeletal muscle function in Holstein cattle (Sadkowski et al., 2008).

The CHR20 contained a single region of interest at 11.5Mb, with PIK3R1 as the only protein coding gene, and the most significant SNP in our analysis on the top of it. The gene itself is involved in various cellular processes including cell survival, growth, proliferation and motility (Donini et al., 2012). In cattle, it has been shown to be associated to milk production traits (Han et al., 2019).

The significant region at CHR21 at 55.1Mb contained a lot of genes, but none of them had a plausible effect on size or growth traits that could be mentioned here.

The most significant SNP on CHR22 was at around 55.3Mb, containing the DNAJB8 gene previously identified as a heat shock protein gene in cattle (Ajayi et al., 2018). Also the RUVBL1 gene nearby appears to contribute to thermo-tolerance mechanisms in African cattle (Taye et al., 2017). The EEFSEC gene in the same region was identified having a pleiotropic effect in milk traits in Nordic Holstein (Cai et al., 2020) and amino acid concentration in Japanese Black beef cattle (Sasago et al., 2018).

The top SNP on CHR23 was just nearby the FOXP4 gene at 15.3Mb. Although there is no specific information related to this gene in particular, the members of the FOXO gene family are known to be involved in numerous gene pathways, including growth in cattle (Sun et al., 2016). The neighboring MDFI gene influences muscle development (Hou et al., 2018). This part of the genome, with all genes around our most impactful SNP in our analysis was also highlighted as being positively selected towards Zebu genotypes in relation to Bovine leucocyte antigen (BoLA) region (Goszczynski et al., 2018).

The most significant SNP on CHR25 at 19.2Mb is directly on the top of the unidentified protein coding ATP-binding cassette sub-family a member 3-like LOC524391 gene, with no further information available on it. The other genes in the region are DNAH3, ZP2 influencing fertility (Hinsch and Hinsch, 1999; Rezende et al., 2018) and feed intake (Chen et al., 2011) in cattle.

On CHR 26 at 14.9 Mb resides the MYOF gene witch has a proven effect on muscle biology (Sorbolini et al., 2017). Apart from this function, members of the ferlin family, of which Myoferyn is part of seem to regulate vascular endothelial growth, similarly to other genes highlighted in the current study. The RBP4 gene also from the same region was found to be involved in the insulin signaling pathways and glucose metabolism, with effects on growth and weight traits in cattle (Wang et al., 2010).

On CHR28 at 10.2Mb the most significant SNP was directly on top of a large gene RYR2, but his was without an apparent connection to growth traits or any other relevant aspect of the current study.

4.3. Genome-wide association for trypanoresistance

The results for genome-wide association for tolerance against trypanosomiasis in the purebred Baoulé cattle (Table 11) indicated two significant genomic regions (Figure 13).

Table 11: Chromosomes with significant effects for Trypanosomosis status

Trypanosomosis status	Chromosome number	Number of analyzed individuals
Purebred Baoulé	16,24	332
Crossbreds	5	278

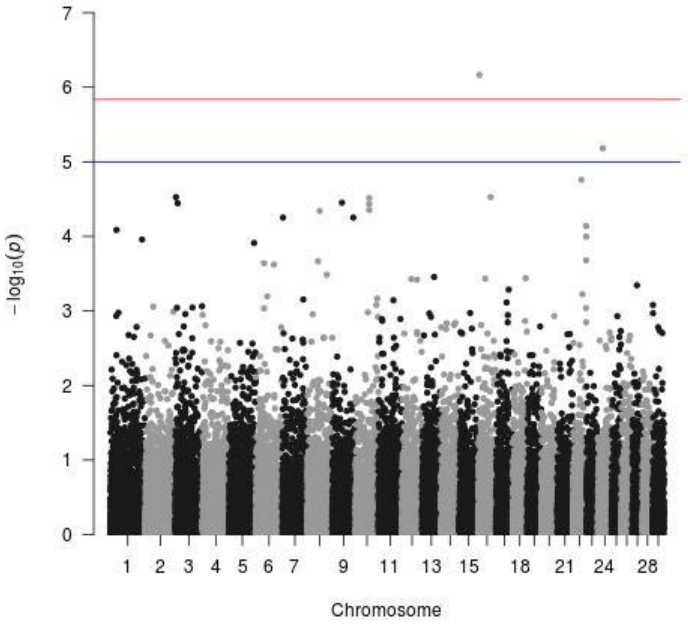

Figure 13: Significant SNPs related to resistance against trypanosomiasis in the purebred Baoulé cattle (blue line = indicative threshold –log10(p) = 5; red line = Bonferroni threshold –log10(p) = 5.86)

The first signal was on CHR16 at 6.4Mb. Just 200kb downstream of our most significant SNP was the CFH gene. This gene was first identified in an epidemiology context in connection to malaria, where it acts as a negative regulator of complement to protect host tissues from aberrant complement activation (Kennedy et al., 2016). Based on these functions, the CFH was selected as a candidate gene as it could produce protein products that are involved in the Human African Trypanosomiasis (Kimuda et al., 2018). In the study of Tiberti et al., (2010), the CFH was not found as a promising candidate, as it did not fulfill the arbitrary criteria to be selected

in this study. Our results in the Baoulé cattle are closer to the findings of Ahouty et al., (2017), who identified CFH as a candidate gene related to African Human Trypanosomiasis. The other of the two protein coding genes in the same region was KCNT2, which does not seem to be relevant for trypanoresistance, although it was found to be connected to other disorders, such as ketosis (Freebern et al., 2020) and metritis (Guarini et al., 2019) in Holstein cattle.

The second significant region for trypanoresistance in our purebred Baoulé cattle data set was on CHR24 at 22.5Mb. The most significant SNP was on the top of the LRRN1 gene, which was not found to be in a direct connection to trypanosomiasis. The CRBN gene however at around 23.1Mb, so around 600kb upstream from our signal is a more promising candidate. The CRBN gene forms the Cereblon protein, and its orthologs are highly conserved from plants to humans, which underscores its physiological importance. Cereblon forms an E3 ubiquitin ligase complex, which in turn was shown to have parasite-specific effects, in particular in connection to malaria (Jain et al., 2017). This pattern of an effect related to parasite and malaria are reminiscent of the CFH gene as discussed above, which was also previously connected to malaria, an another parasite borne disease. Along the same lines, we hypothesize that this gene could be an additional candidate for trypanosomosis resistance that was not highlighted in any of the previous studies. The two additional nearby genes TRNT1 and IL5RA also seem to be involved in immunological processes (Scott et al., 2020; Villarreal-Ramos et al., 2018; Zhu et al., 2020), which could be also relevant for the trypanosomiasis resistance in cattle.

In crossbreds, the most significant SNP was in a gene sparse region of CHR5 (Table 11) at 16.1 Mb (Figure 14).

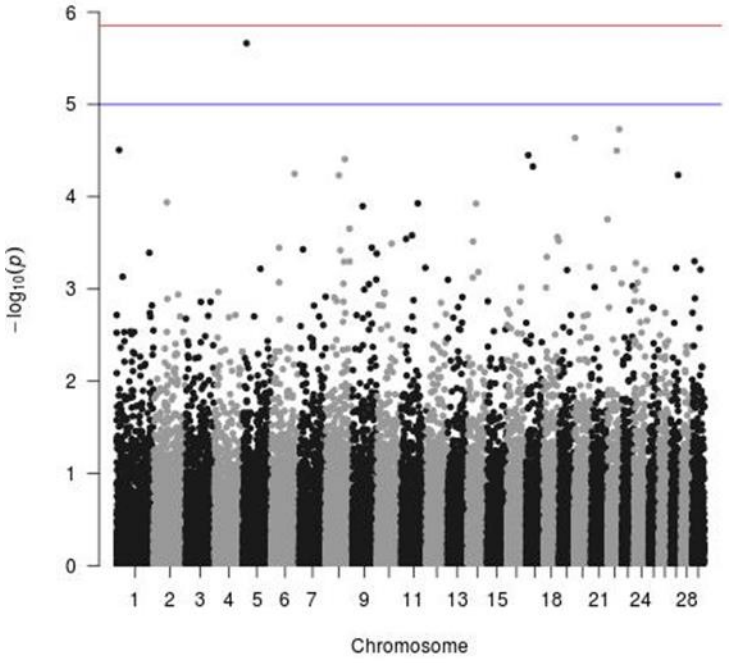

Figure 14: Significant SNPs related to resistance against trypanosomiasis in crossbreds cattle (blue line = indicative threshold –log10 (p) = 5; red line = Bonferroni threshold – log10 (p) = 5.86)

The closest gene to the most significant SNP was the MGAT4C about 150kb downstream, which was found to affect the growth rate in buffaloes (de Araujo Neto et al., 2020), seemingly not in direct connection to trypanosomiasis. An indirect lead to its connection could be that the MGAT4C gene was also identified as a QTL for Cytokynes (Li et al., 2016), which are proteins produced by T-lymphocytes as an immunological response to viral and non-viral antigens.

The second gene about 600kb downstream of the most significant SNP is NTS (Neurotensin), whose degradation is mediated by the enzyme of the *T. brucei* prolyl oligopeptidase gene, providing a clear connection to trypanosomiasis and the sleeping sickness disease that it causes. The POP Tb enzyme of the *T. brucei* might not completely deactivate the peptides, as NTS generated products with weaker affinity for their receptors (Bastos et al., 2010). A similar effect was discussed also in Morty et al., (2006) about the influence of peptidases released by trypanosomes that could affect regulatory peptides such as neurotensin and gastrin. Interestingly, the other genes related to trypanosomiasis, identified in our study (TRNT1 and IL5RA) were also connected to immunological response.

Although the regions identified in our study seem to be relevant to the trypanoresistance, we did not found an overlap between our results and some of the notable previous studies. In

N'Dama cattle Hanotte et al, (2003) mapped QTL associated with trypanotolerance on 18 different cattle autosomes in F2 crosses of trypanotolerant N'Dama and trypanosusceptible Boran cattle. They showed independent genetic control for parasitaemia and body weight, with most QTLs having minor effects and the major ones being located on chromosomes 2, 4, 7, 16 and 27. Subsequently, expression analyses in blood cells reported pathways and genes differentially regulated in trypanotolerant N'Dama and trypanosusceptible Boran (Gachohi et al., 2009; Noyes et al., 2011). Genes such as TICAM1, ARHGAP15, SLC40A1, GFM1 and INHBA have been proposed as candidate genes for trypanotolerance (Dayo, 2009b; Noyes et al., 2011). More recently, full genome sequence analysis reported several candidate genome regions under positive selection in N'Dama cattle including genes with functions related to immunity, anaemia and feeding behaviours that may be linked to the trypanotolerant phenotypes (Kim et al., 2017; Taye et al., 2017). Tijjani, (2019) considered the common candidate genes in Muturu and N'Dama breeds and reported pathways linked to trypanotolerance in West African taurine population as well as selected candidate genes in Muturu cattle only. In total, the authors identified 20 candidate genes in West African taurines. Functional annotation and enrichment analyses based on Reactome pathways in PANTHER ver13.1 (Thomas et al., 2003) confirmed their relevance in response to trypanosome infection pathways. They are all members of the major histocompatibility complex (MHC) class II with related functions in immune responses. Although our results also point into the direction of genes involved in immunological response, we did not find exact overlaps with regions identified in Tijjani, (2019) and Hanotte et al, (2003).

4.4 Global Admixture and local ancestry estimation

The genomes of crossbred Baoulé x Zebu cattle comprise a mosaic of ancestral haplotypes formed by recombination occurring at every generation. The boundaries and origin of each ancestral segment can be reconstructed along each chromosome by statistical methods, which estimate ancestral allele and haplotype frequencies and their distribution in the crossbred populations. The determination of the admixture level and the average ancestry in positive and negative crossbred animals is very important for a better understanding of trypanoresistance in south-west African cattle.

4.4.1. Global admixture of all animals

The individual admixture proportions using the full set of SNPs were estimated for all pure and admixed animals and are presented in Figure 15. The distribution of the global admixture proportions for the 802 animals is presented in (Figure 16). Notably, we detected 91 cattle with a Baoulé ancestry > 0.995 among the presumed crossbreds, which we excluded from the subsequent analysis of local ancestry in admixed animals.

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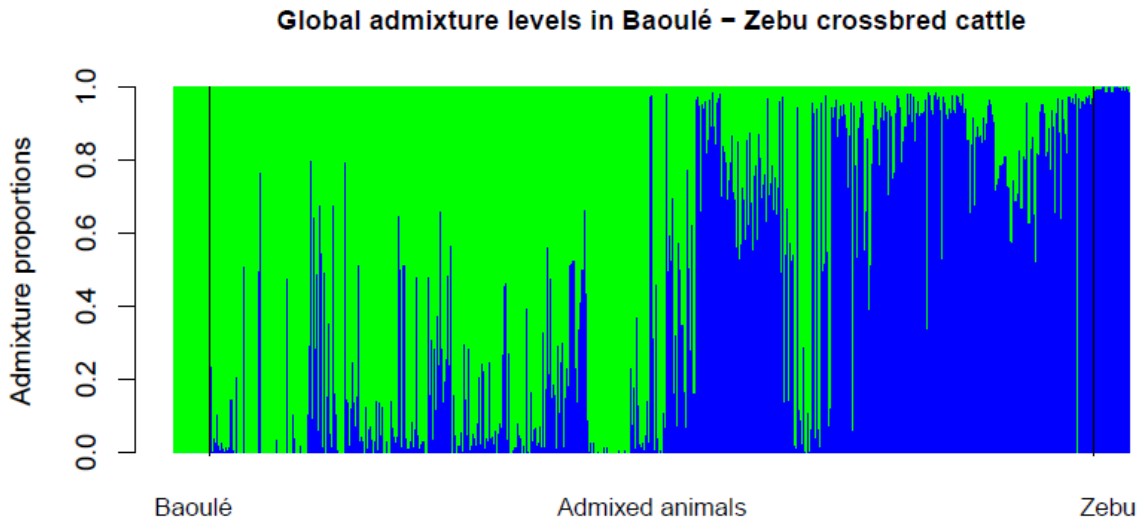

Figure 15: Global Admixture in Baoulé- Zebu Crossbred cattle with the full set of 31612 single nucleotide polymorphisms (SNPs).

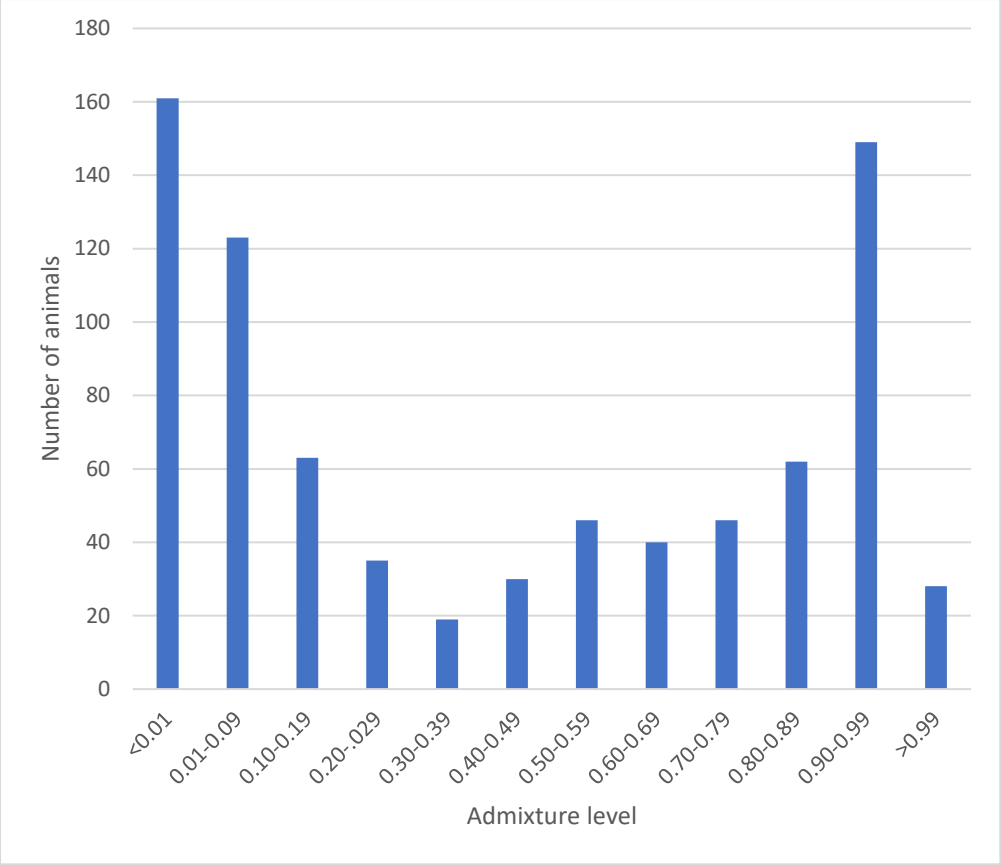

Figure 16: Distribution of the global admixture proportions for 802 animals with the full set of 31612 single nucleotide polymorphisms (SNPs)

The high amounts of global admixture observed in the taurine cattle population in the three studied departments of Burkina Faso indicated mixed genetic backgrounds of the cattle in Borouom-Bouroum, Kampti and Loropeni (Figure 15, 16). The observed admixture levels within the departments are likely due to unrestricted mating among cattle of different genetic backgrounds. Long-distance migrations within and across countries, utilization of communal pastures, exchange of breeding animals, and uncontrolled mating facilitate constant gene flow. Houessou et al., (2019) explained this situation by lack of selection and high levels of gene flow due to cyclical cross-border cattle herd movements known as “transhumance” and extensive commercial transactions of cattle in the West African region.

The uncontrolled mating in extensive production systems, which are typically practiced in West Africa, can lead to the introgression of Zebu genes in the small taurine cattle population, which

represents a threat to their genetic integrity (Dossa and Vanvanhossou, 2016), and might lead to a potential dilution of their trypanotolerance (Albert et al., 2019; Traoré et al., 2015). The increasing importance of Zebu in the south-western region of Burkina Faso might endanger Baoulé cattle in the long term. Thus, suitable management is required for the sustainable use of local breeds, and recently community-based breeding programs (CBBP) for Baoulé cattle and their crossbreds have been implemented (Ouédraogo et al., 2020). Within the CBBP, Zoma et al., (2020) identified four distinct types of cattle production systems sedentary Lobi farms, sedentary crossbreed farms, semi-transhumant Fulani Zebu farms, and transhumant Fulani Zebu farms. The admixture between Zebus and Baoulé cattle observed in this study could be due to differences in the production systems. Furthermore, notable size differences between purebred and crossbred Baoulé were confirmed (Yougbaré et al., 2020) and breeders prefer to have large animals like Zebu cattle. As shown in Figure 15, we identified several purebred Baoulé cattle that had been considered as admixed based on the sampling information. These animals originated from the populations of Loropeni and Bourboum-Bouroum where the farmers have a preference for breeding purebred Baoulé (Zoma et al., 2020).

