Tropical Animal Health and Production
https://doi.org/10.1007/s11250-019-02003-z

REGULAR ARTICLES

Genetic variability and relationships in nine South African cattle breeds using microsatellite markers

Lené van der Westhuizen [1,2] · Michael D. MacNeil [1,2,3] · Michiel M. Scholtz [1,2] · Frederick W. C. Neser [2] · Makglako L. Makgahlela [1] · Japie B. van Wyk [2]

Received: 4 January 2019 / Accepted: 4 July 2019
© Springer Nature B.V. 2019

Abstract

Genetic variability within and between breeds allows adaptation to a changing environment and consequently prepares producers for the future. Eleven bovine-specific microsatellite markers were used to genotype animals from each of nine South African cattle breeds: Afrikaner ($N = 550$), Angus ($N = 550$), Bonsmara ($N = 550$), Boran ($N = 321$), Brahman ($N = 550$), Drakensberger ($N = 550$), Nguni ($N = 550$), Simmental ($N = 550$), and Tuli ($N = 311$). These breeds were drawn from *Bos taurus africanus*, *Bos taurus*, and *Bos indicus*. Genetic variability estimates included unbiased heterozygosity, effective number of alleles, and inbreeding. Ranges of these parameters were 0.569–0.741, 8.818–11.455, and − 0.001–0.050, respectively. Breed private allele and breed pairwise comparison was also used to characterize the breeds. The analysis of population structure with $K = 2$ revealed clusters comprised of Sanga-indicine and taurine, while $K = 3$ included separate clusters of Sanga, indicine, and taurine, and with $K = 9$ showed the breeds arising from unique progenitor populations. This study broke new ground in molecular cattle genetic diversity by genotyping a large sample size per breed and using a larger number of breeds compared with similar studies that have been conducted in the recent past which have either used a smaller number of breeds or smaller sample sizes but with a larger number of marker loci. Thus, opportunities that arise to explore genetic diversity and relationships in both the livestock and wildlife industries in Southern Africa may capitalize on microsatellite marker databases which remain cost-effective and accessible due to their extensive use for parentage verification.

Keywords Cattle · Genetic diversity · Sanga · South Africa

Introduction

Cattle play an essential role in the agricultural economy of Southern African countries including South Africa, Namibia, Botswana, Zimbabwe, and Mozambique. Smallholder and communal cattle farming make important contributions to food production and meet social and economic needs (Bettencourt et al. 2013). Indigenous breeds and their taurine and indicine breed crosses predominate the cattle held by smallholder and communal farmers (Mmbengwa et al. 2015). These breeds, among others, are likely to contribute to current or future traits of interest (Notter 1999), and thus, they are considered important for maintaining future breeding options (Groeneveld et al. 2010). Thus, within- and between-breed genetic variation provides an in situ reservoir to ensure that future market demands can be met through selection or breed substitution (FAO 2010).

Today, breeds of cattle that arise from diverse evolutionary histories are resident in South Africa. Indigenous cattle breeds of Southern Africa comprise of Sanga type and their derivatives that originated from eastern and northern Africa (Rege 1999). They are intermediate crosses between African zebu (*B. indicus*) and humpless taurine cattle (*B. taurus*), have cervico-thoracic humps, and are classified as a subspecies *B. taurus africanus* (Meyer 1984; Rege 1999). In South Africa, the breeds of indigenous Sanga cattle include Afrikaner, Nguni, and Drakensberger. Bonsmara is a Sanga-derived, South African-developed, composite breed which also incorporates Hereford and Shorthorn. Along with these

✉ Lené van der Westhuizen
lenevdwest@gmail.com

[1] ARC-Animal Production, Irene 0062, South Africa

[2] University of the Free State, Bloemfontein 9300, South Africa

[3] Delta G, Miles City 59301, USA

Published online: 06 August 2019

breeds, Tuli and Hugenoot are considered to be landrace cattle breeds of Southern Africa. The indigenous cattle breeds of Southern Africa are adapted to survive and reproduce under harsh environments encountered under extensive ranching in South Africa (Mwai et al. 2015).The Angus breed originated in Scotland during the sixteenth century, with the first animals imported into South Africa during the late 1800s (Scholtz 2010). The South African Aberdeen-Angus Cattle Breeders' Society was established in 1917. The Boran is an East African, i.e., Southern Ethiopia and especially Kenya, developed composite breed. The first Boran embryos were brought to South Africa during the late 1900s (Scholtz 2010). The Boran has genetic influences from European *B. taurus* and African *B. taurus* as well as *B. indicus*. Three Indian breeds of cattle, Guzerat, Nellore, and Gir, were imported into the USA and were used in development of the Brahman breed (http://afs.okstate.edu/breeds/cattle/brahman/). Therefore, Brahman specifically refers to the American developed *B. indicus* breed (Scholtz 2010). The breed was introduced into South Africa during 1954. Simmental was developed in Switzerland, descents from the Aurochs (*B. taurus primigenius*) and indigenous to Europe. The first Simmental animals arrived in South African during 1905 (Scholtz 2010).

Adaptive genetic responses to natural selection may also assist in addressing future challenges such as decreased population size and the consequent increases in inbreeding and climate change which may otherwise threaten indigenous breeds and more broadly agricultural production (Chagunda and Wollny 2003). Challenges created by climate change may include increased surface temperatures, increased drought, and increased frequency of heat stress all of which may negatively affect the productivity of cattle (IPCC 2007). Current adaption of the indigenous breeds to heat and drought may well prove advantageous for future cattle production in South Africa as the projected climatic conditions become hotter and dryer (Maúre et al. 2018).

