


Review

Capitalizing on the Potential of South African Indigenous Beef Cattle Breeds: A Review

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Abstract: Cattle populations arrived in Southern Africa almost 2000 years ago, brought by farming communities migrating southwards. For centuries, cattle have been an integral component of livestock production to meet the animal protein needs of a growing population and they are also important in many cultural and religious events, as repositories of wealth and signifiers of social status. Selection within these cattle populations led to the development of breeds such as the Nguni, Afrikaner and Drakensberger that are well adapted to the local production environment. Genetic information has been generated for most of these populations, providing new insights into their ancestry and indicating moderate levels of diversity and relatively low inbreeding. Indigenous cattle breeds are present in both the well-developed commercial sector as well as the developing South African livestock sector. These breeds have been included in several research studies, mostly focusing on their production and adaptive potential. Genetic improvement of the local cattle populations and breeds, which are often more resilient to local environmental conditions, has the potential to improve the productivity of the small-scale production developing sector and contribute to the alleviation of poverty.

Keywords: cattle; adaptation; ecotype; genomic; production traits



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1. Introduction

In Southern Africa, human populations are expanding and the demand for animal protein is increasing. South Africa currently has an estimated population of 59.6 million people, expected to grow to approximately 72 million by 2050 [1]. Despite ongoing socio-economic transformations and efforts to reach sustainable development goals for a reduction in poverty and zero hunger, inequalities in the South African food system remain [2]. It is estimated that more than two million households are involved in farming or keeping of livestock as part of their livelihoods [3]. Indigenous/local beef cattle populations have an important role to fulfil considering the diverse geography and climate of South Africa, with up to 80% of available land suitable only for livestock farming [4]. These cattle populations are deeply rooted in rural South African communities and form an integral part of cultural and religious events, social status, food production, and livelihoods [5–7]. The sustainable utilization of these populations will ensure their continued contribution to the livestock industry.

The success of local South African cattle populations is the result of their many unique adaptive characteristics, acquired through hundreds of years of natural and directional selection. These bear witness to the complex history of the region and the dualistic nature of its modern agricultural system, consisting of a well-developed commercial sector applying modern farming technologies and a more “developing” sector that consists mainly of

smallholders and subsistence farmers [8,9]. Here we present a comprehensive overview of our current knowledge of South African beef cattle populations combining information from archaeology, history, and genetics.

2. Archaeology, History and the Establishment of South African Cattle Populations

Modern domestic cattle were derived from two wild auroch subspecies from the Near East (taurine cattle) and India (indicine cattle). Taurine cattle were first domesticated over 10,000 years ago in the Near East from where they were spread to North Africa and Asia alongside other farming technologies [10]. Following their introduction to North Africa, cattle likely interbred with local wild auroch populations, potentially contributing to the distinctiveness of African taurine cattle [11].

Although it is unclear whether indicine cattle were domesticated independently (i.e., prior to the arrival of taurine cattle in India), their overall domestication history appears more recent than that of taurine cattle [12]. Both taurine and indicine cattle, as well as hybrids, are common across Africa, including South Africa [13]. Interestingly, recent ancient genomic work suggests that taurine and indicine cattle were likely first hybridized during the Bronze Age, ~4500 years ago, in the Near East to improve the resilience of local cattle populations to recurrent and devastating droughts that took place during the so-called 4.2k event [11]. These highly resilient cattle populations were then likely dispersed to West and East Africa.

Domestic cattle were kept by at least the 7th–6th millennium Before the Common Era (BCE) in what is now the Sahara, but there were substantial time lags before they reached East Africa 5000–4500 years ago [14,15] and Southern Africa around 2000 years ago [16,17]. Cattle, and also sheep and goats, were initially probably ill-adapted to environmental conditions and new diseases they faced in sub-Saharan Africa. This appears to have constrained their spread for thousands of years, until they developed new adaptations that allowed them to survive in these ecosystems [14].

Evidence of the earliest cattle in Southern Africa is scarce. A probable cattle bone found near Lake Ngami in Northern Botswana is radiocarbon dated to approximately 2000 years ago and a tooth from the same site to 1500 years ago [16,17]. Expert assessment, based on size and shape, indicate that these bones probably derive from cattle, but confusion with indigenous wild species is possible. In the case of a horn core from Namaqualand, radiocarbon dated to the fifth/sixth century BCE and morphological identification as cattle was supported by the sequence of a fragment of mitochondrial DNA [18]. In southwestern South Africa, early European sailors (from the late 15th century BCE) and settlers (from the mid-17th century onwards) encountered Khoekhoe herders with large herds of cattle (10,000 animals or more) together with sheep [19]. The Khoekhoe did not cultivate crops; their economy centered on domesticated animals, together with hunting wild animals and gathering wild plant foods.