4.4.2. Different local ancestry in trypanosome positive and negative Baoulé x Zebu crosses

The average ancestry estimation for every single SNP was performed across 29 autosomes for trypanosome positive and negative Baoulé x Zebu crossbreds, respectively. In general, trypanosome negative individuals showed a lower average admixture rate (0.548 ± 0.026) and higher amounts of Baoulé ancestry than positive ones (0.552 ± 0.030) ($p < 0.001$). The permutation tests over all chromosomes indicated significant local ancestry deviation from the average (above the 5% and 10% genome-wide thresholds) in chromosomes 8 and 19 for trypanosome positive crossbreds (Figure 17), and in chromosomes 6, 19, 21 and 22 for trypanosome negative animals, respectively (Figure 18).

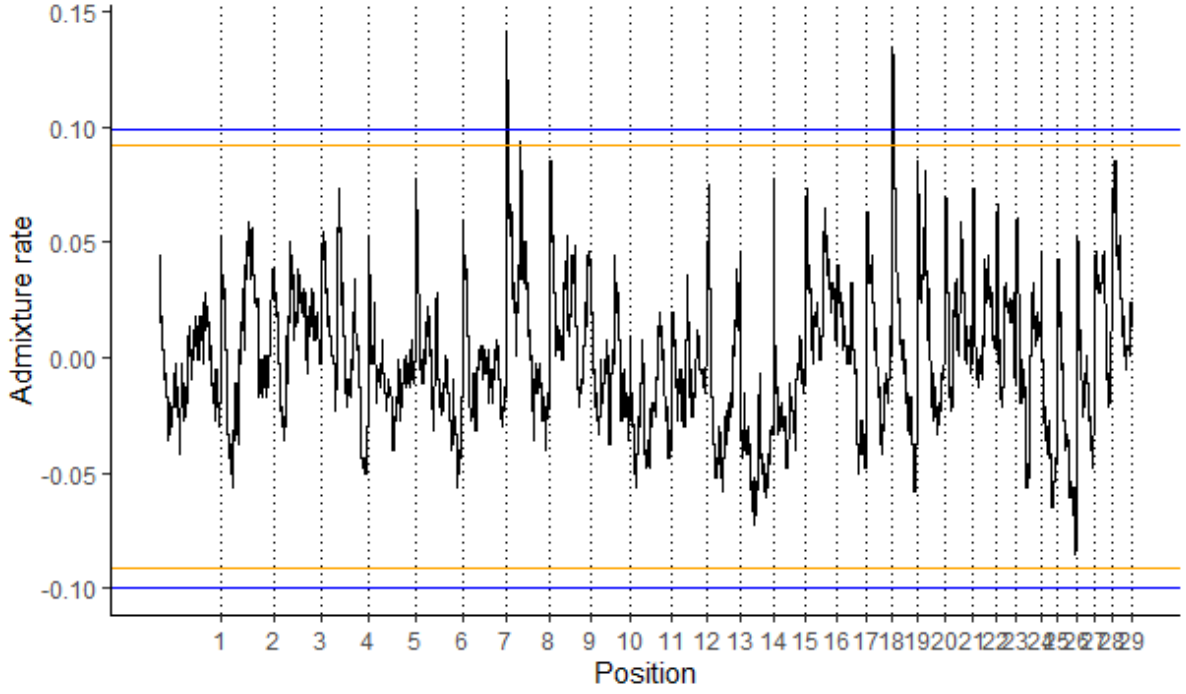

Figure 17: Local ancestry deviations based on the permutation threshold for the 244 positive crossbreds animals. Orange and blue line signify the 5% and 10% genome-wide thresholds

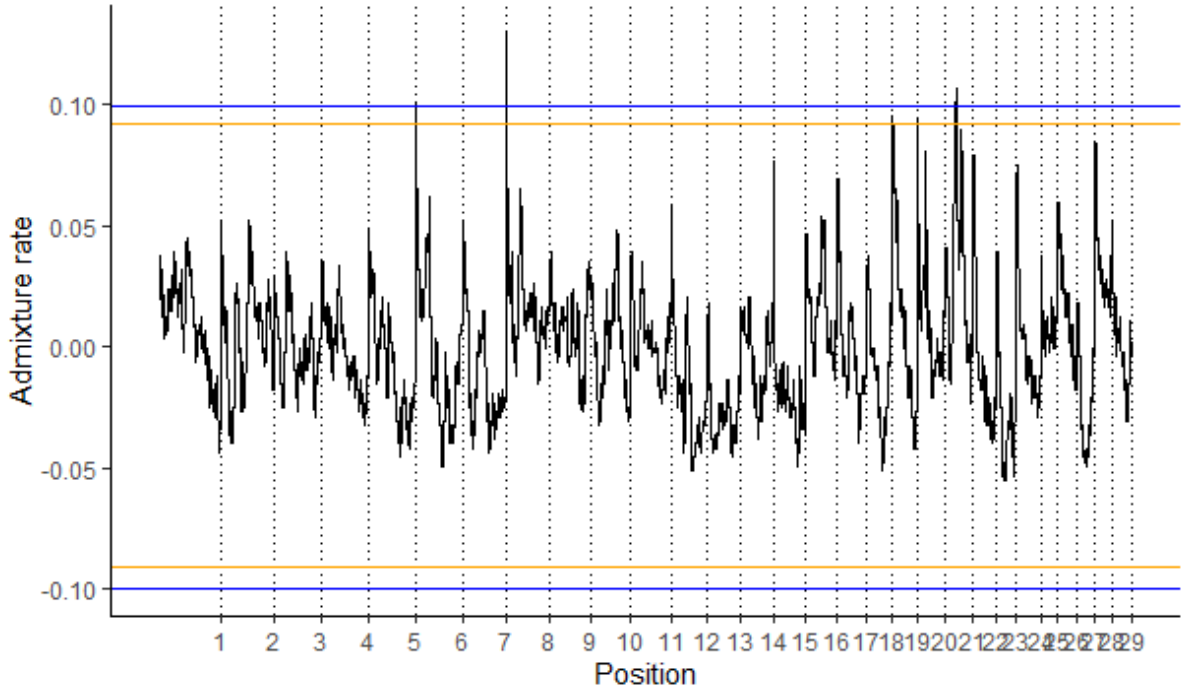

Figure 18: Local ancestry deviations based on the permutation threshold for the 266 negative cossbreds animals. Orange and blue line signify the5% and 10% genome-wide thresholds

The local admixture proportions for these chromosomes are presented in Figure 19 and for all other chromosomes in Figures S1 and S2

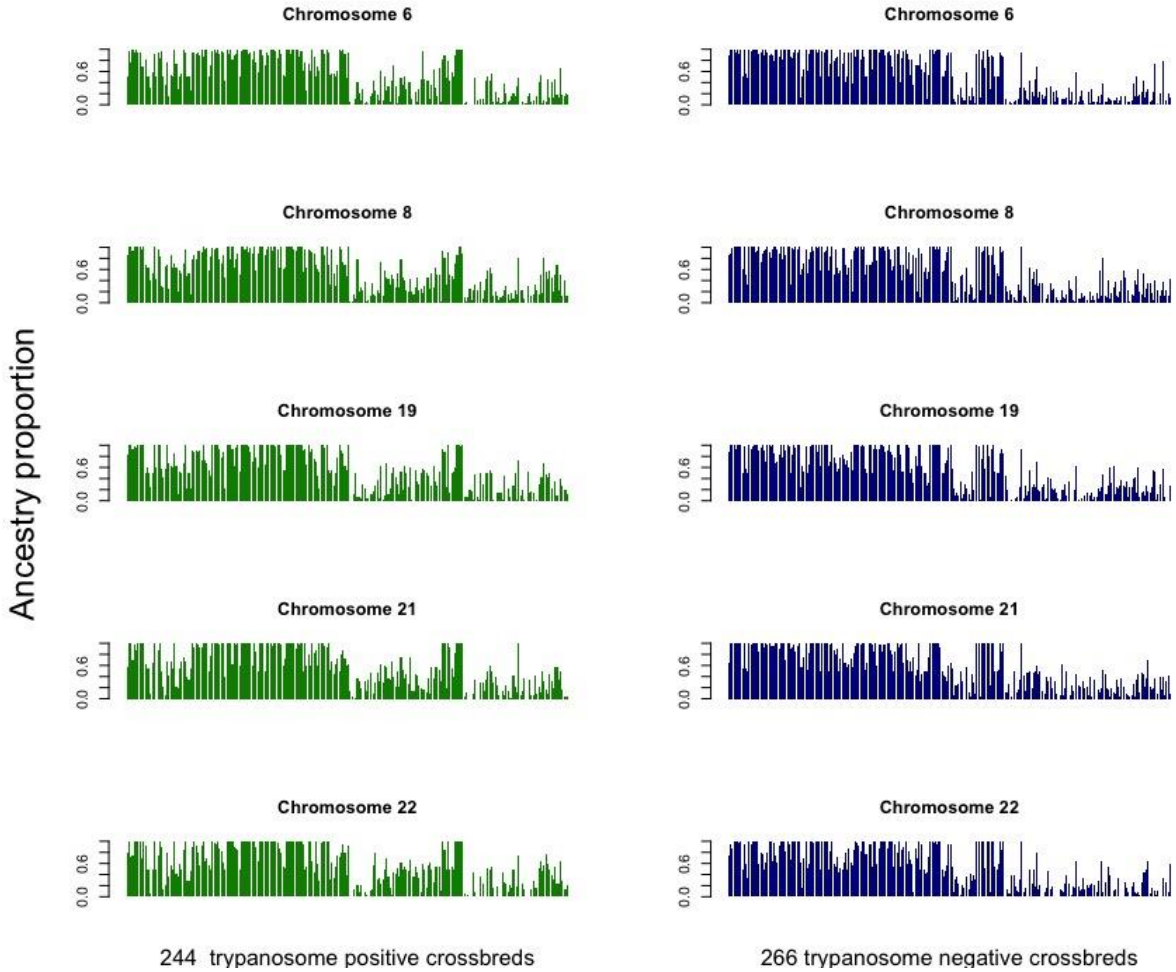

Figure 19: Individual admixture proportions across chromosomes 6, 8,19,21,22 for the 244 trypanosomose positive and 266 negative crossbreds as determined by LAMP

We further visualised the deviations from the average ancestry in the respective chromosomes and identified regions of higher delta ancestry (wide peaks) on chromosome 8 between 35-50 Mb and in chromosome 21 between 20-35 Mb and 40-50 Mb, respectively (Figure 20). The delta ancestry for all other chromosomes in Figures S3 and S4. These genomic regions might harbour candidate genes associated to tolerance or susceptibility of trypanosomosis.

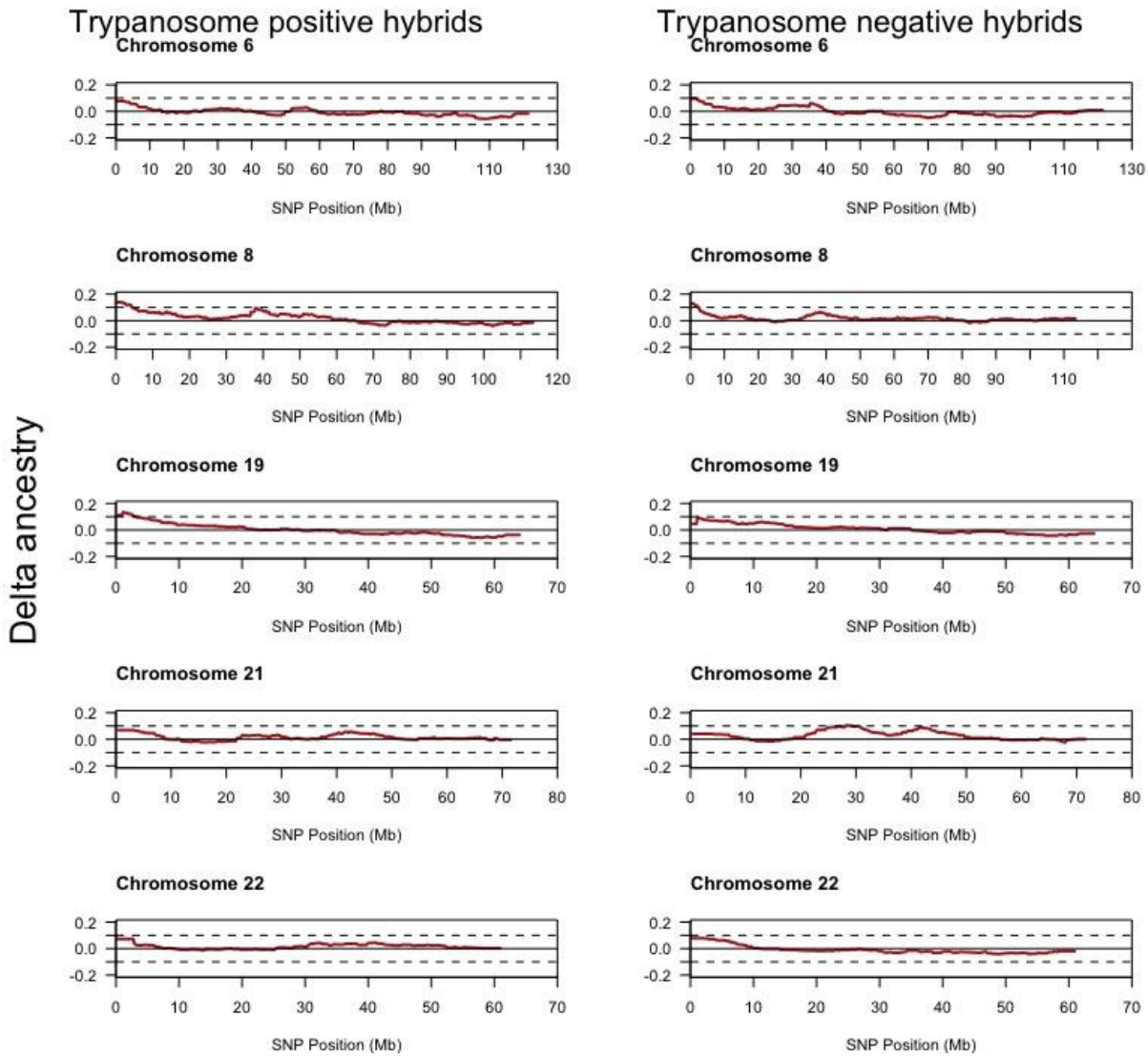

Figure 20: The delta ancestry across chromosomes 6, 8, 19, 21and 22 for the 244 positive and 266 negative crossbreds trypanosomosis status

In a recently admixed population, ancestral populations have been mixing for a relatively small number of generations, resulting in a new population with different proportions from the original populations (Khayatzadeh et al., 2016). Due to recombination events, the genomes of admixed individuals are fragmented into shorter genome regions of different ancestries (Racimo et al., 2015). Local ancestry analysis of admixed populations has been successfully used to detect recent selection in admixed Swiss Fleckvieh cattle (Khayatzadeh et al., 2016). In our study, we applied this approach to identify significantly different local admixture levels

and detected five chromosomes with higher deviation from the average ancestries, with an excess of Baoulé ancestry, which might account for a higher resistance to trypanosomiasis. Similarly, Decker et al., (2014) investigated the population structure of domesticated cattle and calculated Asian indicine (Bos indicus), Eurasian taurine, and African taurine (both Bos taurus) ancestry proportions.

We applied an approach of significance testing and performed a permutation test of circularizing the genome by concatenating the SNPs of all autosomes in a single string, cutting this string once and rearranging the two resulting segments, as proposed by Tang et al., (2007). The permutation approach destroys not only the effects of selection, but also the local effects of genetic drift; the threshold is considered non-conservative. Nevertheless, based on simulations (Tang et al., 2007) outliers are unlikely to be due to genetic drift. Therefore, this procedure is considered robust to correct for multiple testing to find significant signals for selection.

We found regions deviating from the average ancestry with a higher amount of Baoulé proportions on chromosomes 6, 8, and 19 in trypanosome negative individuals. A previous study **(**Noyes et al., 2011) identified *VAV1, PIK3R5, RAC1, VAV2, GAB2, INPP5D* genes on chromosome 8 to be genes under selection in Muturu and N'Dama cattle breeds in response to trypanosomes infection. Surprisingly, we also found higher Baoulé ancestry chromosome 8 (35-50 Mb) also in trypanosome positive cattle, which could indicate that these regions harbor beneficial Baoulé haplotypes which are not connected to trypanosomosis resistance. These regions might harbour genes of general importance for adaptation to the environment. Some, candidate genes on chromosome 6 at 71373513-71421283 (*PDGFRA*) and chromosome 19 at 41185975-41196948 *(CDC6)* for trypanotolerance in West African taurines have been found on these chromosomes (Tijani, 2019). Furthermore, Smetko et al., (2015) identified

chromosomes 7 and 22 as regions with the highest Baoulé ancestry proportion, similar to our results.

4.4.3. Genes under potential selection identified by F_{ST} outlier tests

We screened the genomes of the admixed animals for outlier SNPs with high F_{ST} values and detected seven variants with an FDR corrected threshold of $p < 0.05$ (Figure 21). The seven outlier SNPs with the highest levels of F_{ST} values are presented in Table 12, together with their associated genes.