Historical parentage databases have used microsatellite markers of relatively few loci to validate parentage and forensics and to trace and authenticate meat products for large number of animals (ICAR 2018). In Southern Africa, these markers have been cost-effective for routine use in both livestock (van Marle-Köster and Visser 2017) and wildlife industries (van der Westhuizen et al. 2016). Using relatively few microsatellite markers, Greyling et al. (2008), Pienaar et al. (2018), and Sanarana et al. (2016) characterized contemporary South African populations of Bonsmara, Afrikaner, and Nguni, respectively. Gororo et al. (2018) similarly characterized within and between breed diversity of the Mashona, Nkone, and Tuli breeds from Zimbabwe. Recently, assessments of within- and between-breed genetic variation have used many more SNP markers, albeit with relatively few animals (Makina et al. 2014; Makina et al. 2016). However, comprehensive simultaneous genomic characterization of the landrace and indigenous breeds of cattle from South Africa is virtually lacking from the literature. Thus, the present study obtained data from historical parentage databases, which allowed for use of substantially larger numbers of animals per breed compared with previous investigations, to ascertain within- and between-breed genetic variation and estimate relationships among *B. indicus*, *B. taurus*, *B. taurus africanus* (Sanga), and Sanga-derived South African cattle.

Materials and methods

The present study used existing microsatellite marker databases provided by Breeders' Societies to estimate levels of within breed variability and quantify the genetic relationships between nine cattle breeds of South Africa. All animals (typically seed stock animals, thus representative of each breed) were genotyped by the Animal Genetics Laboratory of the Agricultural Research Council at Irene in response to requests from the industry for parentage verification. Animals were randomly chosen (without prior knowledge of herd name, geographical locations or age) from those available that had no more than two loci with a missing genotype. Eleven bovine-specific microsatellite markers recommended by the International Society of Animal Genetics (ISAG) were used to genotype three Sanga (Afrikaner (AFR, $N = 550$), Drakensberger (DRA, $N = 550$), Nguni (NGU, $N = 550$)), one Zimbabwean landrace (Tuli (TUL, $N = 511$)), one composite (Bonsmara (BON, $N = 550$)), two European taurine (Angus (ANG, $N = 550$) and Simmental (SIM, $N = 550$)), and two indicine (Brahman (BRA, $N = 550$) and Boran (BOR, $N = 321$)) breeds. The microsatellite marker panel was comprised of 11 loci: BM1824, BM2113, SPS115, ETH3, ETH10, ETH225, INRA23, TGLA53, TGLA122, TGLA126, and TGLA127 (Table 1). A direct polymerase chain reaction (PCR) technique was used for genotyping. Hair follicles from each animal were cut into an individual 0.2-mL PCR tube. PCR mixtures contained 1.0 μL of primer mix, 3.67 μL deionized water, 0.18 μL Tween, 0.75 μL dNTPs, 1.50 μL Supertherm Gold reaction buffer (20 mM Tris-HCl pH 8.3, 15 mM MgCl2, 50 mM KCl), and 0.4 μL Supertherm Gold DNA polymerase (5 U/μL) (total volume 7.5 μL). Reaction conditions consisted of a 10-min Hot Start® polymerase activation step at 95 °C, followed by 33 cycles each of 45-s denaturation at 94 °C, 90-s annealing at 61 °C, 60-s extension at 72 °C, and a final extension step at 72 °C for 60 min. Samples were analyzed with a 3130xl Genetic Analyzer, and the resulting genotypes were scored using GeneMapper® Software, version 4.0 (Applied Biosystems, Foster City, CA, USA).

Genetic diversity within breeds expressed as unbiased heterozygosity (H_z) (Nei 1987) and mean number of alleles

Table 1 Microsatellite loci used, primer sequences (5′ to 3′), chromosome number, detected allele size range, annealing temperature, and references

Marker name	Primer sequences (forward and reverse)	Chromosome number	Size range (bp)	Annealing temperature (°C)	Reference
BM1824	F: GAGCAAGGTGTTTTTCCAATC R: CATTCTCCAACTGCTTCCTTG	1	170–218	58	Barendse et al. (1994)
BM2113	F: GCTGCCTTCTACCAAATACCC R: CTTCCTGAGAGAAGCAACACC	2	116–146	55	Sunden et al. (1993)
ETH10	F: GTTCAGGACTGGCCCTGCTAACA R: CCTCCAGCCCACTTTCTCTTCTC	5	198–234	58	Solinas-Tolda et al. (1993)
INRA23	F: GAGTAGAGCTACAAGATAAACTTC R: TAACTACAGGGTGTTAGATGAACTC	3	193–235	55	Vaiman et al. (1994)
SPS115	F: AAAGTGACACAACAGCTTCACCAG R: AACCGAGTGTCCTAGTTTGGCTGTG	15	235–265	55	Baylor College of Medicine (2006)
TGLA53	F: GCTTTCAGAAATAGTTTGCATTCA R: ATCTTCACATGATATTACAGCAGA	16	147–197	58	Georges and Massey (1992)
TGLA122	F: AATCACATGGCAAATAAGTACATAC R: CCCTCCTCCAGGTAAATCAGC	21	134–193	58	Georges and Massey (1992)
TGLA126	F: CTAATTTAGAATGAGAGAGGCTTCT R: TTGGTCCTCTATTCTCTGAATATTCC	20	104–131	55	Georges and Massey (1992)
TGLA227	F: GGAATTCCAAATCTGTTAATTTGCT R: ACAGACAGAAACTCAATGAAAGCA	18	64–115	55	Georges and Massey (1992)
ETH3	F: GAACCTGCCTCTCCTGCATTGG R: ACTCTGCCTGTGGCCAAGTAGG	19	90–135	57	Solinas-Tolda et al. (1993)
ETH225	F: GATCACCTTGCCACTATTTCCT R: ACATGACAGCCAGCTGCTACT	9	136–165	64	Steffen et al. (1993)