In the northern and eastern parts of South Africa, cattle formed part of mixed farming economies. Here, early farmers lived in settled villages, grew crops and worked with iron and other metals as well as keeping domesticated animals [20]. The first sites of this kind date to about 300 BCE, although animal remains from this time are scarce [21]. Later in the first millennium BCE, cattle, sheep and goats were widespread [22–25]. These early farming societies had dynamic histories, with particularly marked changes at the end of the first/beginning of the second millennium BCE. By the 18th and 19th centuries BCE, Nguni-speaking people were living in the eastern coastal regions of South Africa. They kept Nguni cattle, as described further below. Today, there are several Nguni ecotypes, some currently in danger of extinction such as the Shangaan, Pedi, and Nkone, with less than 1000 breeding animals left in each of these populations [26]. Elsewhere, Sotho-Tswana and other communities also kept cattle. The genetic relationships between indigenous cattle in different areas of Southern Africa are of considerable interest, but have yet to be investigated.

Dutch settlers at the Cape acquired Khoekhoe cattle, believed to be of a Sanga type; over time they were subjected to selection for draught power, and beef by the settlers and became known as Afrikaner cattle. The first attempt to import European cattle (in the 1650s) was unsuccessful; the animals apparently died shortly afterwards [27]. A more successful crossbreeding initiative began in about 1780, when Governor van Plettenberg imported a Friesland bull and cow to improve the milk yield of local cattle [19]. The offspring of these and subsequent imports were referred to as the Vaderlanders or home-country cattle. During the early 18th century, the prominent Uys family played an important role in the development of a breed of black cattle by selecting the most hardy and productive animals in their Vaderlander herd [28]. The breed gained popularity and during the Great Trek (which began in 1836) to the north of the country, selection of black-coated and hardy animals, with good conformation, resulted in the Drakensberger [29].

Modern South African cattle now represent a blend of African taurine, African indicine and more recently introduced European cattle [26]. This peculiar evolutionary history suggests that modern indigenous populations from South Africa possess many unique biological features that are the result of years of selection and crossbreeding. These indigenous populations are often classified based on identifiable phenotypic characteristics [30] or according to the geographical area they inhabit or named after the community to which they belong [31,32]. Cattle belonging to different ecotypes are usually found in specific geographic areas and often possess specific color patterns. In sub-Saharan Africa, there are 150 recognized indigenous breeds, which include long- and short-horned taurine cattle, Zebu (*Bos indicus*), Sanga, and Zenga types [26,33]. The Nguni, Tuli, Drakensberger, and Afrikaner are classified as indigenous Sanga (*Bos taurus africanus*) beef breeds and are frequently found in commercial, smallholder and communal beef production systems in South Africa (SA).

3. Genetic Improvement of Local Cattle Populations

The utilization and genetic improvement of SA indigenous populations are embedded in the history of the country and the dualistic nature of the agricultural industry. From the 18th century, South African livestock farmers adopted the principles of selection and improvement of purebred cattle promoted by Sir Robert Bakewell. Several beef and dual-purpose breeds were imported from the UK and Europe during the early 19th century [34]. The commercial livestock sector at the time followed international trends, and in 1905, the SA Studbook Association was founded for registration of pedigree livestock. This was formalized with the declaration of Act 22 of 1920. In 1962, the Act was amended to include locally developed breeds such as the Bonsmara, and in 1977, the Livestock Improvement Act 25 was promulgated [35]. An official beef performance and progeny scheme was established in the early 1960s for recording of phenotypic traits and objective selection [36].

The Afrikaner and Drakensberger breed societies were established in 1912 and 1947, respectively, and they were recognized as official breeds used in beef production. Nguni cattle were not highly regarded and for a short period during 1934, Nguni ecotypes were classified as nondescript [37]. In 1940, the Bartlow Combine Nguni herd was established and performance recording was initiated. Conservation programs to conserve and utilize indigenous SA livestock breeds, including the Nguni [37], were established only during the 1980s and a breed society for SA Nguni cattle was founded in 1986. Although the Tuli originates from Zimbabwe, cattle were imported to SA during the 1970s [38] and the Tuli Cattle Breeders' Society was established in 1994.