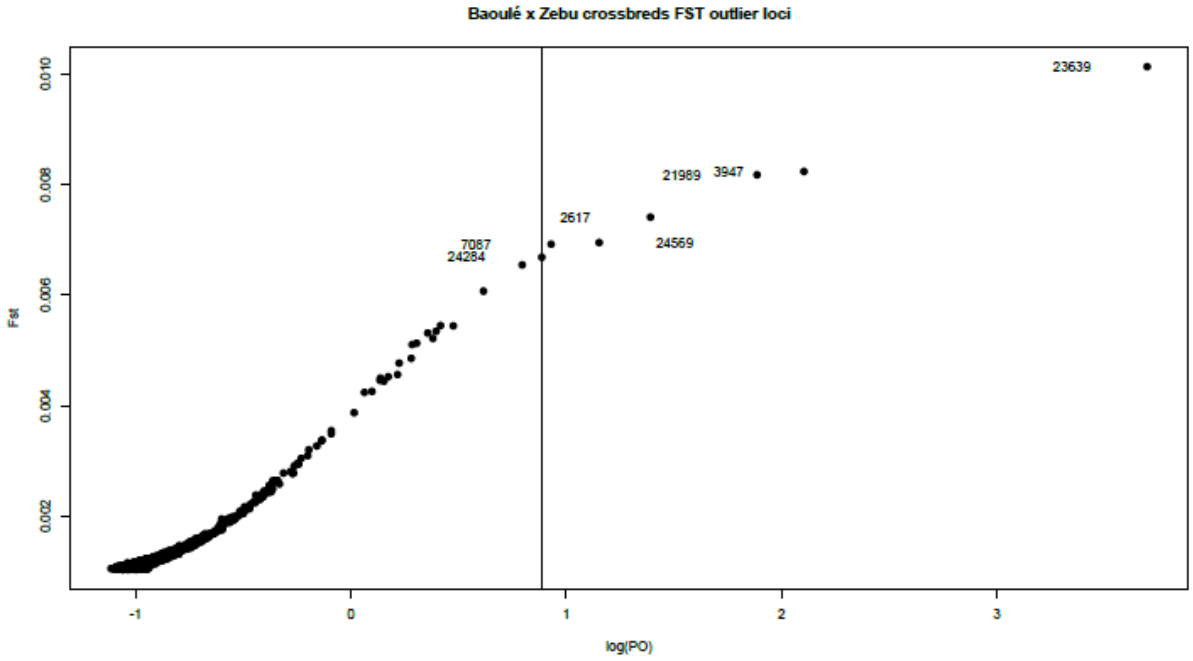

Figure 21: FST outliers between trypanosome positive and negative crossbreds

Table 12: The 7 outlier SNPs with the highest levels of FST values

Chromosome number	SNP name	Position	Genes
2	BovineHD0200021582	75210246	LOC100138101, LOC101902632
3	BovineHD0300017052	56576857	HS2ST1, LMO4, ENSBTAG00000054817, ENSBTAG00000052091
5	ARS-BFGL-NGS-110363	108172899	CACNA1C, DCP1B, CACNA2D4, LRTM2, ADIPOR2, LOC101903199, ERC1, WNT5B, WNK1, RAD52, FBXL14
20	BovineHD2000008166	27620224	ISL1
21	ARS-BFGL-NGS-22971	11067328	LOC107131341, NR2F2, LOC101907985
23	BovineHD4100016034	20992806	CD2AP, ADGRF2, ADGRF4, OPN5, PTCHD4
23	BovineHD2300012802	44142970	PHACTR1, HIVEP1, ADTRP, EDN1

Identifying recent positive selection signatures in domesticated animals can provide information on beneficial mutations and their underlying biological pathways for economically important traits. Global F_{ST} values are one useful method to detect selection signatures across breeds (Biswas and Akey, 2006). The seven outlier SNPs, which we identified between trypanosome positive and negative crossbreds, were on chromosome 2, 3, 5, 20, 21, and 23. The chromosomes BTA 2, 3, 5, and 23 have previously been identified harbouring common candidate genes in Muturu and N'Dama breeds linked to trypanotolerance in West African taurine population as well as selected candidate genes in Muturu cattle only (Tijjani, (2019a). Functional annotation and enrichment analyses based on Reactome pathways in PANTHER

ver 13.1 (Thomas et al., 2003) confirmed their relevance in response to trypanosome infection pathways. In our study, we identified other genes (Table 12) such as *LOC100138101, LMO4, LTRM2, ISL1, PTCHD4, and HIVEP1* as genes potentially responsible for trypanotolerance.

From the previous studies genes such as *TICAM1, ARHGAP15, SLC40A1, GFM1* and *INHBA* have been proposed as candidate genes for trypanotolerance on chromosomes 2, 3 and 5 (Dayo, 2009; Noyes et al., 2011). We have identified on the same chromosomes but not in the same regions. More recently, full genome sequence analysis reported several candidate genome regions under positive selection in N'Dama cattle including genes with functions related to immunity, anaemia and feeding behaviours that may be linked to the trypanotolerant phenotypes (Kim et al., 2017; Taye et al., 2017).

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4.4.4. Ancestry informative markers to detect admixture for routine genetic monitoring.

To reliably detect hybrids even with a smaller SNP set applicable for routine genetic monitoring, we selected the most differentiating SNPs between Baoulé and Zebu cattle. The 100 highest F_{ST} values ranged between 0.98 and 0.79 (Table S1). We estimated admixture levels of the crossbred individuals using the top 15, 25, 50, and 100 SNPs (Figure S5). The Pearson correlation coefficients *r* between the levels of admixture using different ancestry informative SNP sets (allSNPs**,** top100, top50, top25, top15 SNPs) were generally high and ranged between 0.974 (allSNPs/top15) and 0.995 (allSNPs/top100) (Table 3). All Pearson correlation coefficients were statistically significant ($p < 0.001$).

Table 13: Correlation matrix between the levels of admixture using the most ancestry informative SNP sets compared to 31612 SNPs

	Top100	**Top50**	**Top25**	**Top15**
allSNPs	0.995	0.992	0.985	0.974
Top100		0.997	0.990	0.981
Top50			0.993	0.983
Top25				0.992

The indigenous cattle breeds are disappearing because of indiscriminate crossbreeding by individual farmers, and schemes for genetic improvement developed without concern for preserving locally adapted breeds (Belemsaga et al., 2005). Many breeding programs or genetic improvement strategies in developing countries failed due to the lack of involvement of beneficiaries (Duguma et al., 2011). Community-based breeding (CBBP) is recognized to be adapted to low input production systems and this approach requires full participation of farmers in the different steps of implementation(Wurzinger et al., 2011). The implementation of a sustainable community-based breeding program requires a good understanding of production system, selection criteria and breeding goals (Mueller et al., 2015). In many developing countries, livestock crossbreeding has been implemented with poor or no pedigree recording. Thus, ancestry informative markers would provide a great opportunity to estimate the level of admixture in a cost effective way. Sölkner et al., (2010) proposed that individual admixture levels were estimated more accurately based on the genomic data using panels of pure reference animals, compared to estimation based on pedigree. Getachew et al., (2017) indicated that the Ovine 50KSNP array is a powerful tool to identify small sets of AIMs for admixture studies in crossbred sheep populations in Ethiopia.

The minimum set of the 25 highest differentiating SNPs (Table S1) can be used to develop an efficient competitive allele-specific PCR (KASP™, LGC Group, USA) genotyping assay. KASP achieves a bi-allelic discrimination through the competitive binding of the two allele-specific forward primers. If the genotype at a given SNP is homozygous, only one of the two possible fluorescent signals will be generated. If the genotype is heterozygous, a mixed fluorescent signal will be generated. Such an easy and fast genotyping array can be implemented at any laboratory equipped with Real-Time PCR machine and can be used for routine monitoring of hybridisation in Baoulé cattle. Understanding the relationship between genetic admixture and performances is crucial for the success for local cattle breed conservation and crossbreeding programs. Use of small sets of ancestry informative markers (AIMs) is a cost-effective option to estimate the levels of admixture in situations where pedigree recording is difficult like in Burkina Faso.

5. GENERAL REFLECTION AND CONCLUSIONS

Trypanosomosis is a parasitic disease. It is caused by infection with trypanosomes, blood-borne, flagellate protozoan parasites transmitted by tsetse flies (*Glossina spp.*). The trypanosomes replicate in the tsetse fly and are transmitted through saliva when the fly feeds on animal. Trypanosomosis is also mechanically transmitted by tsetse flies and other biting flies through the transfer of blood from one animal to another.

Trypanosomosis is generally a chronic evolving disease which is usually fatal if appropriate treatment is not established. The incubation period varies from 4 to 40 days, depending on the involved trypanosome. The cardinal clinical sign observed is anemia that is characterized by decrease in packed cell volume (PCV), hemoglobin, red blood cell, and white cell levels. Parasitemia can also be observed at clinical level. The most common symptoms are: presence of intermittent fever, edema and loss of condition; depression, lethargy, weakness, anemia, salivation, lacrimation, nasal discharge, change of hair colour (black to metallic brown), accelerated pulse and jugular pulsation, hard breathing. The back of a suffering animal is often arched and the abdomen "tucked up". As said above the symptoms are variable according to the trypanosome that infected the animal, but most of those symptoms are observed with *T. congolense*. Abortion may be seen, and infertility of males and females is a common sequel. The disease can evolve from peracute, acute to chronic disease in cattle and the other susceptible animals (sheep, goats, horses, camels, pigs, dogs) depending again on the trypanosome.

In Burkina Faso, most of the animals at risk are located in the sub-humid zones that represent 32% of the total land area (Soudre, 2011). In contrast, risk of trypanosomosis is lower in the Sahelian domain (Traoré et al., 2015) where it even doesn't exist in some areas. Among the livestock the Baoulé cattle, like most taurine breeds have in general inherited resistance to trypanosomosis (trypanotolerance) that allows them to inhabit areas infested with tsetse flies. In contrast, Zebu cattle possess no innate resistance to trypanosomosis and have only started to penetrate the tsetse infested regions with the assistance of veterinary prophylaxis and other control methods (Dayo et al., 2009). These migrations of zebu cattle pose a serious threat to the genetic integrity of trypanotolerant populations of taurine cattle in the southern areas. In this study, the genomic candidate regions for trypanotolerance and body size with high-density genotype data of purebred Baoulé and crossbred Baoulé and Zebu cattle were investigated.

This study is associated to community-based breeding programs as is recognized to be adapted to low input production systems and this approach requires full participation of farmers in the different steps of implementation. The implementation of a sustainable community-based breeding program requires a good understanding of production system, selection criteria and breeding goals. A breeding objective defines the direction in which the farmer aims to go towards satisfying the demand for specific products and services from the animal.

This thesis presented the differences between purebred Baoulé and their crossbreds with zebu. A total of 421 animals (111 males and 310 females) were included in the study. The quantitative traits were analyzed by fitting a linear model and chi square tests were performed for qualitative traits.

This thesis related to characterization of the Baoulé cattle is also an effort to underline its national and cultural importance. The visual assessments of clear distinction between crossbred and purebred animals were confirmed also in this work, when all of the 24 examined traits were significant (Table 4), and all but one was different between genotypes. The effect of age was significant for 18 traits, and the effect of sex for 12 traits. These apparent and proven differences in morphological and size traits are relevant, considering the importance of the purebred Baoulé cattle in cultural practices. We show that the crossbred status is easily detectable even in an environment where the routine animal recording is not in place, with increased crossbreeding practices potentially leading to diminished purebred stocks and maintenance of cultural practices.

In addition to the differences between purebreds and crossbreds, the crossbred groups kept in different regions and production systems were also distinct (Table 5). The reason for these differences could be feed availability, but also ethnic differences of the livestock breeders and their preferred sedentary or transhumant lifestyle, in response of the seasonal variability in feed resources. Compared to animals from sedentary herds, the animals from transhumant herds tend to be larger, with higher zebu proportions.

The large variability of qualitative traits, such as horn shape and color traits, indicates their lack of importance in the definition of breed characteristics of local breeds. The lack of strong section on these traits is in a stark contrast to e.g. European breeds, where a unified appearance in one of the hallmarks of the breeds.

An additional important advantage of Baoulé cattle, in addition to its cultural relevance, is its trypanoresistance. This characteristic was duly recognized throughout the thesis work, with a main goal to identify genomic regions that harbor genes related to resistance to trypanosomosis. GWAS studies were performed with trypanosomosis positive and negative animals as the observed phenotypes. The recognition of the potential differences between purebred and crossbred Baoulé cattle resulted into separation of these data sets into separate GWAS analyses. The GWAS results were not extremely clear in terms of signals, with only single SNPs denoting regions of importance, and not a large number of SNPs in the same location, as seen in some other studies. In the purebred Baoulé analysis there were two such regions (on CHR16 and CHR24), and in the crossbred set only one (on CHR5). All signals indicated highly relevant genes, however, with direct connection to trypanosomosis, or other similar diseases caused by blood parasites (e.g. malaria). For some of these genes (*CFH, TRNT1, IL5RA, MGAT4C* and *NTS*) we have confirmed results of previous studies by their connection to trypanosomosis, while CRBN was to our knowledge identified in this context for the first time.

The continued fight against trypanosomosis has major importance to the health of both human and livestock populations. The genetics of individuals seem to affect the outcome of the disease, yet there were no genomic regions and genes consistently identified throughout independent association studies. Also, in our case we have identified genes highly relevant to the disease, but did not confirm genes and regions identified in other livestock populations. The reason could be in a generally complex and elusive nature of the genetics of trypanosomosis response, but also in the differences among these response mechanisms between breeds.

The differences in response to trypanosomosis were also apparent among the Baoulé and zebu crossbreds. Few of the crossbreds showed resistance similar to Baoulé cattle, others succumbing to the disease, similar to purebred zebus. These differences were most likely caused by the breed ancestry of respective genomic regions in crossbreds.

The global admixture studies revealed a wide range of admixture, from almost pure Baoulé to almost pure zebu, all being labelled as “crossbred”. This finding was consistent with expectations, given the lack of animal recording and strict breeding practices in the study areas. The global crossbreeding levels were not good indicators of trypanosomosis resistance, however.

More precise analyses of local admixture were performed to uncover genomic regions related to trypanoresistance in crossbreds. The top 10% of the extreme deviations from the average ancestry levels in favour of Baoulé cattle were denoted as potential regions of interest, given the proven trypanoresistance of this breed. Chromosomes 6, 8, 19, 21 and 22 contained such regions of higher ancestry proportions of Baoulé cattle. These results suggest that selection on these regions being of Baoulé ancestry increases the trypanoresistance of crossbreds.

In addition to endeavors related to trypanosomosis we have identified a set of ancestry informative markers that could be used as a cost-effective means of identification of breed proportions in Baoulé x zebu crossbreds. It was shown that a set of 25 carefully selected SNPs could be equally well used to identify breed proportions, even in the absence of pedigree information. The low costs and relatively lower technical requirements associated with this approach allow large scale application of genomics in the breeding programs of Burkina Faso.

Generally, the results of this thesis will serve as basis for further characterization, conservation and improvement strategies for purebred and crossbred populations. Information about best levels of admixture and the most important parts of the Baoulé genome regarding the resistence to trypanosomiasis is a premise of more effective and sustainable use of trypanotolerant types of cattle, in both purebred and crossbred populations.

This study will contribute to a better understanding of the mechanism of trypanotolerance and will allow building a suitable breeding strategy in the south – western region of Burkina Faso. Thus, the following recommendations are given:

• The Baoulé breed, well known for its trypanosomosis resistance, is threatened by crossbreeding with Zebu cattle. The morphometric characterization is the first step and a suitable breeding strategy must be built for its preservation.

• While we were able to identify a number of candidate regions and associated candidate genes with plausible connection to trypanosomiasis and other parasitic diseases, the precise genetic control underlying the trypanoresistance in Baoulé cattle was not confirmed with certainty. In future, research should continue and further studies should be conducted, focused in particular on genomic analyses of targeted case-control trials, involving large cattle cohorts.

• Based on the results from our research it is plausible that the other livestock genetic resources and indigenous breeds of Burkina Faso also harbor genomic regions responsible for adaptive traits in general, and trypanosomiasis resistance in particular. The Ministry of Animal

Resources and Fisheries of Burkina Faso through their genetic conservation section is advised to conduct similar studies on all local breeds in Burkina Faso, to fully capitalize on their genetic potential.

REFERENCES

Adhikari, K., Reales, G., Smith, A.J.P., Konka, E., Palmen, J., Quinto-Sanchez, M., Acuña-Alonzo, V., Jaramillo, C., Arias, W., Fuentes, M., Pizarro, M., Barquera Lozano, R., Macín Pérez, G., Gómez-Valdés, J., Villamil-Ramírez, H., Hunemeier, T., Ramallo, V., Silva de Cerqueira, C.C., Hurtado, M., Villegas, V., Granja, V., Gallo, C., Poletti, G., Schuler-Faccini, L., Salzano, F.M., Bortolini, M.-C., Canizales-Quinteros, S., Rothhammer, F., Bedoya, G., Calderón, R., Rosique, J., Cheeseman, M., Bhutta, M.F., Humphries, S.E., Gonzalez-José, R., Headon, D., Balding, D., Ruiz-Linares, A., 2015. A genome-wide association study identifies multiple loci for variation in human ear morphology. Nat. Commun. 6, 7500. https://doi.org/10.1038/ncomms8500

Aguiar, T.S., Torrecilha, R.B.P., Milanesi, M., Utsunomiya, A.T.H., Trigo, B.B., Tijjani, A., Musa, H.H., Lopes, F.L., Ajmone-Marsan, P., Carvalheiro, R., Neves, H.H. de R., do Carmo, A.S., Hanotte, O., Sonstegard, T.S., Garcia, J.F., Utsunomiya, Y.T., 2018. Association of Copy Number Variation at Intron 3 of HMGA2 With Navel Length in Bos indicus. Front. Genet. 9. https://doi.org/10.3389/fgene.2018.00627

Agyemang, K., 2005. Trypanotolerant Livestock in the Context of Trypanosomiasis Intervention Strategies. Food & Agriculture Org.