(MNA) per locus, and breed private alleles were calculated with the use of Microsatellite-Toolkit (MSToolkit) from Excel (Park 2001). MSToolkit was used to generate input files for several statistical programs such as ARLEQUIN (Excoffier et al. 2005), FSTAT (Goudet 2002), and STRUCTURE (Pritchard et al. 2000). FSTAT (Goudet 2002) was used for the calculation of unbiased *F*-statistics (Weir and Cockerham 1984). Genetic differentiation was also inferred from F_{ST} values calculated by FSTAT software. Significant deviations from the hypothesis of zero differentiation at a level of $p > 0.05$ were also determined.

To describe the genetic structure and genetic relationships between breeds, a Bayesian multi-locus clustering algorithm for association mapping (Pritchard et al. 2000) was implemented using STRUCTURE software (Pritchard et al. 2000). Individuals were assigned to $K = 1$–10 clusters, and admixture proportions of individuals were estimated. The analysis consisted of 15 replicate runs with all runs consisting of a burn-in period of 100,000 Markov Chain Monte Carlo (MCMC) iterations followed by an additional 200,000 MCMC iterations from which the results were extracted. Structure Harvester v0.6.93 (Earl and von Holdt 2012) was chosen as the software to determine the most accurate number of clusters using Delta*K* (ΔK) (Evanno et al. 2005). Furthermore, results from STRUCTURE (Pritchard et al. 2000) were plotted using STRUCTURE PLOT v2.0 software (Ramasamy et al. 2014).

Nei's Da genetic distances (Nei 1987) between the breeds were estimated with the use of TreeFit (Kalinowski 2009). TreeFit was also used to generate a distance matrix to summarize the data that was subsequently used to construct an unrooted neighbor-joining (NJ) tree using MEGA6 software (Tamura et al. 2013).

Results

Across the 11 loci used herein, within-breed variation was described by H_z, MNA, R_s, F_{IS}, and breed private alleles (Table 2). From a genetic diversity perspective, all breeds had large numbers of alleles at each locus and high frequencies of heterozygous genotypes. Afrikaner consistently showed the lowest estimates of H_z (0.569), MNA (8.818), and R_s (7.646), while H_z was the greatest in Bonsmara (0.741), MNA greatest in Angus (11.455), and R_s greatest in Nguni (10.326). Simmental had the highest number of private alleles (i.e., alleles that are unique to only one breed), while Afrikaner and Bonsmara did not have any private alleles.

Simmental had the only negative estimate of F_{IS} (− 0.001) which indicated a slight excess of heterozygous animals relative to expectation. Drakensberger and Boran had low positive estimates of F_{IS} (0.005) which indicated a slight excess of homozygous animals, while Brahman had the greatest estimate of F_{IS} (0.050) which indicated a slight degree of

inbreeding. Estimated F_{IS} statistics for the remaining breeds were intermediate between the Drakensberger or Boran and Brahman.

Multi-locus clustering indicated that portioning the breeds into two groups ($K = 2$) was the most likely description of ancestral structure. The progenitor of the two taurine breeds, Angus and Simmental, was clearly distinct from that of the Afrikaner, Brahman, Boran, Nguni, and Tuli breeds (Fig. 1 and Table 3). With $K = 2$, Drakensberger and Bonsmara were admixed with probabilities of membership in the taurine cluster of 37% and 54%, respectively.

The second most likely number of progenitor populations was three ($K = 3$), with the taurine, indicine, and Sanga breeds grouped separately (Fig. 1 and Table 4). With $K = 3$, the multi-locus clustering algorithm again showed Angus and Simmental to arise from one progenitor population and identified Brahman as arising from a second substantially unique progenitor. The *B. taurus africanus* Afrikaner and Tuli breeds were clearly members of a third multi-locus cluster in which the other Sanga-derived breeds were most likely also to be members. However, various levels of admixture were also indicated for them.

A priori, the hypothesis that each breed arose from a unique ancestry (i.e., $K = 9$) was of interest. Multi-locus clustering with the number of hypothesized progenitor groups equated to the number of breeds illustrated both breed individuality and various degrees of admixture (Fig. 1 and Table 5). Here, the Nguni had a 31% probability of membership in one of the other eight clusters besides the cluster which was its most likely progenitor population. For both Bonsmara and Drakensberger, their probability of membership in another of the eight clusters was 24%. Conversely, Angus and Simmental most likely descended from unique progenitors with probabilities of approximately 90%.

Pairwise estimates of genetic differentiation among breeds (F_{ST} and Nei's genetic distance (Da)) both indicated the greatest divergence between Afrikaner and the *B. taurus* breeds (Table 6). Nguni and Tuli were most closely related.