The Bonsmara is a breed developed from three breeds during the 1960s. In its development, the Afrikaner contributed adaptive traits while the British Hereford and Milk Shorthorn were used for growth traits and mothering ability, resulting in a composite breed with a composition of 5/8 Afrikaner, 3/16 Hereford and 3/16 Milk Shorthorn [39]. The Bonsmara is considered as a South African Landrace breed, which is defined as a locally developed breed [40] well-adapted to diverse climatic regions throughout SA. In Table 1,

a summary of the characteristics of the Afrikaner, Bonsmara, Drakensberger, Nguni, and Tuli is given, as described by their respective breed societies.

Table 1. Summary of the breed characteristics of the Afrikaner, Bonsmara, Drakensberger, Nguni, and Tuli breeds of South Africa.

Breed	Breed Characteristics	Reference
Afrikaner	Medium frame; muscular back and loins; long horns; preferred dam line High quality meat	[41]
Bonsmara	Adapted; preferred dam line; high growth efficiency; superior carcass traits	[42]
Drakensberger	Medium frame; smooth black coat; adapted, low susceptibility to ticks; high fertility	[28]
Nguni	Small frame; adapted to harsh climates; well-pigmented; dam line; low maintenance	[43]
Tuli	Adaptability; fertility; popular crossbreeding; carries <i>Polled</i> gene	[38]

South African indigenous breeds evolved over time due to selection for production, but they are known for their physiological and/or morphological traits, which make them more suited to the high temperatures and humidity of parts of Southern Africa compared to the imported breeds.

Breeds such as the Bonsmara, Drakensberger, and Afrikaner participated in official animal recording from the onset of national animal recording schemes during the 1960s, submitting pedigree and performance records for genetic evaluation. The participation of the different breeds in the official national beef recording has ranged from 42% of Nguni breeders to as high as 82% for the Afrikaner, 85% for the Drakensberger, and 98% for the Bonsmara breed [44]. Table 2 summarizes average performance for fertility traits of indigenous breeds for the periods 1999 to 2008 and 2016.

Table 2. A summary of averaged fertility traits for South Africa (SA) indigenous beef breeds for the periods 1999 to 2008 and 2016 (adapted from [35,44,45]).

Breed	Age at First Calving (Months)		Inter Calving Period (Days)		Cow Weight (kg)	
	1999–2008	2016	1999–2008	2016	1999–2008	2016
Afrikaner	37	35	448	460	476	473
Bonsmara	32	31	414	413	503	506
Drakensberger	36	34	441	424	499	507
Nguni	31	32	404	415	367	366
Tuli	35	35	421	423	453	429

Currently, all indigenous breeds in the developed livestock sector have access to modern breeding technologies, which include the use of artificial insemination (AI), animal recording systems, genetic evaluations (EBV) and genotyping services [46]. Genetic evaluations using best linear unbiased prediction (BLUP) started in the late 1980s in South Africa, providing breeders participating in animal recording with estimated breeding values (EBV) for selection. Ref. [47] analyzed production data for Afrikaner, Drakensberger, Nguni, and Tuli cattle and reported a positive genetic response for weaning weight of 0.549 kg, 0.288 kg, 0.052 kg, and 0.243 kg per year, respectively. The average rate of inbreeding per generation varied from 0.26 for Nguni to 0.56 for the Tuli breed, while effective population sizes ranged between 191 (Nguni), 122 (Drakensberger), 107 (Afrikaner), and 89 (Tuli) based on available data over a period of 10 years.

Research conducted over more than four decades on a range of breeds, including SA indigenous breeds, estimates genetic parameters, production, and adaptability. Table 3 summarizes studies related to genetic improvement; this is not an exhaustive list, but highlights the interest and traits studied in Afrikaner, Bonsmara, Drakensberger, Nguni, and Tuli breeds.

Table 3. Research studies on aspects of production performance for Afrikaner, Bonsmara, Drakensberger, Nguni, and Tuli cattle breeds.