Ahouty, B., Koffi, M., Ilboudo, H., Simo, G., Matovu, E., Mulindwa, J., Hertz-Fowler, C., Bucheton, B., Sidibé, I., Jamonneau, V., MacLeod, A., Noyes, H., N'Guetta, S.-P., Consortium, for the T.R.G. as members of T.H., 2017. Candidate genes-based investigation of susceptibility to Human African Trypanosomiasis in Côte d'Ivoire. PLoS Negl. Trop. Dis. 11, e0005992. https://doi.org/10.1371/journal.pntd.0005992

Ajayi, O.O., Peters, S.O., De Donato, M., Sowande, S.O., Mujibi, F.D.N., Morenikeji, O.B., Thomas, B.N., Adeleke, M.A., Imumorin, I.G., 2018. Computational genome-wide identification of heat shock protein genes in the bovine genome. F1000Research 7. https://doi.org/10.12688/f1000research.16058.1

Al Abri, M.A., Posbergh, C., Palermo, K., Sutter, N.B., Eberth, J., Hoffman, G.E., Brooks, S.A., 2018. Genome-Wide Scans Reveal a Quantitative Trait Locus for Withers Height in Horses Near the ANKRD1 Gene. J. Equine Vet. Sci. 60, 67-73. e1. https://doi.org/10.1016/j.jevs.2017.05.008

Albert, S., Moustapha, G., Stéphane, A.R.T., Amadou, T., Salifou, O.-K., Maria, W., Simone, M., Olivier, H., Anicet, G.O., Johann, S., 2019. Is the introgression of Lobi/Baoul

cattle by zebuine genes in Burkina Faso Lobi cattle threatened ? Afr. J. Biotechnol. 18, 77–85. https://doi.org/10.5897/AJB2018.16467

Alexandre P. A, Ferraz J.B. S, Fukumasu H.,2018. Relationship between hypothalamic transcriptome and feed efficiency in Bos indicus beef cattle. Proceedings of the World Congresson Genetics Applied to Livestock Production,11.233

Alexander, D.H., Novembre, J., Lange, K., 2009. Fast model-based estimation of ancestry in unrelated individuals. Genome Res. 19, 1655–1664. https://doi.org/10.1101/gr.094052.109

Anene, B.M., Onah, D.N., Nawa, Y., 2001. Drug resistance in pathogenic African trypanosomes : what hopes for the future ? Vet. Parasitol. 96, 83–100. https://doi.org/10.1016/S0304-4017(00)00427-1

Bahbahani, H., Salim, B., Almathen, F., Enezi, F.A., Mwacharo, J.M., Hanotte, O., 2018. Signatures of positive selection in African Butana and Kenana dairy zebu cattle. PLOS ONE 13, e0190446. https://doi.org/10.1371/journal.pone.0190446

Balding, D.J., 2006. A tutorial on statistical methods for population association studies. Nat. Rev. Genet. 7, 781–791. https://doi.org/10.1038/nrg1916

Bamshad, M., Wooding, S.P., 2003. Signatures of natural selection in the human genome. Nat. Rev. Genet. 4, 99–110. https://doi.org/10.1038/nrg999

Baran, Y., Pasaniuc, B., Sankararaman, S., Torgerson, D.G., Gignoux, C., Eng, C., Rodriguez-Cintron, W., Chapela, R., Ford, J.G., Avila, P.C., Rodriguez-Santana, J., Burchard, E.G., Halperin, E., 2012. Fast and accurate inference of local ancestry in Latino populations. Bioinformatics 28, 1359–1367. https://doi.org/10.1093/bioinformatics/bts144

Barendse, W., Harrison, B.E., Bunch, R.J., Thomas, M.B., Turner, L.B., 2009. Genome wide signatures of positive selection : The comparison of independent samples and the identification of regions associated to traits. BMC Genomics 10, 178. https://doi.org/10.1186/1471-2164-10-178

Bastos, I.M.D., Motta, F.N., Charneau, S., Santana, J.M., Dubost, L., Augustyns, K., Grellier, P., 2010. Prolyl oligopeptidase of Trypanosoma brucei hydrolyzes native collagen, peptide hormones and is active in the plasma of infected mice. Microbes Infect. 12, 457–466. https://doi.org/10.1016/j.micinf.2010.02.007

Batz, F., 1999. The influence of technology characteristics on the rate and speed of adoption. Agric. Econ. 21, 121–130. https://doi.org/10.1016/S0169-5150(99)00026-2

Belemsaga, D.M.A., Lombo, Y., Thevenon, S., Sylla, S., 2005. Inventory Analysis of West African Cattle Breeds, in : Makkar, H.P.S., Viljoen, G.J. (Eds.), Applications of Gene-Based Technologies for Improving Animal Production and Health in Developing Countries. Springer-Verlag, Berlin/Heidelberg, pp. 167–173. https://doi.org/10.1007/1-4020-3312-5_15

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate : A Practical and Powerful Approach to Multiple Testing. J. R. Stat. Soc. Ser. B Methodol. 57, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Berry et al, 2003. Estimation of genotype environment interactions, in a grass - based system, for milk yield, body condition score and body weight using random regression model. Livest. Prod. Sci. 83 191- 203.

Berthier, D., Chantal, I., Thevenon, S., Sakande, H., Maillard, J.-C., Bengaly, Z., Piquemal, D., Marti, J., Cuny, G., 2008. Study of Bovine Trypanotolerance by Whole Transcriptome Analysis. Ann. N. Y. Acad. Sci. 1149, 71–76. https://doi.org/10.1196/annals.1428.062

Berthier, D., Quéré, R., Thevenon, S., Belemsaga, D., Piquemal, D., Marti, J., Maillard, J.-C., 2003. Serial analysis of gene expression (SAGE) in bovine trypanotolerance : preliminary results. Genet. Sel. Evol. 35, S35–S47. https://doi.org/10.1051/gse:2003015

Bettridge, J.M., Psifidi, A., Terfa, Z.G., Desta, T.T., Lozano-Jaramillo, M., Dessie, T., Kaiser, P., Wigley, P., Hanotte, O., Christley, R.M., 2018. The role of local adaptation in sustainable production of village chickens. Nat. Sustain. 1, 574–582. https://doi.org/10.1038/s41893-018-0150-9

Bishop, S.C., MacKenzie, K.M., 2003. Genetic management strategies for controlling infectious diseases in livestock populations. Genet. Sel. Evol. 35, S3. https://doi.org/10.1186/1297-9686-35-S1-S3

Biswas, S., Akey, J.M., 2006. Genomic insights into positive selection. Trends Genet. 22, 437–446. https://doi.org/10.1016/j.tig.2006.06.005

Blench, R., Marriage, Z., 1999. Drought and livestock in semi-arid Africa and Southwest Asia, Working paper / Overseas Development Institute. London.

Boettcher et al, 2003. Genotype x Environment interaction in Conventional versus pasture - based dairies in Canada. J Dairy Sci 86 383-389.

Boeven, P.H.G., Zhao, Y., Thorwarth, P., Liu, F., Maurer, H.P., Gils, M., Schachschneider, R., Schacht, J., Ebmeyer, E., Kazman, E., Mirdita, V., Dörnte, J., Kontowski, S.,

Horbach, R., Cöster, H., Holzapfel, J., Jacobi, A., Ramgraber, L., Reinbrecht, C., Starck, N., Varenne, P., Starke, A., Schürmann, F., Ganal, M., Polley, A., Hartung, J., Beier, S., Scholz, U., Longin, C.F.H., Reif, J.C., Jiang, Y., Würschum, T., 2020. Negative dominance and dominance-by-dominance epistatic effects reduce grain-yield heterosis in wide crosses in wheat. Sci. Adv. 6, eaay4897. https://doi.org/10.1126/sciadv.aay4897

Bolar, K., 2019. Interactive Document for Working with Basic Statistical Analysis. 2019-04-01 164010 UTC.

Bonfiglio, S., Ginja, C., Gaetano, A.D., Achilli, A., Olivieri, A., Colli, L., Tesfaye, K., Agha, S.H., Gama, L.T., Cattonaro, F., Penedo, M.C.T., Ajmone-Marsan, P., Torroni, A., Ferretti, L., 2012. Origin and Spread of Bos taurus : New Clues from Mitochondrial Genomes Belonging to Haplogroup T1. PLOS ONE 7, e38601. https://doi.org/10.1371/journal.pone.0038601

Bourdon, R.M., 2000. Understanding animal breeding.

Bouyer, J., 2006. Ecologie des glossines du Mouhoun au Burkina Faso : intérêt pour l'épidémiologie et le contrôle des trypanosomoses africaines (These de doctorat). Montpellier 2.

Bouyer, J., Ravel, S., Dujardin, J.-P., De Meeüs, T., Vial, L., Thévenon, S., Guerrini, L., Sidibé, I., Solano, P., 2007. Population Structuring of Glossina palpalis gambiensis (Diptera : Glossinidae) According to Landscape Fragmentation in the Mouhoun River, Burkina Faso. J. Med. Entomol. 44, 788–795. https://doi.org/10.1093/jmedent/44.5.788

Bradley, D.G., MacHugh, D.E., Cunningham, P., Loftus, R.T., 1996. Mitochondrial diversity and the origins of African and European cattle. Proc. Natl. Acad. Sci. U. S. A. 93, 5131–5135.

Brisbin, A., Bryc, K., Byrnes, J., Zakharia, F., Omberg, L., Degenhardt, J., Reynolds, A., Ostrer, H., Mezey, J.G., Bustamante, C.D., 2012. PCAdmix : Principal Components-Based Assignment of Ancestry along Each Chromosome in Individuals with Admixed Ancestry from Two or More Populations. Hum. Biol. 84, 343–364. https://doi.org/10.3378/027.084.0401

Burrow, H.M., 2012. Importance of adaptation and genotype × environment interactions in tropical beef breeding systems. Animal 6, 729–740. https://doi.org/10.1017/S175173111200002X

Cai, Z., Dusza, M., Guldbrandtsen, B., Lund, M.S., Sahana, G., 2020. Distinguishing pleiotropy from linked QTL between milk production traits and mastitis resistance in Nordic Holstein cattle. Genetics Selection Evolution 52, 19. https://doi.org/10.1186/s12711-020-00538-6

Chang, C.C., Chow, C.C., Tellier, L.C., Vattikuti, S., Purcell, S.M., Lee, J.J., 2015. Second-generation PLINK : rising to the challenge of larger and richer datasets. GigaScience 4, 7.

Chen et al., 2010. Zebu cattle are an exclusive legacy of the South Asia Neolithic. Mol. Biol. Evol. 27 1–6.

Chen, Y., Gondro, C., Quinn, K., Herd, R.M., Parnell, P.F., Vanselow, B., 2011. Global gene expression profiling reveals genes expressed differentially in cattle with high and low residual feed intake. Anim. Genet. 42, 475–490. https://doi.org/10.1111/j.1365-2052.2011.02182.x

Churchhouse, C., Marchini, J., 2013. Multiway Admixture Deconvolution Using Phased or Unphased Ancestral Panels. Genet. Epidemiol. 37, 1–12. https://doi.org/10.1002/gepi.21692

Cordell, H.J., Clayton, D.G., 2005. Genetic association studies. The Lancet 366, 1121–1131. https://doi.org/10.1016/S0140-6736(05)67424-7

Courtin, D., Berthier, D., Thevenon, S., Dayo, G.-K., Garcia, A., Bucheton, B., 2008. Host genetics in African trypanosomiasis. Infect. Genet. Evol. 8, 229–238. https://doi.org/10.1016/j.meegid.2008.02.007

D'Ieteren, G.D., Authié, E., Wissocq, N., Murray, M., 1998. Trypanotolerance, an option for sustainable livestock production in areas at risk from trypanosomosis. Rev. Sci. Tech. Int. Off. Epizoot. 17, 154–175.

Dargie, J.D., Murray, P.K., Murray, M., Grimshaw, W.R.T., McIntyre, W.I.M., 1979. Bovine trypanosomiasis : the red cell kinetics of Ndama and Zebu cattle infected with Trypanosoma congolense. Parasitology 78, 271–286. https://doi.org/10.1017/S0031182000051143

Dayo, G.-K., 2009a. Recherche de marqueurs génétiques associés à la tolérance et/ou sensibilité des bovins aux trypanosomoses africaines (thesis). Montpellier 2.

Dayo, G.-K., 2009b. Recherche de marqueurs génétiques associés à la tolérance et/ou sensibilité des bovins aux trypanosomoses africaines (These de doctorat). Montpellier 2.

Dayo, G.-K., Thevenon, S., Berthier, D., Moazami-Goudarzi, K., Denis, C., Cuny, G., Eggen, A., Gautier, M., 2009. Detection of selection signatures within candidate regions underlying trypanotolerance in outbred cattle populations. Mol. Ecol. 18, 1801–1813. https://doi.org/10.1111/j.1365-294X.2009.04141.x

De Araujo Neto, F.R., Santos, D.J. de A., Fernandes Júnior, G.A., Aspilcueta-Borquis, R.R., Nascimento, A.V. do, de Oliveira Seno, L., Tonhati, H., de Oliveira, H.N., 2020. Genome-wide association studies for growth traits in buffaloes using the single step genomic BLUP. J. Appl. Genet. 61, 113–115. https://doi.org/10.1007/s13353-019-00528-5

Decker, J.E., McKay, S.D., Rolf, M.M., Kim, J., Alcalá, A.M., Sonstegard, T.S., Hanotte, O., Götherström, A., Seabury, C.M., Praharani, L., Babar, M.E., Regitano, L.C. de A., Yildiz, M.A., Heaton, M.P., Liu, W.-S., Lei, C.-Z., Reecy, J.M., Saif-Ur-Rehman, M., Schnabel, R.D., Taylor, J.F., 2014a. Worldwide Patterns of Ancestry, Divergence, and Admixture in Domesticated Cattle. PLOS Genet. 10, e1004254. https://doi.org/10.1371/journal.pgen.1004254

Decker, J.E., McKay, S.D., Rolf, M.M., Kim, J., Alcalá, A.M., Sonstegard, T.S., Hanotte, O., Götherström, A., Seabury, C.M., Praharani, L., Babar, M.E., Regitano, L.C. de A., Yildiz, M.A., Heaton, M.P., Liu, W.-S., Lei, C.-Z., Reecy, J.M., Saif-Ur-Rehman, M., Schnabel, R.D., Taylor, J.F., 2014b. Worldwide Patterns of Ancestry, Divergence, and Admixture in Domesticated Cattle. PLOS Genet. 10, e1004254. https://doi.org/10.1371/journal.pgen.1004254

Delespaux, V., Geysen, D., Van den Bossche, P., Geerts, S., 2008. Molecular tools for the rapid detection of drug resistance in animal trypanosomes. Trends Parasitol. 24, 236–242. https://doi.org/10.1016/j.pt.2008.02.006

Desquesnes, M., Bengaly, Z., Dia, M.L., 2003. Evaluation de la persistance des anticorps détectés par Elisa-indirect Trypanosoma vivax après traitement trypanocide chez des. Rev. D'élevage Médecine Vét. Pays Trop. 56, 141–144. https://doi.org/10.19182/remvt.9855

Desta, T.T., Ayalew, W., Hegde, B.P., 2011. Breed and trait preferences of Sheko cattle keepers in southwestern Ethiopia. Trop. Anim. Health Prod. 43, 851–856. https://doi.org/10.1007/s11250-010-9772-2

Doerge, R.W., Churchill, G.A., 1996. Permutation Tests for Multiple Loci Affecting a Quantitative Character. Genetics 142, 285–294.

Doko, A., Verhulst, A., Pandey, V.S., Stuyft, P.V.D., 1997. Trypanosomose expérimentale à Trypanosoma brucei brucei chez les taurins Holstein et les zébus Bororo blancs. Rev. D'élevage Médecine Vét. Pays Trop. 50, 23–28. https://doi.org/10.19182/remvt.9597

Dolan, R.B., Alushula, H., Munga, L., Mutugi, M., Mwendia, C., Okech, G., Sayer, P.D., Stevenson, P.G.W., Baker, R.L., Magadi, M., 1994. The Orma Boran - ten years of field observations.

Donini, C.F., Di Zazzo, E., Zuchegna, C., Di Domenico, M., D'Inzeo, S., Nicolussi, A., Avvedimento, E.V., Coppa, A., Porcellini, A., 2012. The p85α regulatory subunit of PI3K mediates cAMP-PKA and retinoic acid biological effects on MCF7 cell growth and migration. Int. J. Oncol. 40, 1627–1635. https://doi.org/10.3892/ijo.2012.1383

Dossa, L.H., Vanvanhossou, F.U.S., 2016. The indigenous Somba cattle of the hilly Atacora region in North-West Benin : threats and opportunities for its sustainable use. Trop. Anim. Health Prod. 48, 349–359. https://doi.org/10.1007/s11250-015-0958-5

Doyle, J.L., Berry, D.P., Veerkamp, R.F., Carthy, T.R., Walsh, S.W., Evans, R.D., Purfield, D.C., 2020. Genomic Regions Associated With Skeletal Type Traits in Beef and Dairy Cattle Are Common to Regions Associated With Carcass Traits, Feed Intake and Calving Difficulty. Front. Genet. 11. https://doi.org/10.3389/fgene.2020.00020

Duguma, G., Mirkena, T., Haile, A., Okeyo, A.M., Tibbo, M., Rischkowsky, B., Sölkner, J., Wurzinger, M., 2011. Identification of smallholder farmers and pastoralists' preferences for sheep breeding traits : choice model approach. Animal 5, 1984–1992. https://doi.org/10.1017/S1751731111001029

Duvallet, G., 1987. Trypanosomoses humaine et animale en Afrique de l'Ouest : recherches épidémiologiques et immunoparasitologiques (These de doctorat). Paris 11.

Eck et al., 2009. Whole. Genome sequencing of a single Bos taurus animal for single nucleotide polymorphism. Discov. Genome Biol 10 R82 Httpgenomebiologycom2009108R82.

Edea, Z., Jung, K.S., Shin, S.-S., Yoo, S.-W., Choi, J.W., Kim, K.-S., 2020. Signatures of positive selection underlying beef production traits in Korean cattle breeds [WWW Document]. J. Anim. Sci. Technol. https://doi.org/10.5187/jast.2020.62.3.293

Epstein, H., 1971. The origin of the domestic animals of Africa. Africana Publishing Corporation.

FAO, 2012. Phenotypic characterization of animal genetic resources. Food Agric. Organ. U. N. Rome Ital. Anim. Prod. Health Guidel. 11 144 Available Httpwwwfaoorgdocrep015i2686e00htm.

Fisher, P., Hedeler, C., Wolstencroft, K., Hulme, H., Noyes, H., Kemp, S., Stevens, R., Brass, A., 2007. A systematic strategy for large-scale analysis of genotype–phenotype correlations : identification of candidate genes involved in African trypanosomiasis. Nucleic Acids Res. 35, 5625–5633. https://doi.org/10.1093/nar/gkm623

Foll, M., Gaggiotti, O., 2008. A Genome-Scan Method to Identify Selected Loci Appropriate for Both Dominant and Codominant Markers : A Bayesian Perspective. Genetics 180, 977–993. https://doi.org/10.1534/genetics.108.092221

Fox et al, J., 2019. Companion to Applied Regression. 2019-05-27 162003 UTC.