Discussion

Microsatellite marker data drawn from an extensive database that has been accumulated over time in validating parentage of seed stock animals was used to characterize nine *B. indicus*, *B. taurus*, and *B. taurus africanus* beef breeds. The obvious differences between this study and other research with nominally similar objectives (Makina et al. 2014, 2016; Zwane et al. 2016) include the substantially greater numbers of animals sampled in the present study and the far greater number of markers used in the latter studies. However, MacHugh et al. (1998) has shown the effectiveness of using only eight microsatellite loci, by assigning genotypes representative of breeds including Angus, Hereford, Jersey, Kerry, and Simmental with > 99% accuracy. Further, Pritchard et al. (2000) demonstrated that population structure could be accurately inferred using modest numbers of loci, e.g., seven microsatellite loci in an example using genotype data from an endangered bird species. In comparison with the present results, fewer alleles per locus were observed in previous studies which genotyped microsatellite loci in Angus and Simmental (MacNeil et al. 2017), Nguni (Sanarana et al. 2016), Bonsmara, (Greyling et al. 2008), and Tuli (Gororo et al. 2018) cattle. Levels of heterozygosity also tended to be less, although not as markedly, with the smaller numbers of animals being genotyped in the aforementioned studies. In sampling over 2-fold more Afrikaner cattle, Pienaar et al. (2018) observed greater numbers of alleles per locus than were found here.

Increasing the number of animals representing each of the breeds was expected to provide greater opportunity to detect rare alleles and genotypes (Crossa 1989). However, statistical power also may be increased either adding loci or selecting more polymorphic loci (Selkoe and Toonen 2006). Without increasing sample size, using more polymorphic loci can inflate the experimental error (Kalinowski 2005). Ascertainment bias that results from marker discovery largely in *B. taurus* (Matukumalli et al. 2009) may result in diversity and genetic relationships being underestimated (FAO 2010).

Table 2 Genetic variability estimates (mean ± SD) of nine beef cattle breeds in South Africa. The parameters included unbiased heterozygosity (H_z), mean number of alleles (MNA), allelic richness (R_s), within breed inbreeding (F_{IS}), and number of breed private alleles (PA)

Breed	Abbr.	N	$H_z \pm$ SD	MNA ± SD	$R_s \pm$ SD	F_{IS}	PA
Afrikaner	AFR	550	0.569 ± 0.055	8.818 ± 2.639	7.646 ± 2.177	0.013	0
Angus	ANG	550	0.703 ± 0.022	11.455 ± 3.417	9.552 ± 2.524	0.028	7
Bonsmara	BON	550	0.741 ± 0.039	10.273 ± 2.901	9.489 ± 2.783	0.025	0
Boran	BOR	321	0.696 ± 0.033	9.000 ± 2.490	8.536 ± 2.301	0.005	3
Brahman	BRA	550	0.707 ± 0.036	11.091 ± 3.506	10.170 ± 3.422	0.050	6
Drakensberger	DRA	550	0.740 ± 0.036	10.636 ± 3.171	9.927 ± 2.765	0.005	3
Nguni	NGU	550	0.731 ± 0.041	11.182 ± 3.371	10.326 ± 3.260	0.024	5
Simmental	SIM	550	0.712 ± 0.028	10.909 ± 3.534	9.374 ± 3.176	− 0.001	9
Tuli	TUL	511	0.720 ± 0.028	11.000 ± 3.435	9.662 ± 2.644	0.020	2