Research Topic	Breeds Included	Reference
Production performance at Mara Research Station (semiarid subtropics); pure and crossbred performance	Bonsmara, Afrikaner, Hereford, Simmentaler	[48,49]
Variance components and heritability estimates for growth traits, maternal traits	Nguni	[50,51]
Breed performance in developing areas	Nguni, Afrikaner, Bonsmara	[52]
Production and product traits tested under intensive feeding conditions	Bonsmara and Nguni	[53]
Long-term selection experiment—genetic parameters and genotype X environment for calf growth traits	Afrikaner	[54]
Comparison of meat quality traits between Sanga, Sanga-derived and Brahman cattle	Nguni, Tuli, Nguni, Drakensberger, Bonsmara and Brahman	[55,56]
Population structure and genetic trends	Afrikaner, Drakensberger, Nguni and Tuli and Boran	[47]
Genetic relationships between weaning weight and milk yield	Nguni and Bonsmara	[57]
Coat traits associated with tick counts; genetic parameters for tick counts and resistance	Nguni, Afrikaner, Bonsmara and Drakensberger	[58–60]
Effect of bioregion and environmental factors on cow size and reproduction	Bonsmara	[61]
Morphology and physiology of claw quality	Bonsmara	[62]

These breeds are well-established in the developed sector and make a major contribution to beef production and food security in South Africa. The implementation of selection programs in the developing sector, however, is facing multiple challenges particularly because there is often a lack of phenotypic (i.e., performance) and pedigree data. This lack of structured selection programs leads to indiscriminate crossbreeding and potentially the loss of important adaptive traits in breeds such as the Nguni and Tuli.

4. Genetic and Genomic Characterization

Over the last decade, genetic and (more recently) genomic tools have been employed to study the ancestry and genetic diversity of SA cattle populations. Microsatellite data from Afrikaner, Bonsmara, Drakensberger, Nguni, and Tuli populations have been used to show that these populations possess moderate to high levels of genetic diversity. Refs. [32] and [63] both observed high levels of heterozygosity in the SA Nguni population, with expected heterozygosity estimates of 0.70–0.75, estimated with panels of 22 and 25 microsatellite markers, respectively (16 common microsatellites). Ref. [64] supported these findings and reported a heterozygosity level of 0.73 in a reduced panel of 11 microsatellite markers for the SA Nguni. In this study, similarly high diversity levels were reported for the Bonsmara (0.74), Drakensberger (0.74), and Tuli (0.72), but a significantly lower level of genetic diversity for the Afrikaner (0.57).

Studies based on Single Nucleotide Polymorphism (SNP) arrays reported moderate levels of heterozygosity for the Afrikaner (0.22–0.24), Bonsmara (0.36), Drakensberger (0.25–0.35), and Nguni (0.23–0.28) [65–67]. Inbreeding coefficients reported in the same studies were negligible to low for all breeds. These studies indicated sufficient genetic diversity to exploit in breeding programs for genetic improvement. The reliability of these estimates, however, is questionable, given that SNP markers were ascertained in European cattle and therefore are unlikely to capture the true extent of the genetic diversity of African taurine and indicine cattle. A proper characterization of the ancestry, genetic diversity, and levels of inbreeding in indigenous cattle populations will be key to evaluate breeding strategies and improve or conserve this unique genetic resource.

Genome-wide SNP data from South African cattle populations provided new insights into their origin. SNP data from Sanga populations confirmed that these populations were indeed crosses between African taurine and Zebu cattle [68]. Both the Nguni and Afrikaner lineages possessed more African taurine ancestry (60–70%) than indicine ancestry. The Bonsmara and Drakensberger populations consisted of roughly similar amounts of African (42–38%) and European taurine (41–46%) ancestry, as well as a smaller (16–15%) indicine component. Ref. [68] suggested that African Sanga cattle appeared to possess unique indicine ancestry, highly differentiated from that found in modern populations such as Nelore and Brahman.

A small number of studies have also investigated the genetic architecture of adaptive traits in indigenous cattle. Interestingly, ref. [69] did not identify any selection signatures that were shared between the South African indigenous (Afrikaner, Bonsmara, Drakensberger and Nguni) and two *Bos taurus* breeds (Angus and Holstein). The study did, however, identify genes associated with adaptation to tropical environments, such as keratin and heat shock genes, under selection in Nguni cattle and these might contribute to the breed's superior temperature regulation and tick tolerance. Several additional candidate genes involved in reproductive pathways, growth and muscle development, and immune response were detected as being under selection in indigenous breeds. Ref. [70] identified candidate genes under selection in the reproductive and immune response pathways of Nguni cattle using a Copy Number Variation approach. Recently, ref. [71] identified novel polymorphisms in the heat shock protein gene in Nguni crossbreds. These mutations may play a role in the Nguni's superior adaptive characteristics, such as heat tolerance and tick resistance.

These genomic studies on South African indigenous breeds, however, included mostly animals from populations subjected to artificial selection. Thus, the genetic architecture of traits found in local (and often admixed) indigenous populations remains unclear. In fact, there is a general lack of genomic information from populations kept by communal or smallholder farmers, although they represent the majority of cattle in Southern Africa.