Freebern, E., Santos, D.J.A., Fang, L., Jiang, J., Parker Gaddis, K.L., Liu, G.E., VanRaden, P.M., Maltecca, C., Cole, J.B., Ma, L., 2020. GWAS and fine-mapping of livability and six disease traits in Holstein cattle. BMC Genomics 21, 41. https://doi.org/10.1186/s12864-020-6461-z

Freeman, A.R., Bradley, D.G., Nagda, S., Gibson, J.P., Hanotte, O., 2006. Combination of multiple microsatellite data sets to investigate genetic diversity and admixture of domestic cattle. Anim. Genet. 37, 1–9. https://doi.org/10.1111/j.1365-2052.2005.01363.x

Freeman, A.R., Meghen, C.M., MacHUGH, D.E., Loftus, R.T., Achukwi, M.D., Bado, A., Sauveroche, B., Bradley, D.G., 2004a. Admixture and diversity in West African cattle populations. Mol. Ecol. 13, 3477–3487. https://doi.org/10.1111/j.1365-294X.2004.02311.x

Freeman, A.R., Meghen, C.M., MacHUGH, D.E., Loftus, R.T., Achukwi, M.D., Bado, A., Sauveroche, B., Bradley, D.G., 2004b. Admixture and diversity in West African cattle populations : GENETIC SURVEY OF WEST AFRICAN CATTLE. Mol. Ecol. 13, 3477–3487. https://doi.org/10.1111/j.1365-294X.2004.02311.x

Freyer, M.W., Lewis, E.A., 2008. Isothermal Titration Calorimetry : Experimental Design, Data Analysis, and Probing Macromolecule/Ligand Binding and Kinetic Interactions, in: Methods in Cell Biology, Biophysical Tools for Biologists, Volume One: In Vitro Techniques. Academic Press, pp. 79–113. https://doi.org/10.1016/S0091-679X(07)84004-0

Gachohi, J.M., Bett, B.K., Murilla, G.A., 2009. Factors influencing the prevalence of trypanosomosis in Orma Boran (trypanotolerant) and Teso zebu (trypanosusceptible) cattle crosses in Teso District, western Kenya. Livest. Res. Rural Dev.

Garcia, P.R.J.M., Sharma, P., De Massis, A., Wright, M., Scholes, L., 2019. Perceived Parental Behaviors and Next-Generation Engagement in Family Firms : A Social

Cognitive Perspective. Entrep. Theory Pract. 43, 224–243. https://doi.org/10.1177/1042258718796087

Gautier et al., 2009. A whole genome Bayesian scan for adaptive genetic divergence in West African cattle. Bio Med Cent. Genomics 10, 550. https://doi.org/doi

Gautier, M., Naves, M., 2011. Footprints of selection in the ancestral admixture of a New World Creole cattle breed. Mol. Ecol. 20, 3128–3143. https://doi.org/10.1111/j.1365-294X.2011.05163.x

Geerts, S., Raes, D., 2009. Deficit irrigation as an on-farm strategy to maximize crop water productivity in dry areas. Agric. Water Manag. 96, 1275–1284. https://doi.org/10.1016/j.agwat.2009.04.009

Getachew, T., Huson, H.J., Wurzinger, M., Burgstaller, J., Gizaw, S., Haile, A., Rischkowsky, B., Brem, G., Boison, S.A., Mészáros, G., Mwai, A.O., Sölkner, J., 2017. Identifying highly informative genetic markers for quantification of ancestry proportions in crossbred sheep populations : implications for choosing optimum levels of admixture. BMC Genet. 18, 80. https://doi.org/10.1186/s12863-017-0526-2

Goddard, M.E., Hayes, B.J., 2009. Mapping genes for complex traits in domestic animals and their use in breeding programmes. Nat. Rev. Genet. 10, 381–391. https://doi.org/10.1038/nrg2575

Goszczynski, D.E., Corbi-Botto, C.M., Durand, H.M., Rogberg-Muñoz, A., Munilla, S., Peral-Garcia, P., Cantet, R.J.C., Giovambattista, G., 2018. Evidence of positive selection towards Zebuine haplotypes in the BoLA region of Brangus cattle. Animal 12, 215–223. https://doi.org/10.1017/S1751731117001380

Gouveia, V.V., Milfont, T.L., Guerra, V.M., 2014. The functional theory of human values : From intentional overlook to first acknowledgement—A reply to Schwartz (2014). Personal. Individ. Differ. 68, 250–253. https://doi.org/10.1016/j.paid.2014.03.025

Gregory, K.E., Trail, J.C.M., 1981. Rotation Crossbreeding with Sahiwal and Ayrshire Cattle in the Tropics1. J. Dairy Sci. 64, 1978–1984. https://doi.org/10.3168/jds.S0022-0302(81)82800-7

Guarini, A.R., Lourenco, D.A.L., Brito, L.F., Sargolzaei, M., Baes, C.F., Miglior, F., Misztal, I., Schenkel, F.S., 2019. Genetics and genomics of reproductive disorders in Canadian Holstein cattle. J. Dairy Sci. 102, 1341–1353. https://doi.org/10.3168/jds.2018-15038

Hamadou, S., Kamuanga, M., 2004. Farmers' perceptions and assessment of cattle traits in periurban dairy systems of Bobo-Dioulasso (Burkina Faso).

Han, B., Yuan, Y., Shi, L., Li, Y., Liu, L., Sun, D., 2019. Identification of single nucleotide polymorphisms of PIK3R1 and DUSP1 genes and their genetic associations with milk production traits in dairy cows. J. Anim. Sci. Biotechnol. 10, 81. https://doi.org/10.1186/s40104-019-0392-z

Hanotte et al, 2003. Mapping of quantitative trait loci controlling trypanotolerance in a cross of tolerant West African N'Dama and susceptible East African Boran cattle. Proc Natl Acad Sci USA 100, 7443–744. https://doi.org/doi : 10.1073/pnas.1232 392100

Hanotte, O., 2002. African Pastoralism : Genetic Imprints of Origins and Migrations. Science 296, 336–339. https://doi.org/10.1126/science.1069878

Hansen, P.J., 2004. Physiological and cellular adaptations of zebu cattle to thermal stress. Anim. Reprod. Sci., Research and Practice III. 15th International Congress on Animal Reproduction 82–83, 349–360. https://doi.org/10.1016/j.anireprosci.2004.04.011

Heid, H.W., Werner, E., Franke, W.W., 1986. The complement of native α-keratin polypeptides of hair-forming cells : A subset of eight polypeptides that differ from epithelial cytokeratins. Differentiation 32, 101–119. https://doi.org/10.1111/j.1432-0436.1986.tb00562.x

Hill, E.W., O'Gorman, G.M., Agaba, M., Gibson, J.P., Hanotte, O., Kemp, S.J., Naessens, J., Coussens, P.M., MacHugh, D.E., 2005. Understanding bovine trypanosomiasis and trypanotolerance : the promise of functional genomics. Vet. Immunol. Immunopathol., Functional Genomics of Host-Pathogen Interactions in Species of Veterinary Importance 105, 247–258. https://doi.org/10.1016/j.vetimm.2005.02.004

Hill, W.G., Mackay, T.F.C., 2004. D. S. Falconer and Introduction to Quantitative Genetics. Genetics 167, 1529–1536.

Hinsch, K.D., Hinsch, E., 1999. The zona pellucida "receptors" ZP1, ZP2 and ZP3. Andrologia 31, 320–322.

Hoffmann, I., 2010. Climate change and the characterization, breeding and conservation of animal genetic resources. Anim. Genet. 41, 32–46. https://doi.org/10.1111/j.1365-2052.2010.02043.x

Hoste, C., Chalon, E., D'Ietezen, G., Trail, J.C.M., 1988. Le bétail trypanotolérant en Afrique occidentale et centrale. Vol. 3. Bilan d'une décennie. FAO.

Hoste, C.H., Chalon, E., D'Ieteren, G., Trail, J.C.M., 1992. Trypanotolerant livestock in west and central Africa, vol. 3 : a decade's results. Trypanotolerant Livest. West Cent. Afr. Vol 3 Decades Results.

Hou, L., Xu, J., Jiao, Y., Li, H., Pan, Z., Duan, J., Gu, T., Hu, C., Wang, C., 2018. MiR-27b Promotes Muscle Development by Inhibiting MDFI Expression. Cell. Physiol. Biochem. 46, 2271–2283. https://doi.org/10.1159/000489595

Houessou, S.O., Dossa, L.H., Diogo, R.V.C., Ahozonlin, M.C., Dahouda, M., Schlecht, E., 2019. Confronting pastoralists' knowledge of cattle breeds raised in the extensive production systems of Benin with multivariate analyses of morphological traits. PLOS ONE 14, e0222756. https://doi.org/10.1371/journal.pone.0222756

Hu, Y., Willer, C., Zhan, X., Kang, H.M., Abecasis, G.R., 2013. Accurate Local-Ancestry Inference in Exome-Sequenced Admixed Individuals via Off-Target Sequence Reads. Am. J. Hum. Genet. 93, 891–899. https://doi.org/10.1016/j.ajhg.2013.10.008

Isaac, J.L., 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Rev. 35, 101–115. https://doi.org/10.1111/j.1365-2907.2005.00045.x

Jabbar, M.A., Diedhiou, M.L., 2003. Does breed matter to cattle farmers and buyers?: Evidence from West Africa. Ecol. Econ., Valuing Animal Genetic Resources 45, 461–472. https://doi.org/10.1016/S0921-8009(03)00097-1

Jain, J., Jain, S.K., Walker, L.A., Tekwani, B.L., 2017. Inhibitors of ubiquitin E3 ligase as potential new antimalarial drug leads. BMC Pharmacol. Toxicol. 18, 40. https://doi.org/10.1186/s40360-017-0147-4

Jiang, Y., Schmidt, R.H., Zhao, Y., Reif, J.C., 2017. A quantitative genetic framework highlights the role of epistatic effects for grain-yield heterosis in bread wheat. Nat. Genet. 49, 1741–1746. https://doi.org/10.1038/ng.3974

Juszczuk-Kubiak, E., Flisikowski, K., Wicińska, K., 2011. Nucleotide sequence and variations of the bovine myocyte enhancer factor 2C (MEF2C) gene promoter in Bos taurus cattle. Mol. Biol. Rep. 38, 1269–1276. https://doi.org/10.1007/s11033-010-0226-8

Juszczuk-Kubiak, E., Wicińska, K., Starzyński, R.R., 2014. Postnatal expression patterns and polymorphism analysis of the bovine myocyte enhancer factor 2C (Mef2C) gene. Meat Sci. 98, 753–758. https://doi.org/10.1016/j.meatsci.2014.06.015

K, M., Pa, C., 1998. The wound repair-associated keratins 6, 16, and 17. Insights into the role of intermediate filaments in specifying keratinocyte cytoarchitecture. Subcell. Biochem. 31, 173–204.

Kaneko, J.J., Harvey, J.W., Bruss, M.L., 2008. Clinical Biochemistry of Domestic Animals. Academic Press.

Katongole et al, 1994. Morphological Characterisation of the Tswana goat. In Small Ruminant Research and Development in Africa. Proceeding of the third Biennal Conference of the african Small Ruminant Research Network. UICC, Kampala, Uganda, 43-47. [WWW Document]. URL https://www.google.com/search?client=firefox-b-ab&q=Katongole,+J.B.,+Sebolai,+D.B.+%26+Madinabe+(1994).+Morphological+Characterisation+of+the+Tswana+goat.+In+Small+Ruminant+Research+and+Development+in+Africa.+Proceeding+of+the+third+Biennal+Conferenceof+the+african+Small+Ruminant+Research+Network.+UICC,+Kampala,Uganda,+43-47.&spell=1&sa=X&ved=0ahUKEwiWj8zP_OrfAhWRZ1AKHaoeDtkQBQgpKAA&biw=1233&bih=613 (accessed 1.13.19).

Kearney et al, 2004a. Genotype x environment interaction for grazing versus confinment. I. Production traits. J Dairy Sci 872501-509.

Kennedy, A.T., Schmidt, C.Q., Thompson, J.K., Weiss, G.E., Taechalertpaisarn, T., Gilson, P.R., Barlow, P.N., Crabb, B.S., Cowman, A.F., Tham, W.-H., 2016. Recruitment of Factor H as a Novel Complement Evasion Strategy for Blood-Stage Plasmodium falciparum Infection. J. Immunol. 196, 1239–1248. https://doi.org/10.4049/jimmunol.1501581

Keogh, K., Kenny, D.A., Waters, S.M., 2019. Gene co-expression networks contributing to the expression of compensatory growth in metabolically active tissues in cattle. Sci. Rep. 9, 6093. https://doi.org/10.1038/s41598-019-42608-w

Khan, M.S., Ahmad, N., Khan, M.A., 2007. GENETIC RESOURCES AND DIVERSITY IN DAIRY BUFFALOES OF PAKISTAN 7.

Khayatzadeh, N., Mészáros, G., Utsunomiya, Y.T., Garcia, J.F., Schnyder, U., Gredler, B., Curik, I., Sölkner, J., 2016. Locus-specific ancestry to detect recent response to selection in admixed Swiss Fleckvieh cattle. Anim. Genet. 47, 637–646. https://doi.org/10.1111/age.12470

Kim, J., Hanotte, O., Mwai, O.A., Dessie, T., Bashir, S., Diallo, B., Agaba, M., Kim, K., Kwak, W., Sung, S., Seo, M., Jeong, H., Kwon, T., Taye, M., Song, K.-D., Lim, D., Cho, S., Lee, H.-J., Yoon, D., Oh, S.J., Kemp, S., Lee, H.-K., Kim, H., 2017. The genome landscape of indigenous African cattle. Genome Biol. 18, 34. https://doi.org/10.1186/s13059-017-1153-y

Kimuda, M.P., Noyes, H., Mulindwa, J., Enyaru, J., Alibu, V.P., Sidibe, I., Ngoyi, D.M., Hertz-Fowler, C., MacLeod, A., Bishop, Ö.T., Matovu, E., Consortium, T.R.G. as

members of T.H., 2018. No evidence for association between APOL1 kidney disease risk alleles and Human African Trypanosomiasis in two Ugandan populations. PLoS Negl. Trop. Dis. 12, e0006300. https://doi.org/10.1371/journal.pntd.0006300

Kinghorn, B.P., 1983. A review of quantitative genetics in fish breeding. Aquaculture 31, 283–304. https://doi.org/10.1016/0044-8486(83)90320-4

Kitajiri, S., Sakamoto, T., Belyantseva, I.A., Goodyear, R.J., Stepanyan, R., Fujiwara, I., Bird, J.E., Riazuddin, Saima, Riazuddin, Sheikh, Ahmed, Z.M., Hinshaw, J.E., Sellers, J., Bartles, J.R., Hammer, J.A., Richardson, G.P., Griffith, A.J., Frolenkov, G.I., Friedman, T.B., 2010. Actin-Bundling Protein TRIOBP Forms Resilient Rootlets of Hair Cell Stereocilia Essential for Hearing. Cell 141, 786–798. https://doi.org/10.1016/j.cell.2010.03.049

Kreitman, M., 2000. Methods to Detect Selection in Populations with Applications to the Human. Annu. Rev. Genomics Hum. Genet. 1, 539–559. https://doi.org/10.1146/annurev.genom.1.1.539

Kristjanson, P.M., Swallow, B.M., Rowlands, G.J., Kruska, R.L., de Leeuw, P.N., 1999. Measuring the costs of African animal trypanosomosis, the potential benefits of control and returns to research. Agric. Syst. 59, 79–98. https://doi.org/10.1016/S0308-521X(98)00086-9

Lauvergne, J.-J., 1985. I.L. Mason (editor), 1985. — Evolution of domesticated animals Longman. J. Agric. Tradit. Bot. Appliquée 32, 251–252.

Leak, S.G.A., Kemp, S.J., Teale, A.J., 1993. Responses of N'Dama X Boran crossbred cattle to experimental infection with Trypanosoma congolense.

Lenth, R., 2018. Least-Squares Means. 2018-11-02 235011 UTC.

Leroy, G., Baumung, R., Boettcher, P., Besbes, B., From, T., Hoffmann, I., 2018. Animal genetic resources diversity and ecosystem services. Glob. Food Secur. 17, 84–91. https://doi.org/10.1016/j.gfs.2018.04.003

Leroy, G., Besbes, B., Boettcher, P., Hoffmann, I., Capitan, A., Baumung, R., 2016. Rare phenotypes in domestic animals : unique resources for multiple applications. Anim. Genet. 47, 141–153. https://doi.org/10.1111/age.12393

Leroy, G., Boettcher, P., Besbes, B., Peña, C.R., Jaffrezic, F., Baumung, R., 2020. Food securers or invasive aliens ? Trends and consequences of non-native livestock introgression in developing countries. Glob. Food Secur. 26, 100420. https://doi.org/10.1016/j.gfs.2020.100420

Lhoste, P., 1991. Cattle genetic resources of West Africa [WWW Document]. Cattle Genet. Ressour. Ressour. Génétiques Bov. URL https://agritrop.cirad.fr/394721/ (accessed 3.2.20).

Li, N., Stephens, M., 2003. Modeling Linkage Disequilibrium and Identifying Recombination Hotspots Using Single-Nucleotide Polymorphism Data. Genetics 165, 2213–2233.

Li, Y., Gao, Y., Kim, Y.-S., Iqbal, A., Kim, J.-J., 2017. A whole genome association study to detect additive and dominant single nucleotide polymorphisms for growth and carcass traits in Korean native cattle, Hanwoo. Asian-Australas. J. Anim. Sci. 30, 8–19. https://doi.org/10.5713/ajas.16.0170

Li, Y., Oosting, M., Smeekens, S.P., Jaeger, M., Aguirre-Gamboa, R., Le, K.T.T., Deelen, P., Ricaño-Ponce, I., Schoffelen, T., Jansen, A.F.M., Swertz, M.A., Withoff, S., van de Vosse, E., van Deuren, M., van de Veerdonk, F., Zhernakova, A., van der Meer, J.W.M., Xavier, R.J., Franke, L., Joosten, L.A.B., Wijmenga, C., Kumar, V., Netea, M.G., 2016. A Functional Genomics Approach to Understand Variation in Cytokine Production in Humans. Cell 167, 1099-1110.e14. https://doi.org/10.1016/j.cell.2016.10.017

Lippman, Z.B., Zamir, D., 2007. Heterosis : revisiting the magic. Trends Genet. 23, 60–66. https://doi.org/10.1016/j.tig.2006.12.006

Littlejohn, M.D., Henty, K.M., Tiplady, K., Johnson, T., Harland, C., Lopdell, T., Sherlock, R.G., Li, W., Lukefahr, S.D., Shanks, B.C., Garrick, D.J., Snell, R.G., Spelman, R.J., Davis, S.R., 2014. Functionally reciprocal mutations of the prolactin signalling pathway define hairy and slick cattle. Nat. Commun. 5, 5861. https://doi.org/10.1038/ncomms6861

Loftus, G.R., Masson, M.E.J., 1994. Using confidence intervals in within-subject designs. Psychon. Bull. Rev. 1, 476–490. https://doi.org/10.3758/BF03210951

Long, S.P., 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO2 concentrations : Has its importance been underestimated ? Plant Cell Environ. 14, 729–739. https://doi.org/10.1111/j.1365-3040.1991.tb01439.x

MacDonald, K.C., MacDonald, R.H., 2000. The Origins and Development of Domesticated Animals in Arid West Africa, in : Blench, R.M., MacDonald, K.C. (Eds.), The Origins and Development of African Livestock: Archaeology, Genetics, Linguistics and Ethnography. UCL Press, London, pp. 127–162.