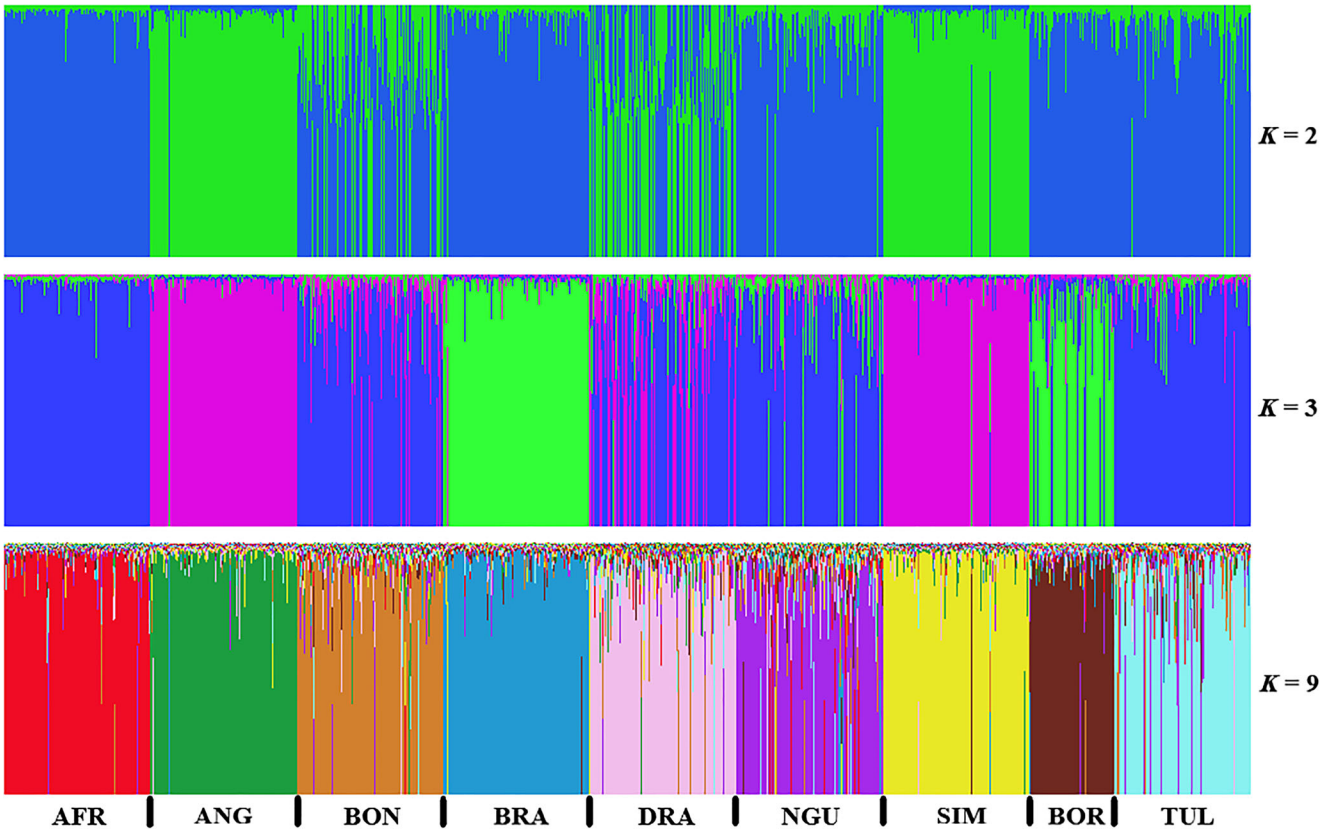

Fig. 1 STRUCTURE bar plots of proportions of genetic membership identified within clusters where $K = 2$, $K = 3$, and $K = 9$. Each animal is represented by a vertical line

Inbreeding effects on fitness and an accompanying loss of evolutionary potential are of concern for many breeds of livestock (Kristensen et al. 2015). Waples (2015) describes how positive values of F_{IS} indicate heterozygote deficiency and a corresponding excess of homozygous individuals or inbreeding. Here, the F_{IS} values were near zero as has been previously observed for Afrikaner (Makina et al. 2014; Pienaar et al. 2018), Angus (Makina et al. 2014; MacNeil et al. 2017), Bonsmara (Greyling et al. 2008; Makina et al. 2014), Brahman (Gómez et al. 2013), Drakensberger (Makina et al. 2014), Nguni (Makina et al. 2014), and Simmental cattle (MacNeil et al. 2017) cattle. This finding appears robust to the variations in numbers of markers and animals as Makina et al. (2014) used 50k SNP data for genotyping approximately 50 animals from each Sanga breed. Both the present study and Makina et al. (2014) indicate lower levels of H_z in Afrikaner in comparison with other *B. taurus* and *B. taurus africanus* beef breeds. Contributing

Table 3 Proportion of membership of each breed to two identified clusters ($K = 2$)

Breed	Inferred clusters	
	1	2
AFR	0.958	0.042
BOR	0.929	0.071
BRA	0.928	0.072
NGU	0.881	0.119
TUL	0.868	0.132
BON	0.635	0.365
DRA	0.462	0.538
ANG	0.044	0.956
SIM	0.045	0.955

Table 4 Proportion of membership of each breed to three identified clusters ($K = 3$)

Breed	Inferred clusters		
	1	2	3
AFR	0.959	0.027	0.014
TUL	0.910	0.040	0.050
NGU	0.814	0.129	0.057
BON	0.775	0.041	0.185
DRA	0.562	0.077	0.361
BRA	0.023	0.947	0.030
BOR	0.181	0.780	0.039
SIM	0.023	0.016	0.961
ANG	0.021	0.019	0.961

Table 5 Proportion of membership of the analyzed South African beef cattle breeds in each of the nine clusters ($K = 9$)

Predefined populations	Inferred clusters								
	1	2	3	4	5	6	7	8	9
AFR	0.009	0.016	0.009	0.015	0.007	0.031	0.011	0.026	0.877
ANG	0.012	0.015	0.908	0.009	0.026	0.008	0.005	0.012	0.005
BON	0.013	0.033	0.031	0.036	0.024	0.040	0.019	0.760	0.044
BOR	0.028	0.013	0.010	0.015	0.008	0.022	0.880	0.012	0.012
BRA	0.897	0.012	0.010	0.009	0.015	0.014	0.020	0.014	0.009
DRA	0.013	0.761	0.033	0.033	0.023	0.047	0.023	0.047	0.020
NGU	0.030	0.044	0.018	0.051	0.016	0.694	0.042	0.040	0.064
SIM	0.006	0.020	0.037	0.011	0.894	0.010	0.007	0.010	0.006
TUL	0.013	0.020	0.016	0.774	0.014	0.072	0.023	0.048	0.020

to this observation may be the potential, but small, bottleneck in the evolutionary history of the Afrikaner population (Pienaar et al. 2015). Thus, in concurrence with the previously referenced studies and Pekkala et al. (2014), levels of inbreeding found herein are unlikely to be problematic for any of the breeds that were studied.