5. Capitalizing on Indigenous Breeds as a Genetic Resource

Given their complex evolutionary history, South African cattle populations likely possess a wealth of unique genetic material shaped through long-term natural and artificial selection. The SA local cattle breeds discussed in this review have become established local breeds, which are often found in both developed and developing sectors and hold the advantage of being well-adapted to a range of climatic conditions. Despite the higher production potential of the European types, they are often ill-adapted to African environmental conditions, and will suffer further with climate change [72,73].

South African producers and farmers have capitalized on the adapted traits of local beef cattle populations, and by crossbreeding them with certain European breeds the productivity was improved, while maintaining their resilience. This led to the development of several composites that have evolved using indigenous resources as well as indicine breeds such as the Brahman (Braford and Brangus). The Nguni has been used to develop the Pin2Zyl, a cross between the Pinzgauer and the Nguni (<https://www.zz.co.za/products/livestock>, accessed on 16 February 2021), the Borguni, a cross between the Boran and Nguni, and the Charolais and Afrikaner were have been crossbred to form the Huguenot SA. These composites have the adaptive traits of the indigenous breed and the growth potential required for entering the formal market and recognized as SA composite breeds [45] more, it has been reported that indigenous breeds such as the Nguni have similar carcass quality compared to the European/British breeds; the variation in frame size will determine their suitability for feedlot finishing [56].

South Africa has indigenous resources to utilize for sustainable beef production, but constraints other than genetics are preventing their optimal use in the various production systems. The commercial sector has adopted various technologies to provide the developing sector with the genetics and the means to ensure conservation of adapted

characteristics. In the developing sector, a lack of extension services, financial support to purchase good indigenous genetics, lick supplementation, and infrastructure to weigh cattle all inhibit utilization and improvement of indigenous cattle resources in the smallholder market-oriented sector [7,74,75].

The advent of high throughput DNA sequencing platforms has paved the way for Genomic Selection, a method that uses genome wide information to estimate the genomic breeding value of animals [76]. This technology has revolutionized animal breeding in many parts of the developed world, in both dairy and beef cattle. In the USA, for example, the implementation of large genomic selection programs in dairy cattle have led to a substantial increase in the rate of genetic gain in yield traits of between 50 % and 100% [77]. A major benefit in application of genomic selection in beef cattle breeds is the increase in reliability, especially of traits with low heritability and hard-to-measure traits such as disease resistance. In South Africa, the Beef Genomic Program (BGP) contributed to the establishment of reference populations for a number of beef breeds, including the Nguni, Tuli, Drakensberger, and Bonsmara breeds [78]. The Bonsmara and Drakensberger breeds, which are well-established in the developed sector, have implemented genomic enhanced breeding values in their selection programs [64], while breeds such as the Nguni and Tuli have smaller reference populations with sufficient phenotypic and genotypic information. Limitations for the implementation of genomic selection in the indigenous breeds include the sizes of the reference populations and the lack of pedigrees and performance recordings; these challenges have also been reported for indigenous breeds elsewhere in Africa [79]. The application of this technology in local South African cattle, which are more resilient to local conditions than European and North American breeds, could prove hugely beneficial for the local economy while reducing the environmental burden associated with meat production.

Deploying large genomic selection programs in Southern Africa, however, remains challenging particularly as genotyping can be prohibitively expensive for developing countries. Reliable low-cost genotyping technologies are being developed, including methods using low-density SNP panels and imputation [80]. Enabling these technologies will require sequencing high-quality genomes from South African breeds, to better understand their uniqueness (e.g., potentially map adaptation), characterize genetic diversity, and create large imputation panels [81]. In combination, these new technologies will allow the livestock sector to capitalize on the unique genetic resources available in South Africa and improve the sustainability of local production in a changing world.

6. Conclusions

The uniqueness of the history of South Africa is mirrored in the complex genetic makeup of its indigenous/local cattle populations. Since the 19th century, South African local breeds have been subjected to selection in a well-developed commercial sector and there is evidence of genetic improvement and utilization of adaptive traits. The indigenous populations in the developing sector, however, face pressures of indiscriminate crossbreeding, which results in nondescript cattle populations with limited opportunities to enter the formal market. Despite the availability of favourable traits among the South African breeds, several constraints need to be addressed before these resources can be utilized to their full extent, particularly in the development sector. Future developments of structured breeding programs, and use of genomic selection in the development sector will allow the livestock industry to breed more productive and resilient cattle populations, which will ultimately assist with alleviating poverty and reducing hunger.

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