MacHugh, D.E., Shriver, M.D., Loftus, R.T., Cunningham, P., Bradley, D.G., 1997. Microsatellite DNA Variation and the Evolution, Domestication and Phylogeography of Taurine and Zebu Cattle (Bos taurus and Bos indicus). Genetics 146, 1071–1086.

MacLennan, K.J.R., 1981. Tsetse-transmitted trypanosomiasis in relation to the rural economy in Africa. Pt. 2 : Techniques in use for the control or eradication of tsetse infestations. Rev. Mond. Zootech. FAO - Rev. Mund. Zootec. FAO.

Magnani, S.D., Ancey, V., Hubert, B., 2019. "(Dis)ordered intensification ?" Techno-political models, resource access and pastoralist/agribusiness relations in the Middle Valley of the Senegal River. Nomadic Peoples 23, 5–27. https://doi.org/10.3197/np.2019.230102

Makina, S.O., Muchadeyi, F.C., van Marle-Köster, E., Taylor, J.F., Makgahlela, M.L., Maiwashe, A., 2015. Genome-wide scan for selection signatures in six cattle breeds in South Africa. Genet. Sel. Evol. 47, 92. https://doi.org/10.1186/s12711-015-0173-x

Mäki-Tanila, A., 2007. An overview on quantitative and genomic tools for utilising dominance genetic variation in improving animal production. Agric. Food Sci. 16, 188–198. https://doi.org/10.2137/145960607782219337

Mammo, M., Alemayehu, K., Tassew, A., 2017. Conformation traits of dairy cattle populations in selected Districts of Northwestern Amhara, Ethiopia. Biodiversitas J. Biol. Divers. 18, 1669–1679. https://doi.org/10.13057/biodiv/d180447

Mani, M., Marichatou, H., Issa, M., Chaïbou, I., Sow, A., Chaibou, M., Sawadogo, J.G., 2014. Caractéristiques phénotypiques de la chèvre du sahel au Niger par analyse des indices de primarité et des paramètres qualitatifs. Anim. Genet. Resour. Inf. Bull. Inf. Sur Ressour. Génétiques Anim. Bol. Inf. Sobre Recur. Genéticos Anim. 11–19.

Marshall, F., Hildebrand, E., 2002. Cattle Before Crops : The Beginnings of Food Production in Africa. J. World Prehistory 16, 99–143.

Marshall, K., Gibson, J.P., Mwai, O., Mwacharo, J.M., Haile, A., Getachew, T., Mrode, R., Kemp, S.J., 2019. Livestock Genomics for Developing Countries – African Examples in Practice. Front. Genet. 10. https://doi.org/10.3389/fgene.2019.00297

Mattioli, R.C., Faye, J.A., Büscher, P., 1999. Susceptibility of N'Dama cattle to experimental challenge and cross-species superchallenges with bloodstream forms of Trypanosoma congolense and T. Vivax. Vet. Parasitol. 86, 83–94. https://doi.org/10.1016/S0304-4017(99)00117-X

Meng, J.-F., Fingerlin, T.E., 2008. Linear Models for Analysis of Multiple Single Nucleotide Polymorphisms with Quantitative Traits in Unrelated Individuals. Ann. Zool. Fenn. 45, 429–440. https://doi.org/10.5735/086.045.0506

Miao, L., Wang, Y., Xia, H., Yao, C., Cai, H., Song, Y., 2013. SPOCK1 is a novel transforming growth factor-β target gene that regulates lung cancer cell epithelial-mesenchymal transition. Biochem. Biophys. Res. Commun. 440, 792–797. https://doi.org/10.1016/j.bbrc.2013.10.024

Moll, R.H., Lonnquist, J.H., Fortuno, J.V., Johnson, E.C., 1965. The Relationship of Heterosis and Genetic Divergence in Maize. Genetics 52, 139–144.

Moradi, M.H., Abedini, M., 2012. A combination of genetic algorithm and particle swarm optimization for optimal DG location and sizing in distribution systems. Int. J. Electr. Power Energy Syst. 34, 66–74. https://doi.org/10.1016/j.ijepes.2011.08.023

Morty, R.E., Bulau, P., Pellé, R., Wilk, S., Abe, K., 2006. Pyroglutamyl peptidase type I from Trypanosoma brucei : a new virulence factor from African trypanosomes that de-blocks regulatory peptides in the plasma of infected hosts. Biochem. J. 394, 635–645. https://doi.org/10.1042/BJ20051593

Mottet, A., de Haan, C., Falcucci, A., Tempio, G., Opio, C., Gerber, P., 2017. Livestock: On our plates or eating at our table? A new analysis of the feed/food debate. Glob. Food Secur., Food Security Governance in Latin America 14, 1–8. https://doi.org/10.1016/j.gfs.2017.01.001

Moussa, M., Issa, M., Traoré, A., Moustapha, G., Hamani, M., Fernández, I., Soudré, A., Álvarez, I., Sanou, M., Tamboura, H., Alhassane, Y., Goyache, F., 2017. Morphological assessment of the Zebu Bororo (Wodaabé) cattle of Niger in the West African zebu framework. Arch. Anim. Breed. 60, 363–371. https://doi.org/10.5194/aab-60-363-2017

Msalya, G., Kim, E.-S., Laisser, E.L.K., Kipanyula, M.J., Karimuribo, E.D., Kusiluka, L.J.M., Chenyambuga, S.W., Rothschild, M.F., 2017. Determination of Genetic Structure and Signatures of Selection in Three Strains of Tanzania Shorthorn Zebu, Boran and Friesian Cattle by Genome-Wide SNP Analyses. PLOS ONE 12, e0171088. https://doi.org/10.1371/journal.pone.0171088

Mudadu, M.A., Porto-Neto, L.R., Mokry, F.B., Tizioto, P.C., Oliveira, P.S.N., Tullio, R.R., Nassu, R.T., Niciura, S.C.M., Tholon, P., Alencar, M.M., Higa, R.H., Rosa, A.N., Feijó, G.L.D., Ferraz, A.L.J., Silva, L.O.C., Medeiros, S.R., Lanna, D.P., Nascimento, M.L., Chaves, A.S., Souza, A.R.D.L., Packer, I.U., Torres, R.A.A., Siqueira, F.,

Mourão, G.B., Coutinho, L.L., Reverter, A., Regitano, L.C.A., 2016. Genomic structure and marker-derived gene networks for growth and meat quality traits of Brazilian Nelore beef cattle. BMC Genomics 17, 235. https://doi.org/10.1186/s12864-016-2535-3

Mueller, J.P., Rischkowsky, B., Haile, A., Philipsson, J., Mwai, O., Besbes, B., Zárate, A.V., Tibbo, M., Mirkena, T., Duguma, G., Sölkner, J., Wurzinger, M., 2015. Community-based livestock breeding programmes : essentials and examples. J. Anim. Breed. Genet. 132, 155–168. https://doi.org/10.1111/jbg.12136

Murray, M., Morrison, W.I., Whitelaw, D.D., 1982. Host Susceptibility to African Trypanosomiasis : Trypanotolerance, in : Baker, J.R., Muller, R. (Eds.), Advances in Parasitology. Academic Press, pp. 1–68. https://doi.org/10.1016/S0065-308X(08)60274-2

Murray, M., Trail, J.C., Dieteren, G., 1990. Trypanotolerance in cattle and prospects for the control of trypanosomiasis by selective breeding. Rev. Sci. Tech. https://doi.org/10.20506/RST.9.2.506

Murray, N.E., Bruce, S.A., Murray, K., 1979. Molecular cloning of the DNA ligase gene from bacteriophage T4: II. Amplification and preparation of the gene product. J. Mol. Biol. 132, 493–505. https://doi.org/10.1016/0022-2836(79)90271-7

Musemwa, L., Muchenje, V., Mushunje, A., Zhou, L., 2012. The Impact of Climate Change on Livestock Production amongst the Resource-Poor Farmers of Third World Countries: A Review [WWW Document]. Asian J. Agric. Rural Dev. https://doi.org/ISSN(P): 2304-1455

Mwai, O., Hanotte, O., Kwon, Y.-J., Cho, S., 2015. African Indigenous Cattle : Unique Genetic Resources in a Rapidly Changing World. Asian-Australas. J. Anim. Sci. 28, 911–921. https://doi.org/10.5713/ajas.15.0002R

Nayeri, S., Stothard, P., 2016. Tissues, Metabolic Pathways and Genes of Key Importance in Lactating Dairy Cattle. Springer Science Reviews 4, 49–77. https://doi.org/10.1007/s40362-016-0040-3

Noyes, H., Brass, A., Obara, I., Anderson, S., Archibald, A.L., Bradley, D.G., Fisher, P., Freeman, A., Gibson, J., Gicheru, M., Hall, L., Hanotte, O., Hulme, H., McKeever, D., Murray, C., Oh, S.J., Tate, C., Smith, K., Tapio, M., Wambugu, J., Williams, D.J., Agaba, M., Kemp, S.J., 2011. Genetic and expression analysis of cattle identifies

candidate genes in pathways responding to Trypanosoma congolense infection. Proc. Natl. Acad. Sci. 108, 9304–9309. https://doi.org/10.1073/pnas.1013486108

O'Gorman, G.M., Park, S.D., Hill, E.W., Meade, K.G., Coussens, P.M., Agaba, M., Naessens, J., Kemp, S.J., MacHugh, D.E., 2009. Transcriptional profiling of cattle infected with Trypanosoma congolense highlights gene expression signatures underlying trypanotolerance and trypanosusceptibility. BMC Genomics 10, 207. https://doi.org/10.1186/1471-2164-10-207

Oleksyk, T.K., Smith, M.W., O'Brien, S.J., 2010. Genome-wide scans for footprints of natural selection. Philos. Trans. R. Soc. B Biol. Sci. 365, 185–205. https://doi.org/10.1098/rstb.2009.0219

Ouédraogo, D., Soudré, A., Ouédraogo-Koné, S., Zoma, B.L., Yougbaré, B., Khayatzadeh, N., Burger, P.A., Mészáros, G., Traoré, A., Mwai, O.A., Wurzinger, M., Sölkner, J., 2020. Breeding objectives and practices in three local cattle breed production systems in Burkina Faso with implication for the design of breeding programs. Livest. Sci. 232, 103910. https://doi.org/10.1016/j.livsci.2019.103910

Paling, R.W., Moloo, S.K., Scott, J.R., Mcodimba, F.A., Enfrey, L.L.L.-H., Murray, M., Williams, D.J.L., 1991. Susceptibility of N'Dama and Boran cattle to tsetse-transmitted primary and rechallenge infections with a homologous serodeme of Trypanosoma congolense. Parasite Immunol. 13, 413–425. https://doi.org/10.1111/j.1365-3024.1991.tb00294.x

Pérez O'Brien, A.M., Mészáros, G., Utsunomiya, Y.T., Sonstegard, T.S., Garcia, J.F., Van Tassell, C.P., Carvalheiro, R., da Silva, M.V.B., Sölkner, J., 2014. Linkage disequilibrium levels in Bos indicus and Bos taurus cattle using medium and high density SNP chip data and different minor allele frequency distributions. Livest. Sci., Genomics Applied to Livestock Production 166, 121–132. https://doi.org/10.1016/j.livsci.2014.05.007

Pérez- Pardal et al.,2010a, 2010a. Multiple paternal origins of domestic cattle revealed by Y-specific interspersed multilocus microsatellites. Hered. 105 511–519.

Polák, J., Frynta, D., 2010. Patterns of sexual size dimorphism in cattle breeds support Rensch's rule. Evol. Ecol. 24, 1255–1266. https://doi.org/10.1007/s10682-010-9354-9

Price, P., Stephenson, S.M., 2009. Learning to promote occupational development through co-occupation. J. Occup. Sci. 16, 180–186. https://doi.org/10.1080/14427591.2009.9686660

Quéval, R., Bambara, L., 1984. Le polymorphisme de l'albumine dans la race Baoulé et une population de zébus de type soudanien. Rev. Elev. Médecine Vét. Pays Trop.

R. Roschinsky et al, 2014. Smallholder experiences with dairy cattle crossbreeding in the tropics: from introduction to impact. PO Box 5689 Addis Ababa Ethiop.

Racimo, F., Sankararaman, S., Nielsen, R., Huerta-Sánchez, E., 2015. Evidence for archaic adaptive introgression in humans. Nat. Rev. Genet. 16, 359–371. https://doi.org/10.1038/nrg3936

Rege et al., 1994. Shorthorn cattle of West and Central Africa. 1. Origin, distribution, classification and population statistic. Rev. Mond. Zootech. 78 2-13.

Rennie, C., Hulme, H., Fisher, P., Hall, L., Agaba, M., Noyes, H.A., Kemp, S.J., Brass, A., 2008. A Systematic, Data-driven Approach to the Combined Analysis of Microarray and QTL Data. Anim. Genomics Anim. Health 132, 293–299. https://doi.org/10.1159/000317174

Rezende, F.M., Dietsch, G.O., Peñagaricano, F., 2018. Genetic dissection of bull fertility in US Jersey dairy cattle. Anim. Genet. 49, 393–402. https://doi.org/10.1111/age.12710

Rosenberg, N.A., Huang, L., Jewett, E.M., Szpiech, Z.A., Jankovic, I., Boehnke, M., 2010. Genome-wide association studies in diverse population. Nat. Rev. Genet. 11, 356–366. https://doi.org/10.1038/nrg2760

Sabeti, P.C., Reich, D.E., Higgins, J.M., Levine, H.Z.P., Richter, D.J., Schaffner, S.F., Gabriel, S.B., Platko, J.V., Patterson, N.J., McDonald, G.J., Ackerman, H.C., Campbell, S.J., Altshuler, D., Cooper, R., Kwiatkowski, D., Ward, R., Lander, E.S., 2002. Detecting recent positive selection in the human genome from haplotype structure. Nature 419, 832–837. https://doi.org/10.1038/nature01140

Sadkowski, T., Jank, M., Zwierzchowski, L., Siadkowska, E., Oprządek, J., Motyl, T., 2008. Gene expression profiling in skeletal muscle of Holstein-Friesian bulls with single-nucleotide polymorphism in the myostatin gene 5'-flanking region. J. Appl. Genet. 49, 237–250. https://doi.org/10.1007/BF03195620

Sahana, G., Guldbrandtsen, B., Bendixen, C., Lund, M.S., 2010. Genome-wide association. Mapping for female fertility traits in Danish and Swedish Holstein cattle. Anin Genet 41, 579–588.

Saleem, M., Rahim, I., Jalali, S., Rueff, H., Khan, M., Maselli, D., Wiesmann, U., Muhammad, S., 2013. Morphological characterization of Achai cattle in sedentary and transhumant systems in Pakistan. Anim. Genet. Resour. Génétiques Anim. Genéticos Anim. 52, 83–90. https://doi.org/10.1017/S207863361200080X

Sankararaman, S., Sridhar, S., Kimmel, G., Halperin, E., 2008. Estimating Local Ancestry in Admixed Populations. Am. J. Hum. Genet. 82, 290–303. https://doi.org/10.1016/j.ajhg.2007.09.022

Sasago, N., Takeda, M., Ohtake, T., Abe, T., Sakuma, H., Kojima, T., Sasaki, S., Uemoto, Y., 2018. Genome-wide association studies identified variants for taurine concentration in Japanese Black beef. Anim. Sci. J. 89, 1051–1059. https://doi.org/10.1111/asj.13030

Scott, M.A., Woolums, A.R., Swiderski, C.E., Perkins, A.D., Nanduri, B., Smith, D.R., et al2020. Whole blood transcriptomic analysis of beef cattle at arrival identifies potential predictive molecules and mechanisms that indicate animals that naturally resist bovine respiratory disease. PLOS ONE 15, e0227507. https://doi.org/10.1371/journal.pone.0227507

Seabury, C.M., Oldeschulte, D.L., Saatchi, M., Beever, J.E., Decker, J.E., Halley, Y.A., Bhattarai, E.K., Molaei, M., Freetly, H.C., Hansen, S.L., Yampara-Iquise, H., Johnson, K.A., Kerley, M.S., Kim, J., Loy, D.D., Marques, E., Neibergs, H.L., Schnabel, R.D., Shike, D.W., Spangler, M.L., Weaber, R.L., Garrick, D.J., Taylor, J.F., 2017. Genome-wide association study for feed efficiency and growth traits in U.S. beef cattle. BMC Genomics 18, 386. https://doi.org/10.1186/s12864-017-3754-y

Seldin, M.F., Pasaniuc, B., Price, A.L., 2011. New approaches to disease mapping in admixed populations. Nat. Rev. Genet. 12, 523–528. https://doi.org/10.1038/nrg3002

Shao, G., 2009. Understanding the appeal of user-generated media: a uses and gratification perspective. Internet Res. 19, 7–25. https://doi.org/10.1108/10662240910927795

Shaw, A.P.M., Hoste, C., 1991. Les échanges internationaux de bovins trypanotolérants. I. Historique et synthèse. Rev. D'élevage Médecine Vét. Pays Trop. 44, 221–228. https://doi.org/10.19182/remvt.9203

Silbermayr, K., Li, F., Soudré, A., Müller, S., Sölkner, J., 2013. A Novel qPCR Assay for the Detection of African Animal Trypanosomosis in Trypanotolerant and Trypanosusceptible Cattle Breeds. PLoS Negl. Trop. Dis. 7. https://doi.org/10.1371/journal.pntd.0002345

Sölkner J, Frkonja A, Raadsma HW, Jonas E, Thaller G. Gootwine E, et al. Estimation of Individual Levels of Admixture in Crossbred Populations from SNP Chip Data : Examples with Sheep and Cattle Populations. 2010:62–6.