Estimated genetic distances were least within the *B. indicus*, *B. taurus*, and *B. taurus africanus* groups of breeds. The genetic distances among breeds were illustrated by using Nei's genetic distance to construct an NJ tree wherein the indicine and taurine breeds are clearly separated from each other with the *B. taurus africanus* breeds being intermediate (Fig. 2). The lowest F_{ST} existed between Nguni and Tuli. The Nguni migrated southward along the eastern part of Southern Africa where Tuli was especially prevalent in Zimbabwe (Scholtz 2010; Pienaar et al. 2016). Also closely related in the present study, Nguni and Afrikaner cattle were previously observed on the gradient between the indicine and African taurine breeds, and nearer to the taurine (Makina et al. 2016). Not surprisingly, the Bonsmara is shown to be closely related to its Afrikaner progenitor as well as the taurine breeds, results which are consistent with its development as a composite of 5/8 Afrikaner, 3/16 Shorthorn, and 3/16 Hereford (http://www.bonsmara.co.za). Origins of the Drakensberger breed are unknown (Scholtz 2010), with Makina et al. (2016) suggesting ancestry that is 46% *B. taurus*, 38% *B. taurus africanus*, and 15% *B. indicus*. In addition to the analysis of population structure, the genetic distance estimates support the speculation that the *B. taurus africanus* breeds may be more closely related to *B. indicus* breeds than to European *B. taurus*.

This study found it feasible to assess genetic diversity by capitalizing on microsatellite marker databases which remain cost-effective and accessible due to their continued use for parentage verification in South Africa. Such databases facilitate use of large numbers of animals in these assessments, although with a relatively small number of markers. Breeds whose molecular phylogeny indicates a substantial separation from other breeds are likely to have developed unique features arising from specific alleles and/or particular epistatic combinations (Felius et al. 2015). Among the breeds that are indigenous to South Africa, the Afrikaner appears to most closely satisfy this criterion.

Table 6 Breed pairwise estimates of genetic differentiation (F_{ST}, below diagonal) and Nei's genetic distance (Da, above diagonal) measures between Southern African Sanga and exotic cattle breeds

Breed	AFR	ANG	BON	BOR	BRA	DRA	NGU	SIM	TUL
AFR	–	0.389	0.140	0.225	0.296	0.213	0.117	0.412	0.172
ANG	0.229	–	0.196	0.348	0.379	0.170	0.257	0.138	0.275
BON	0.095	0.106	–	0.182	0.237	0.108	0.090	0.217	0.108
BOR	0.153	0.173	0.103	–	0.154	0.185	0.126	0.372	0.184
BRA	0.198	0.196	0.139	0.082	–	0.247	0.179	0.369	0.272
DRA	0.140	0.083	0.062	0.093	0.135	–	0.099	0.192	0.140
NGU	0.075	0.128	0.047	0.067	0.108	0.048	–	0.275	0.086
SIM	0.229	0.071	0.110	0.174	0.191	0.076	0.127	–	0.292
TUL	0.117	0.143	0.055	0.100	0.150	0.071	0.034	0.136	–

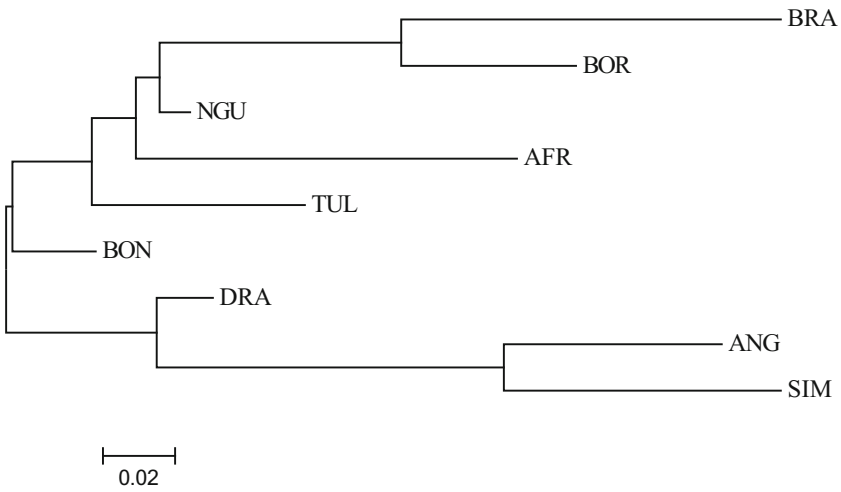

Fig. 2 Neighbor-joining tree depicting the genetic distances between nine Southern African landrace and exotic beef cattle breeds

Acknowledgments The authors acknowledge the work done by the ARC Animal Genetics Laboratory at the Animal Production for the genotypes. The authors also thank Eddington Gororo, Chinhoyi University of Technology, for a thoughtful and comprehensive review of an earlier version of this paper.

Funding information Funding for the research was provided by Red Meat Research and Development, South Africa (RMRD-SA).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Barendse, W., Armitage, S.M., Kossarek, L.M., Shalom, A., Kirkpatrick, B.W., Ryan, A.M., Clayton, D., Li, L., Neibergs, H.L. and Zhang, N., 1994. A genetic linkage map of the bovine genome, Nature Genetics, 6, 227–235.

Baylor College of Medicine Human Genome Sequencing Center., 2006. Bovine Whole Genome Assembly release Btau_3.1, http//www.hgsc.bcm.tmc.edu/projects/bovine/.

Bettencourt, E.M.V., Tilman, M., Henriques, P.D.D.S., Narciso, V. and Carvalho, M.L.D.S., 2013. The economic and socio-cultural role of livestock in the wellbeing of rural communities of Timor-Leste, CEFAGE-UE Working Paper 2013/01, 1–18.

Chagunda, M.G.G. and Wollny, C.B.A., 2003. Conserving and managing the biodiversity of Malawian farm animal genetic resources: A case of Malawi zebu cattle. In: Abdi-Khalil, E. (ed.). The dynamics of food production systems and adoption of technologies in a village economy, (University of Malawi, Malawi).