Smetko, A., Soudre, A., Silbermayr, K., Müller, S., Brem, G., Hanotte, O., Boettcher, P.J., Stella, A., Mészáros, G., Wurzinger, M., Curik, I., Müller, M., Burgstaller, J., Sölkner, J., 2015. Trypanosomosis : potential driver of selection in African cattle. Front. Genet. 6. https://doi.org/10.3389/fgene.2015.00137

Sorbolini, S., Bongiorni, S., Cellesi, M., Gaspa, G., Dimauro, C., Valentini, A., Macciotta, N.P.P., 2017. Genome wide association study on beef production traits in Marchigiana cattle breed. J. Anim. Breed. Genet. 134, 43–48. https://doi.org/10.1111/jbg.12227

Sorensen, J., Kondrup, J., Prokopowicz, J., Schiesser, M., Krähenbühl, L., Meier, R., Liberda, M., 2008. EuroOOPS : An international, multicentre study to implement nutritional risk screening and evaluate clinical outcome. Clin. Nutr. 27, 340–349. https://doi.org/10.1016/j.clnu.2008.03.012

Soro, B., Sokouri, D.P., Dayo, G.K., N'Guetta, A.S.P., Yapi, C.V., 2015. Caractérisation des bovins de race Baoulé dans le "Pays Lobi" de Côte d'Ivoire : rôles socio-économiques, modes d'élevage et contraintes de production 14.

Soudre, A., 2011. Trypanosomosis, genetic diversity and admixture in cattle breeds of Burkina Faso.

SUN, Y., XUE, J., GUO, W., LI, M., HUANG, Y., LAN, X., LEI, C., ZHANG, C., CHEN, H., 2016. Haplotypes of bovine FoxO1 gene sequence variants and association with growth traits in Qinchuan cattle. J. Genet. 93, 8–14. https://doi.org/10.1007/s12041-013-0209-3

Tang, H., Choudhry, S., Mei, R., Morgan, M., Rodriguez-Cintron, W., Burchard, E.G., Risch, N.J., 2007. Recent Genetic Selection in the Ancestral Admixture of Puerto Ricans. Am. J. Hum. Genet. 81, 626–633. https://doi.org/10.1086/520769

Taye, M., Kim, J., Yoon, S.H., Lee, W., Hanotte, O., Dessie, T., Kemp, S., Mwai, O.A., Caetano-Anolles, K., Cho, S., Oh, S.J., Lee, H.-K., Kim, H., 2017. Whole genome scan reveals the genetic signature of African Ankole cattle breed and potential for higher quality beef. BMC Genet. 18, 11. https://doi.org/10.1186/s12863-016-0467-1

The R Development Core Team, 2008. A Language and Environment for Statistical Computing. ISBN 3-900051-07-0.

Thomas, P.D., Kejariwal, A., Campbell, M.J., Mi, H., Diemer, K., Guo, N., Ladunga, I., Ulitsky-Lazareva, B., Muruganujan, A., Rabkin, S., Vandergriff, J.A., Doremieux, O., 2003. PANTHER: a browsable database of gene products organized by biological function, using curated protein family and subfamily classification. Nucleic Acids Res. 31, 334–341. https://doi.org/10.1093/nar/gkg115

Tiberti, N., Hainard, A., Lejon, V., Robin, X., Ngoyi, D.M., Turck, N., Matovu, E., Enyaru, J., Ndung'u, J.M., Scherl, A., Dayon, L., Sanchez, J.-C., 2010. Discovery and Verification of Osteopontin and Beta-2-microglobulin as Promising Markers for

Staging Human African Trypanosomiasis. Mol. Cell. Proteomics 9, 2783–2795. https://doi.org/10.1074/mcp.M110.001008

Tijjani, A., 2019. Genome diversity and adaptation of African Taurine and Zebu cattle [WWW Document]. URL http://eprints.nottingham.ac.uk/55806/ (accessed 10.15.20).

Trail, J.C.M., d'Ieteren, G.D.M., Feron, A., Kakiese, O., Mulungo, M., Pelo, M., 1990. Effect of trypanosome infection, control of parasitaemia and control of anaemia development on productivity of N'Dama cattle. Acta Trop. 48, 37–45. https://doi.org/10.1016/0001-706X(90)90063-6

Traoré, A., Koudandé, D.O., Fernández, I., Soudré, A., Álvarez, I., Diarra, S., Diarra, F., Kaboré, A., Sanou, M., Tamboura, H.H., Goyache, F., 2016. Multivariate characterization of morphological traits in West African cattle sires. Arch. Anim. Breed. 59, 337–344. https://doi.org/10.5194/aab-59-337-2016

Traoré, A., Koudandé, D.O., Fernández, I., Soudré, A., Granda, V., Álvarez, I., Diarra, S., Diarra, F., Kaboré, A., Sanou, M., Tamboura, H.H., Goyache, F., 2015. Geographical assessment of body measurements and qualitative traits in West African cattle. Trop. Anim. Health Prod. 47, 1505–1513. https://doi.org/10.1007/s11250-015-0891-7

Ulbrich, S.E., Schoenfelder, M., Thoene, S., Einspanier, R., 2004. Hyaluronan in the bovine oviduct—modulation of synthases and receptors during the estrous cycle. Mol. Cell. Endocrinol. 214, 9–18. https://doi.org/10.1016/j.mce.2003.12.002

van der Waaij, E.H., Hanotte, O., van Arendonk, J.A.M., Kemp, S.J., Kennedy, D., Gibson, J.P., Teale, A., 2003. Population parameters for traits defining trypanotolerance in an F2 cross of N'Dama and Boran cattle. Livest. Prod. Sci. 84, 219–230. https://doi.org/10.1016/S0301-6226(03)00078-2

Villarreal-Ramos, B., Berg, S., Whelan, A., Holbert, S., Carreras, F., Salguero, F.J., et al2018. Experimental infection of cattle with Mycobacterium tuberculosis isolates shows the attenuation of the human tubercle bacillus for cattle. Scientific Reports 8, 894. https://doi.org/10.1038/s41598-017-18575-5

Voight, B.F., Kudaravalli, S., Wen, X., Pritchard, J.K., 2006. A Map of Recent Positive Selection in the Human Genome. PLOS Biol. 4, e72. https://doi.org/10.1371/journal.pbio.0040072

Wang, M., Lai, X., Yu, H., Wang, J., Chen, Z.-Q., Lan, X.-Y., Lei, C.-Z., Chen, H., 2010. Two novel single nucleotide polymorphisms (SNPs) and 4-bp deletion mutation of

RBP4 gene in Chinese cattle. J. Genet. 89, 233–236. https://doi.org/10.1007/s12041-010-0031-0

Wason, J.M., Dudbridge, F., 2010. Comparison of multimarker logistic regression models, with application to a genomewide scan of schizophrenia. BMC Genet. 11, 80. https://doi.org/10.1186/1471-2156-11-80

Wei, X., Zhang, J., 2018. The optimal mating distance resulting from heterosis and genetic incompatibility. Sci. Adv. 4, eaau5518. https://doi.org/10.1126/sciadv.aau5518

Weir, B.S., Cockerham, C.C., 1984. Estimating F-Statistics for the Analysis of Population Structure. Evolution 38, 1358–1370. https://doi.org/10.2307/2408641

Wendorf, F., Schild, R., 1994. Are the early holocene cattle in the eastern sahara domestic or wild? Evol. Anthropol. Issues News Rev. 3, 118–128. https://doi.org/10.1002/evan.1360030406

Wesdorp, M., van de Kamp, J.M., Hensen, E.F., Schraders, M., Oostrik, J., Yntema, H.G., Feenstra, I., Admiraal, R.J.C., Kunst, H.P.M., Tekin, M., Kanaan, M., Kremer, H., Pennings, R.J.E., 2017. Broadening the phenotype of DFNB28 : Mutations in TRIOBP are associated with moderate, stable hereditary hearing impairment. Hear. Res., Hearing loss and auditory plasticity 347, 56–62. https://doi.org/10.1016/j.heares.2016.12.017

Wood, W., Carden, L., 2014. Elusiveness of menstrual cycle effects on mate preferences : Comment on Gildersleeve, Haselton, and Fales (2014). Psychol. Bull. 140, 1265–1271. https://doi.org/10.1037/a0036722

Wurzinger, M., Sölkner, J., Iñiguez, L., 2011. Important aspect and limitations in considering community-based breeding programs for low-input smallholder livestock systems. Small Rumin. Res., Special Issue : Technological development and associative attempts to a sustainable goat production 98, 170–175. https://doi.org/10.1016/j.smallrumres.2011.03.035

Xu, Z., Gong, J., Maiti, D., Vong, L., Wu, L., Schwarz, J.J., Duh, E.J., 2012. MEF2C Ablation in Endothelial Cells Reduces Retinal Vessel Loss and Suppresses Pathologic Retinal Neovascularization in Oxygen-Induced Retinopathy. Am. J. Pathol. 180, 2548–2560. https://doi.org/10.1016/j.ajpath.2012.02.021

Yakubu, A., Ogah, D.M., Idahor, K.O., 2009. PRINCIPAL COMPONENT ANALYSIS OF THE MORPHOSTRUCTURAL INDICES OF WHITE FULANI CATTLE. Trakia J. Sci. 7, 8.

Yougbaré, B., Soudré, A., Ouédraogo, D., Zoma, B.L., Tapsoba, A.S.R., Sanou, M., Ouédraogo-Koné, S., Burger, P., Wurzinger, M., Khayatzadeh, N., Tamboura, H.H., Traoré, A., Sölkner, J., Mészáros, G., 2020. Morphometric characterization of purebred and crossbred Baoulé cattle in Burkina Faso. Acta Agric. Scand. Sect. — Anim. Sci. 0, 1–10. https://doi.org/10.1080/09064702.2020.1825785

Zafindrajaona, P.S., Zeuh, V., Goudarzi, K.M., Laloë, D., Bourzat, D., Idriss, A., Grosclaude, F., 1999. Etude du statut phylogénétique du bovin Kouri du lac Tchad à l'aide de marqueurs moléculaires. Rev. D'élevage Médecine Vét. Pays Trop. 52, 155–162. https://doi.org/10.19182/remvt.9690

Zhang, H.M., Xia, H.L., Jiang, H.R., Mao, Y.J., Qu, K.X., Huang, B.Z., Gong, Y.C., Yang, Z.P., 2018. Longissimus dorsi muscle transcriptomic analysis of Yunling and Chinese simmental cattle differing in intramuscular fat content and fatty acid composition. Genome. https://doi.org/10.1139/gen-2017-0164

Zhang, Y., Xiao, M., Zhang, Shulan, Xia, P., Cao, W., Jiang, W., Chen, H., Ding, X., Zhao, H., Zhang, H., Wang, C., Zhao, J., Sun, X., Tian, R., Wu, W., Wu, D., Ma, J., Chen, Y., Zhang, D., Xie, J., Yan, X., Zhou, X., Liu, Z., Wang, J., Du, B., Qin, Y., Gao, P., Qin, X., Xu, Y., Zhang, W., Li, T., Zhang, F., Zhao, Y., Li, Y., Zhang, Shuyang, 2020. Coagulopathy and Antiphospholipid Antibodies in Patients with Covid-19. N. Engl. J. Med. 382, e38. https://doi.org/10.1056/NEJMc2007575

Zhou, X., Stephens, M., 2012. Genome-wide efficient mixed-model analysis for association studies. Nat. Genet. 44, 821–824. https://doi.org/10.1038/ng.2310

Zhu, C., Sun, B., Nie, A., Zhou, Z., 2020. The tRNA-associated dysregulation in immune responses and immune diseases. Acta Physiologica 228, e13391. https://doi.org/10.1111/apha.13391

ANNEXES

Annex 1. Questionnaire

MORPHOLOGICAL TRAITS CHARACTERIZATION OF TRYPANOTOLERANT ANIMALS

INDIVIDUAL DATA OF INQUIRY
MEASUREMENTS AND OBSERVATIONS PHENOTYPIC (1)

IDENTIFICATION OF SURVEY

Name and first name of investigator: _____ **Number of questionnaires:**

Date of investigation : __/__/__ Province : _____

Village/Site : _____ site code : _____

IDENTIFICATION OF ANIMAL

Identification: _____ Date of birth: __/__/__ Age: _____ Sexe: M / F

Type genetic _____ Date entry in the herd: __/__/__ Entry mode: Birth / Buy

Genetic type of mother: _____ Identification of mother: _____

Genetic type of father: _____ Identification of father: _____

HEAD AND HORN MEASUREMENT

Head length	
Head width	
Cranial length	
Cranial width	
Facial length	
Facial width	
Muzzle circumference	
Horn length	
Distance Point -point horn	
Distance Base-Base horn	

Earn length	

* Bind the order number in herd number: for example, order number 1.3 for the first herd and 3rd herd animal in the province

Head profile

Concave ☐
Convex ☐
Rectilinear ☐

Ears position

Horizontal ☐
Drawn ☐
Falling ☐

Color of muzzle

Pigmented ☐
No pigmented ☐

Head Tache

Yes ☐
No ☐

Eyelid pigmentation

Pigmentation (black) ☐
Not pigmentation (white)☐

Color hoof

Pigmented ☐
No pigmented☐

Color of horn

Black ☐
White ☐
Brown ☐
Grey ☐
Two coloured ☐

Cephalic profile

Concave ☐
Convex ☐
straight ☐

Dewlap size

Well developed ☐
Poorly developed ☐
Small developped ☐

Hump position

Absence ☐
thoracic ☐
Cervicothoracic ☐

Presence of horn:

Yes ☐
No ☐

Backline

straight ☐
Concave ☐
Convex ☐

Horn shape

Short ☐
Long ☐
Polled ☐
Cup ☐
Crescent ☐
Lyre ☐
Wheel ☐
Crown ☐
Spirale ☐
Backwards ☐

MEASUREMENT OF BODY

Heigth at weithers	
Thorax depth	
Heigth at sacrum	
Length of scapula-Ischium	
Chest depth	
Chest width	
Tail length	
Shoulder Width	
Hip width	
Height at hips	
Ischium width	
Pelvic width	
Basin lenght	
Height of the hump	
Rump length	

Heart girth	
Teat Length	
Body length	

COLOUR OF COAT

General of the dress appearance:

Uniform ☐

Presence ☐

Pied ☐

Absence ☐

Speckled ☐

Type of hair

Black hair in legs

Short ☐

Medium ☐

Long ☐

Curly ☐

Straight ☐

Coat color

Black ☐

black - pied ☐

White ☐

Red ☐

Red- pie ☐

Roan ☐

Fawn ☐

Sand ☐

Grey ☐

Diluted fawn ☐

blond ☐

fawn-blond ☐

dun-red ☐

Fawn-red ☐

Blackness

slightly charred ☐

medium charred ☐

charred strongly ☐

Spotting pattern

Absence ☐

Pied ☐

Spotted ☐

Sooty pattern

Absence ☐

Light ☐

Apparent ☐

Strong ☐

white variegations

Irregular ☐

white head ☐

lateral color ☐

white belt ☐

lateral depigmentation ☐

Brindling

slightly brindle ☐

Medium brindle ☐

strongly brindle ☐

Brindle

Absence ☐
Light ☐
Apparent ☐
Strong ☐

Particular of the coat

stripe mullet

Inverse ☐
Dark ☐

Extremity

Charred ☐
faded ☐

Color of chignon

Yes ☐
No ☐

Discolored abdomen

Yes ☐
No ☐

If yes, specify color----------

Speckle

Yes ☐
No ☐

Colored belly

Presence
Absence

White blazens

Presence
Absence

Dorsal stripe

Absence ☐
Black ☐
Presence ☐

Local name of the breed _____

BREATS OF THE FEMALE

Development of breasts

Developed ☐
Medium ☐
Small ☐

BLOOD SAMPLE

The blood of animal was taked? Yes ☐ **If yes, specify the tube code:**

Annex 2. Supplementary table

Table S1: The 100 highest differentiating SNPs according the FST value

Chromosome number	SNP-Name	Position	FST-Value
5	BovineHD0500014038	48684632	0.983051
5	ARS-BFGL-NGS-4763	56585423	0.964319
7	BovineHD0700014767	50596886	0.949183
13	BovineHD1300012337	42418952	0.949183
3	ARS-BFGL-NGS-67960	34263481	0.92997
13	BovineHD1300010688	36956520	0.915361
13	BovineHD1300014423	49869007	0.913063
18	ARS-BFGL-NGS-11936	25653308	0.912438
5	BovineHD0500018676	66809794	0.911919
7	BovineHD0700019952	68127848	0.911919
12	BovineHD1200008699	29542838	0.911919
7	BovineHD0700015011	51739128	0.911294
5	ARS-BFGL-NGS-100547	66784879	0.906898
2	BovineHD0200008300	28396626	0.898467
3	BovineHD0300016644	55064457	0.898467
4	BovineHD0400011124	40104459	0.898467
12	BTA-31783-no-rs	19982250	0.898467
9	BovineHD0900021248	76270904	0.897829
5	BovineHD0500006844	23543325	0.895597
5	BovineHD0500026582	93664518	0.894536
5	BovineHD0500035017	119886893	0.894536
15	BovineHD1500020125	69707369	0.893883
18	Hapmap52308-rs29009652	54470798	0.893871
16	ARS-BFGL-NGS-101656	41992472	0.891385
7	BovineHD0700021133	71697239	0.881588
9	BovineHD0900021283	76385110	0.881588
2	BovineHD0200020386	70972553	0.880937
6	BovineHD0600032704	115296748	0.880937
5	Hapmap41950-BTA-72999	26082666	0.878144
7	ARS-BFGL-NGS-15459	23756162	0.877495
7	BovineHD0700008786	31011979	0.876847
2	Hapmap30596-BTA-161397	69939162	0.874726
16	BovineHD1600011216	39118839	0.874726
11	BovineHD1100014651	49934803	0.864721
2	ARS-BFGL-NGS-83221	70719167	0.864058
13	BovineHD1300022886	79109584	0.863395
2	BovineHD0200020335	70770040	0.862019
10	BovineHD1000017894	61946034	0.860705
4	BovineHD0400019264	70100877	0.859211
5	BovineHD4100003413	9211843	0.857857