Crossa, J., 1989. Methodologies for estimating the sample size required for genetic conservation of outbreeding crops, Theoretical and Applied Genetics, 77, 153–161.

Earl, D.A. and vonHoldt, B.M., 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method, Conservation Genetics Resources, 4, 359–361, (http://taylor0.biology.ucla.edu/structureHarvester/).

Evanno, G., Regnaut, S. and Goudet, J., 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study, Molecular Ecology, 14, 2611–2620.

Excoffier, L., Laval, G. and Schneider, S., 2005. Arlequin, version 3.5: an integrated software package for Population Genetics Data Analysis, Evolutionary bioinformatics online, 1, 47, (http://cmpg.unibe.ch/software/arlequin3).

FAO., 2010. Progress report of the FAO on selected activities related to agricultural biodiversity, http://www.fao.org/docrep/meeting/018/k5700e.pdf.

Felius, M., Theunissen, B. and Lenstra, J.A., 2015. Conservation of cattle genetic resources: the role of breeds, Journal of Agricultural Science, 153, 152–162.

Georges, M. and Massey, J., 1992. Polymorphic DNA markers in Bovidae: World Intellectual Property Organization, Geneva, Patent application WO PUBL NO 92/13102).

Gómez, Y.M., Fernández, M., Rivera, D., Gómez, G. and Bernal, J.E., 2013, Genetic characterization of Colombian Brahman cattle using microsatellites markers, Russian Journal of Genetics, 49, 737–745.

Gororo, E., Makuza, S.M., Chatiza, F.P., Chidzwondo, F. and Sanyika, T.W., 2018. Genetic diversity in Zimbabwean Sanga cattle breeds using microsatellite markers, South African Journal of Animal Science, 48, 128–141.

Goudet, J., 2002. FSTAT, a program to estimate and test gene diversities and fixation indices version 2.9.3.2, (http://www2.unil.ch/popgen/softwares/fstat.htm).

Greyling, B.J., Kryger, P., du Plessis, S., van Hooft, W.F., van Helden, P., Getz, W.M. and Bastos, A.D.S., 2008. Development of a high-throughput microsatellite typing approach for forensic and population genetic analysis of wild and domestic African Bovini, African Journal of Biotechnology, 7, 655–660.

Groeneveld, L.F., Lenstra, J.A., Eding, H., Toro, M.A., Scherf, B., Pilling, D., Negrini, R., Finlay, E.K., Jianlin, H., Groeneveld, E., Weigend, S. and GLOBALDIV Consortium., 2010. Genetic diversity in farm animals – a review, Animal Genetics, 41(S1), 6–31.

ICAR., 2018. Section 4 - Guidelines for DNA Technology, In: ICAR Guidelines, https://www.icar.org/index.php/icar-recording-guidelines/.

IPCC., 2007. Climate change: impacts, adaptation and vulnerability, Summary for Policy Makers, http://www.ipcc.cg/SPM13ap07.pdf.

Kalinowski, S.T., 2005. Do polymorphic loci require large sample sizes to estimate genetic distances?, Heredity, 94, 33–36.

Kalinowski, S.T., 2009. How well do evolutionary trees describe genetic relationships between populations?, Heredity, 102, 506–513.

Kristensen, T.N., Pertoldi, A.A.C. and Stronen, A.V., 2015. What can livestock breeders learn from conservation genetics and *vice versa*? Frontiers in Genetics, 6, 38.

MacHugh, D.E., Loftus, R.T., Cunningham, P. and Bradley, D.G., 1998. Genetic structure of seven European cattle breeds assessed using 20 microsatellite markers, Animal Genetics, 29, 333–340.

MacNeil, M.D., Alexander, L.J., Kantanen, J., Ammosov, I.A., Ivanova, Z.I., Popov, R.G., Ozerov, M., Millbrooke, A. and Cronin, M.A., 2017. Potential emigration of Siberian cattle germplasm on Chirikof Island, Alaska, Journal of Genetics, 96, 47–51.

Makina, S.O., Muchadeyi, F.C., van Marle-Köster, E., MacNeil, M.D. and Maiwashe, A., 2014., Genetic diversity and population structure among six cattle breeds in South Africa using a whole genome SNP panel, Frontiers in Genetics, 5, 33.

Makina, S.O., Whitacre, L.K., Decker, J.E., Taylor, J.F., MacNeil, M.D., Scholtz, M.M., Muchadeyi, F.C., van Marle-Köster, E., Makgahlela, M.L. and Maiwashe A., 2016. Insight into the genetic composition of South African Sanga cattle using dense SNP data from cattle breeds worldwide, Genetics Selection Evolution, 48, 88.

Matukumalli, L.K., Lawley, C.T., Schnabel, R.D., Taylor, J.F., Allan, M.F., Heaton, M.P., O'Connell, J., Moore, S.S., Smith, T.P., Sonstegard, T.S. and Van Tassell, C.P., 2009. Development and characterization of a high density SNP genotyping assay for cattle, PLoS ONE 4, e5350.

Maúre, G., Pinto, I., Ndebele-Murisa, M., Muthige, M., Lennard, C., Nikulin, G., Dosio, A. and Meque, A., 2018. The southern African climate under 1.5 °C and 2 °C of global warming as simulated by CORDEX regional climate models, Environmental Research Letters, 13, 065002.

Meyer, E.H.H., 1984. Chromosomal and biochemical genetic markers of cattle breeds in Southern Africa, Proceedings of the 2nd World Congress on Sheep and Beef Cattle Breeding, Pretoria, South Africa, 328–339.

Mmbengwa, V., Nyhodo, B., Myeki, L., Ngethu, X. and van Schalkwyk, H., 2015. Communal livestock farming in South Africa: Does this farming system create jobs for poverty stricken rural areas? SYLWAN, 159, 176–192.

Mwai, O., Hanotte, O., Kwon Y-J. and Cho, S., 2015. African indigenous cattle: Unique genetic resources in a rapidly changing world, Asian-Australasian Journal of Animal Sciences, 28, 911–921.

Nei, M., 1987. Molecular Evolutionary Genetics, (Columbia University Press, New York).

Notter, D., 1999. The importance of genetic diversity in livestock populations of the future. Journal of Animal Science, 77, 61–69.

Park, S.D.E., 2001. Trypanotolerance in West African cattle and the population genetic effects of selection, (PhD thesis, Trinity College, University of Dublin).

Pekkala, N., Knott, K.E., Kotiaho, J.S., Nissinen, K. and Puurtinen, M., 2014. The effect of inbreeding rate on fitness, inbreeding depression and heterosis over a range of inbreeding coefficients, Evolutionary Applications, 7, 1107–1119.

Pienaar, L., Neser, F.W.C., Grobler, J.P., Scholtz, M.M. and MacNeil, M.D., 2015. Pedigree analysis of the Afrikaner cattle breed, Animal Genetic Resources, 57, 51–56.

Pienaar, L., Scholtz, M.M., Makina, S.O. and Neser, F.W.C., 2016. History and origin of the Afrikaner cattle. In: Scholtz, M.M., Neser, F.W.C. and Tissier, L (eds). The Afrikaner breed of cattle: South Africa's heritage for food security, (Agricultural Research Council, Pretoria).

Pienaar, L., Grobler, J.P., Scholtz, M.M., Swart, H., Ehlers, K., Marx, M., MacNeil, M.D. and Neser, F.W.C., 2018. Genetic diversity of the Afrikaner cattle breed, Tropical Animal Health and Production, 50, 399–404.

Pritchard, J.K., Stephens, M., Rosenberg, N.A. and Donnelly, P., 2000. Association mapping in structured populations, American Journal of Human Genetics, 67, 170–181.

Ramasamy, R.K., Ramasamy, S., Bindroo, B.B. and Naik, V.G., 2014. STRUCTURE PLOT: a program for drawing elegant STRUCTURE bar plots in user friendly interface, SpringerPlus, 3, 431.

Rege, J.E.O., 1999. The state of African cattle genetic resources. I. Classification framework and identification of threatened and extinct breeds, Animal Genetic Resources Information, 25, 1–25.

Sanarana, Y., Visser, C., Bosman, L., Nephawe, K., Maiwashe, A. and van Marle-Köster, E., 2016. Genetic diversity in South African Nguni cattle ecotypes based on microsatellite markers, Tropical Animal Health and Production, 48, 379–385.

Scholtz, M.M., 2010. Beef Breeding in South Africa, (Agricultural Research Council, Pretoria).

Selkoe, K.A. and Toonen, R.J., 2006. Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers, Ecology Letters, 9, 615–629.

Solinas-Tolda, S., Fries, R., Steffen, P., Neibergs, H.L., Barendse, W., Womack, J.E., Hetzel, D.J.S. and Stranzinger, G., 1993. Physically mapped, cosmid-derived microsatellite markers as anchor loci on bovine chromosomes, Mammalian Genome, 4, 720–727.

Steffen, P., Eggen, A., Dietz, A.B., Womack, J.E., Stranzinger, G. and Fries, R., 1993. Isolation and mapping of polymorphic microsatellites in cattle, Animal Genetics, 24, 121–124.

Sunden, S.L., Stone, R.T., Bishop, M.D., Kappes, S.M., Keele, J.W. and Beattie, C.W., 1993. A highly polymorphic bovine microsatellite locus: BM2113, Animal Genetics, 24, 69.

Tamura, K., Stecher, G., Peterson, D., Filipski, A. and Kumar, A., 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0, Molecular Biology and Evolution, 30, 2725–2729.

Vaiman, D., Mercier, D., Moazami-Goudarzi, K., Eggen, A., Ciampolini, R., Lépingle, A., Velmala, R., Kaukinen, J., Varvio, S.L., Martin, P., Leveziel, H. and Guerin, G., 1994. A set of 99 cattle microsatellites: characterization, synteny mapping, and polymorphism, Mammalian Genome, 5, 288–297.

van der Westhuizen, L., Neser, F.W.C. and Louw, R., 2016. Genetic variability of Cape buffalo populations in South Africa, 9th International Wildlife Ranching Symposium (IWRS) & IUCN 2nd African Buffalo Symposium, Windhoek.

van Marle-Köster, E. and Visser, C., 2017. Genomics for the advancement of livestock production: A South African perspective, South African Journal of Animal Science 48, 808–817.

Waples, R.S., 2015. Testing for Hardy-Weinberg proportions: Have we lost the plot? Journal of Heredity, 106, 1–19.

Weir, B.S. and Cockerham, C.C., 1984. Estimating F-Statistics for the analysis of population structure, Evolution, 38, 1358–1370.

Zwane, A.A., Maiwashe, A., Makgahlela, M.L., Choudhury, A., Taylor, J.F. and van Marle-Köster, E., 2016. Genome-wide identification of breed-informative single-nucleotide polymorphisms in three South African indigenous cattle breeds, South African Journal of Animal Science, 46, 302–312.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.