12	BovineHD1200008803	29864049	0.855593
6	BovineHD0600013238	48243519	0.855501
3	Hapmap57282-ss46526266	95924827	0.85154
13	BovineHD1300008042	27686629	0.84787
19	UA-IFASA-6210	59715027	0.84787
10	BovineHD1000025823	90327707	0.847194
11	BovineHD1100011251	37930714	0.847194
6	BovineHD4100004930	46808748	0.846518
20	BovineHD2000004622	15282042	0.844948
12	BovineHD1200007107	23573797	0.843281
14	BovineHD1400012544	44320278	0.843281
11	BovineHD1100014397	48966315	0.83987
4	BovineHD0400022404	81050716	0.8392
3	BovineHD0300035702	117337293	0.836942
7	BovineHD0700015218	52757805	0.836942
9	BovineHD4100007585	76516167	0.831153
11	ARS-BFGL-BAC-11783	74603943	0.831034
19	BovineHD1900006203	21678830	0.831034
3	Hapmap51282-BTA-67903	55187147	0.830345
4	BTA-70284-no-rs	41895490	0.830345
12	BovineHD1200008483	28644619	0.830345
20	BTB-01300413	15253542	0.830345
10	BovineHD1000011295	36041911	0.829655
10	ARS-BFGL-NGS-28776	17377774	0.8219
13	BovineHD1300016722	58378178	0.8219
18	ARS-BFGL-NGS-15837	62591127	0.8219
12	BovineHD1200014463	52404316	0.820535
7	BovineHD0700014460	49961510	0.816846
4	BovineHD0400014383	52024984	0.816167
7	Hapmap35191-BES11_Contig367_1030	55144387	0.815489
5	BovineHD0500018581	66379267	0.814215
6	Hapmap33430-BTC-037618	41588847	0.814215
17	BovineHD1700000823	3479572	0.814215
13	BovineHD1300022893	79143377	0.813875
2	BovineHD0200002852	10166949	0.813512
4	BovineHD0400022134	80034734	0.813512
13	BovineHD1300009238	31608219	0.813512
3	BovineHD0300027088	94006679	0.812808
8	BovineHD0800021888	72806242	0.812808
18	BovineHD1800016466	56446320	0.812104
3	Hapmap53284-rs29015774	55327770	0.809708
3	BovineHD0300028475	98991477	0.808481
6	BTB-00272418	96493695	0.808481
11	BovineHD1100004099	12441952	0.807782

6	BovineHD0600015761	57608133	0.806384
4	BovineHD0400011578	41938042	0.803254
13	BovineHD1300016713	58347218	0.803245
1	BovineHD0100013052	45719178	0.800582
6	BovineHD0600032874	115853782	0.800582
7	BovineHD0700010226	35704892	0.800582
9	BovineHD0900017167	62432661	0.800582
11	Hapmap40862-BTA-100125	62144546	0.800582
6	BovineHD0600012731	46730204	0.798352
5	BovineHD0500025003	88134041	0.797661
1	BovineHD0100003512	11155914	0.797414
2	BovineHD0200002816	9928973	0.797414
4	BovineHD0400033226	114860030	0.797414
14	BovineHD1400014933	52870232	0.797414
15	BovineHD1500012190	43894485	0.797414
16	BTB-01226007	32591482	0.797241

Annex 3. Supplementary figures

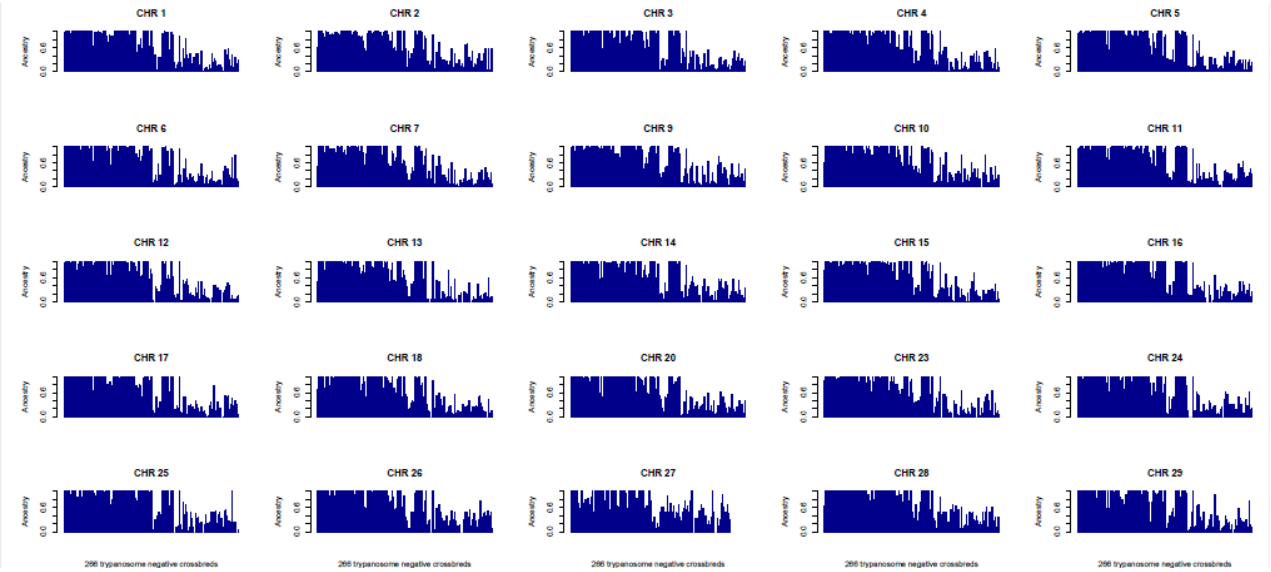


Figure S1: The local ancestry estimation plot for 29 autosomes chromosomes for 266 trypanosomes negative, in Baoulé X Zebu crossbred cattle, excluding CHR 6,8,19, 21, and 22 which are presented in Figure 19

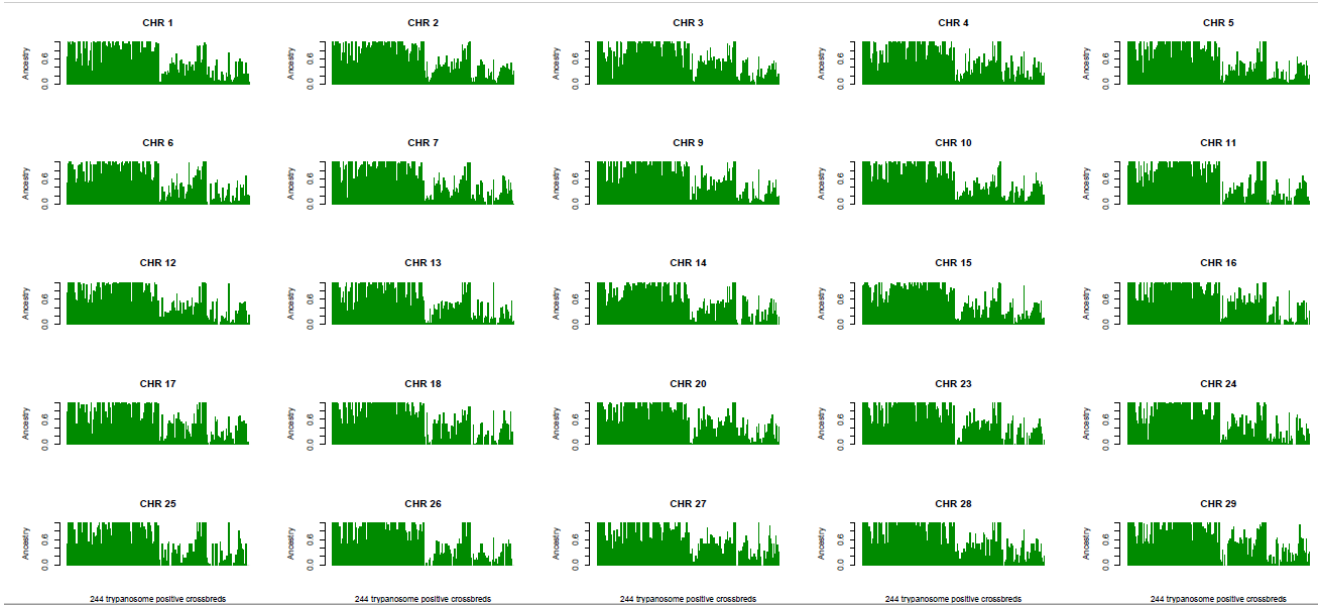


Figure S2: The local ancestry estimation plot for 29 autosomes chromosomes for 244 trypanosomes positive, in Baoulé X Zebu crossbred cattle, excluding CHR 6, 8,19,21,22 which are presented in Figure 19

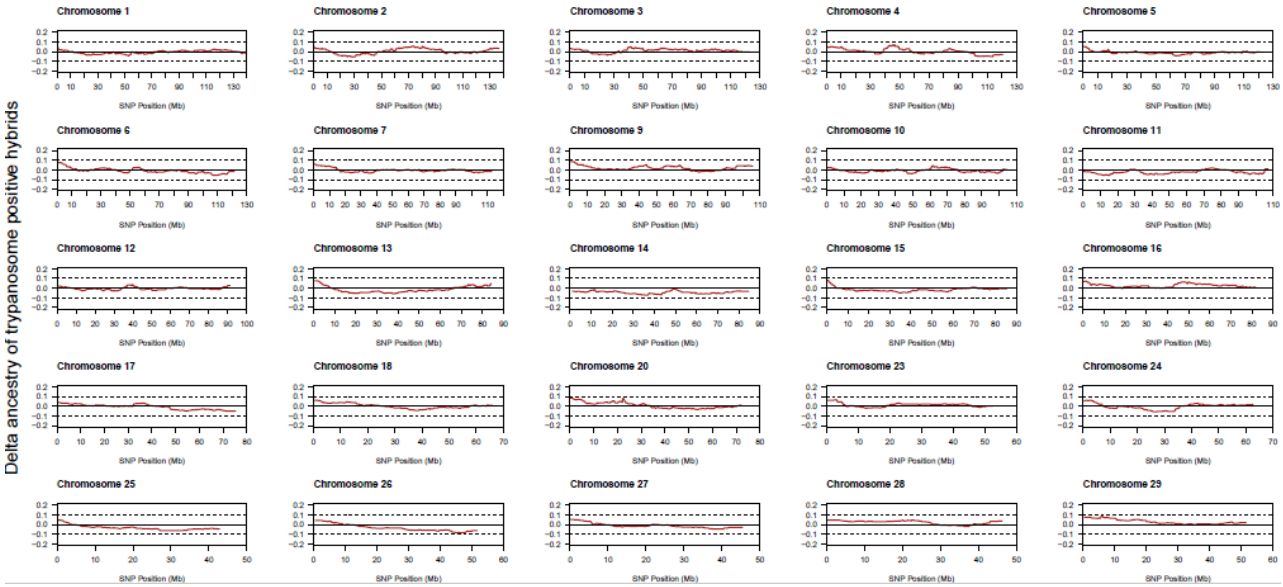


Figure S3: The delta ancestry for 29 autosomes chromosomes for 244 trypanosomes positive, in Baoulé X Zebu crossbred cattle, excluding CHR 6, 8,19,21,22 which are presented in Figure 20

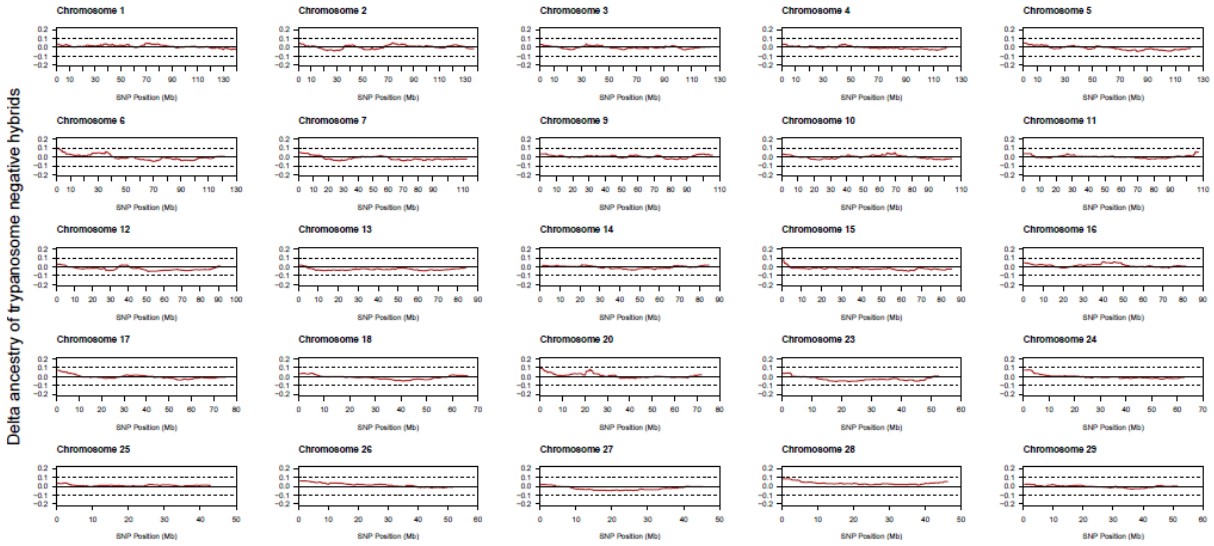
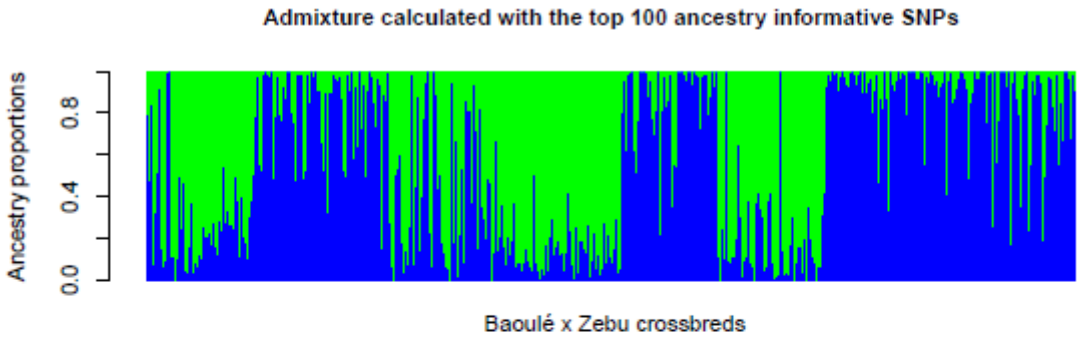
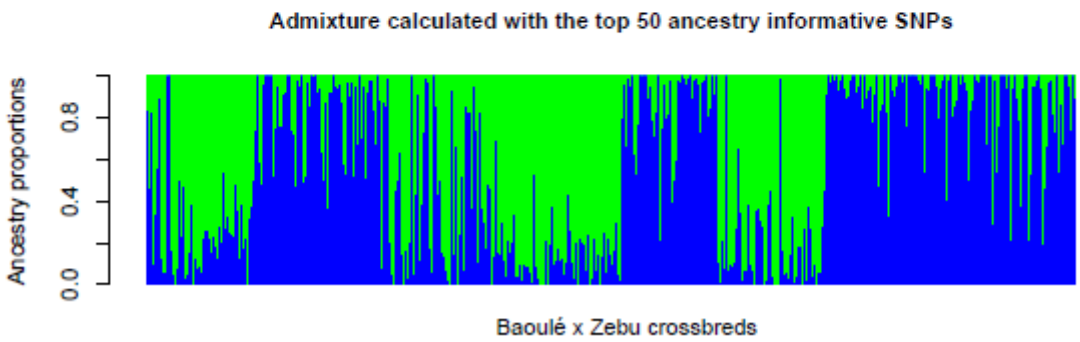
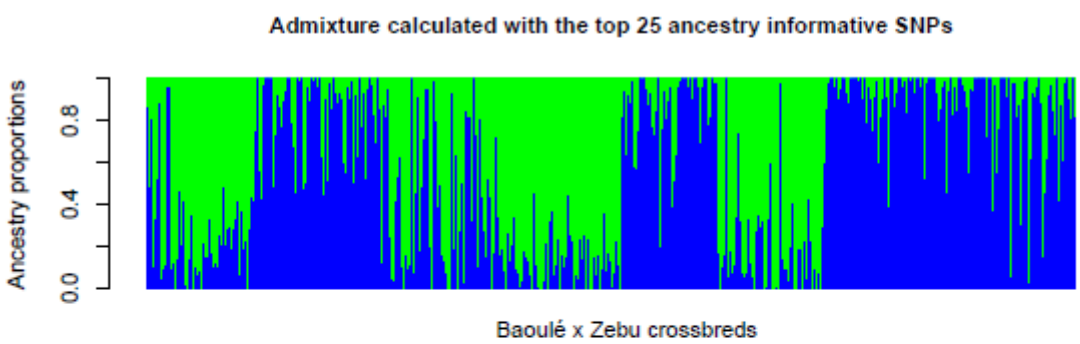


Figure S4: The delta ancestry for 29 autosomes chromosomes for 266 trypanosomes negative, in Baoulé X Zebu crossbred cattle, excluding CHR 6, 8,19,21,22 which are presented in Fig. 5which are presented in Figure 20


Admixture calculated with the top 100 ancestry informative SNPs
Ancestry proportions
0.0
0.4
0.8
Baoulé x Zebu crossbreds


Admixture calculated with the top 50 ancestry informative SNPs
Ancestry proportions
0.0
0.4
0.8
Baoulé x Zebu crossbreds


Admixture calculated with the top 25 ancestry informative SNPs
Ancestry proportions
0.0
0.4
0.8
Baoulé x Zebu crossbreds

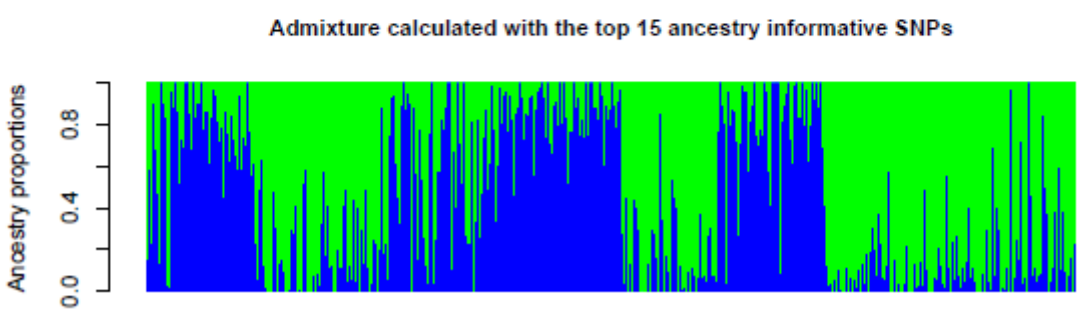

Admixture calculated with the top 15 ancestry informative SNPs
Ancestry proportions
0.0
0.4
0.8

Figure S5: the admixture rate of the top 100, 50, 25 and 15 differentiating SNPs according the F_{ST} value