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Genetics underlying phenotypic diversity in South African sheep breeds

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ABSTRACT

This study investigates genetic diversity and morphological trait-associated genes in 897 genotyped animals from 14 African sheep breeds. The breeds include Blackhead Persian (BHP), Damara (DAM), Dorper (DOR), Fat-tail (FTT), Karakul (KAR), Meatmaster (MMR), Merino (MER), Namakwa Afrikaner (NAM), Pedi (PED), White Dorper (WDOR), Zulu (ZUL), Ethiopian Menz (EMZ), Ronderib Afrikaner (RDA), and Red Massai (RMA), with the latter three obtained from the WIDDE platform. Results showed lowest genomic heterozygosity in ZUL (0.308) and highest in MER (0.352). PCA analysis based on genome-wide SNPs revealed clustering mostly according to pre-defined populations. Morphological traits were analysed using pairwise F_{ST} values and overlapping ROH for tail length, fibre type, coat colour, and horn presence. Coat colour-related genes (*ASIP*, *MC1R*, *TYRP1*) were near regions with the highest F_{ST} values. In the horned phenotype population, overlapping ROH was found near the *HOXD1* gene, linked to horn development. For hair phenotypes, two keratin-associated genes (*KRTAP6–1*, *LOC101104027)*, and *FGF5*, which regulates the hair cycle, were identified. The wool phenotype featured *DLX3*, related to wool quality. Five genes associated with tail growth were identified in the fat-tailed phenotype populations, including *PDGFD*, identified in both F_{ST} analyses of long and short fat-tailed phenotypes. High differentiation at the *BMP2* gene that is linked to tail fat deposition was noted between long fat-tailed and thin-tailed phenotypes. Using SNP genotypes, we clarified the phylogenetic relationships between various indigenous and locally developed sheep breeds and confirmed the conservation of certain genomic areas associated with morphological traits in local populations.

1. Introduction

The domestication process of livestock species includes different evolutionary events, such as inbreeding, genetic drift, natural selection, and artificial selection (Mignon-Grasteau et al., 2005). This has resulted in over one thousand breeds of sheep being recognised worldwide (FAO, 2022), showing a wide range of phenotypes and substantial differences between both production and type traits (Grasso et al., 2014).

Modern sheep breeds were developed through centuries of artificial selection, as well as natural selection. Varying environmental conditions and cultures resulted in the selection of specific breeds in certain areas (Erhardt and Weimann, 2007). Morphological traits that can vary widely among breeds include tails, horns, coat colour and fleece type. In harsh environments, some sheep breeds developed large-fat tails as an energy reserve (Moradi et al., 2012), while the thin-tail phenotype is generally more desirable for commercial producers owing to the negative impacts of fat-tails on locomotion, food conversion and mating (Orihuela and Ungerfeld, 2019). Large horns have historically been important for defence against predators and during mating competition, however, hornless, or polled phenotypes are increasingly desired by producers to minimise injuries to handlers and animals (Johnston et al., 2011). Furthermore, coat colour serves a purpose in protection from predators by allowing prey to blend in with their environment (Sponenberg et al., 1997), while specific production systems desire appropriate colour patterns, such as white wool being preferable for most wool producing breeds (Koseniuk et al., 2018).

Archaeological evidence suggests that sheep first migrated to southern Africa about 2000 years ago. The fat-tailed indigenous breeds that travelled south with the Khoi, Bapedi, and Nguni peoples include the Damara, Namaqua Afrikaner, Ronderib Afrikaner, Pedi, Swazi, and Zulu sheep. Among these, the fat-tailed Namaqua Afrikaner is one of the oldest sheep breeds found in the region (Cloete et al., 2014), while the Damara breed, which originated in Eastern Asia and Egypt, was introduced to South Africa around 2000 years ago (Soma et al., 2012). South

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African Persian breeds, believed to have originated from Somalia or Saudi Arabia, have been present in South Africa for several centuries (Soma et al., 2012). The Blackhead Persian, a small-framed, fat-tailed sheep from Somalia, was imported to South Africa in 1870 (Soma et al., 2012).

The Dorper, a locally developed composite thin-tailed meat breed, emerged from one of South Africa's most successful long-term livestock improvement programs (Milne, 2000). It was created by crossing Blackhead Persian and Dorset Horn sheep (Cloete et al., 2016). Another locally developed breed is the Meatmaster, which is a composite meat breed (Peters et al., 2010). Its composition includes 50 % Damara, along with contributions from Dorper and varying amounts of Ile de France, Van Rooy, SA Mutton Merino, Dormer, Wiltshire Horn, and other breeds (Peters et al., 2010). As a result of the Meatmasters' origins containing both fat-tailed and thin-tailed sheep, there is variation in the tail phenotype of the breed. The only commercial wool-producing thin--tailed breed included in this study is the Merino, which originated in Spain and was introduced to South Africa in 1789 (Vink, 2009).

Sheep production is an important aspect of agriculture in South Africa. The aridity of the country has resulted in extensive small stock production being one of the predominant agricultural ventures in large areas of the country (Cloete and Olivier, 2012). South Africa's sheep stock totalled approximately 21.43 million heads in 2022 (Statista, 2023). Studies investigating the genetic diversity of different breeds, as well as inbreeding levels and relatedness of breeds and individuals are important in allowing sustainable selection and breeding of diverse and adaptable sheep breeds for South Africa.

Research on sheep genetics in South Africa is somewhat limited but has provided valuable insights. Early studies using random amplified polymorphic DNA (RAPD) profiles (Kunene et al., 2009) and microsatellite loci (Peters et al., 2010; Soma et al., 2012; Qwabe et al., 2013) reported medium to high levels of genetic variation within a range of sheep populations, and well-preserved genetic diversity despite potential bottlenecks from intensive early selection. Sandenbergh et al. (2016) and Molotsi et al. (2017) made use of the OvineSNP50 array to investigate genetic diversity and population structure of South African commercial and smallholder sheep breeds, respectively. Their results generally supported the previously reported findings with regards to diversity levels. Greyvenstein et al. (2016) performed a genome-wide association study investigating horn development in Damara sheep, while Dlamini et al. (2019) investigated *Haemonchus contortus* resistance in a Dohne Merino flock.

Characterizing diversity within and among breeds is an important tool for sustainable management practices, conservation programs as well as the development of breeding strategies (Bravo et al., 2019). Various studies performed on sheep populations identified selection signatures linked to morphological traits, such as coat colour (Purfield et al., 2012; Bertolini et al., 2018; Kumar et al., 2018), horn morphology (Molotsi et al., 2018; Signer-Hasler et al., 2017; Guo et al., 2021), and fat deposition (Mastralengo et al., 2019).

The aim of this study was to validate previously identified genes in under-researched South African sheep breeds, by identifying selection signatures using pairwise F_{ST} values between phenotypes within trait classes, and detecting overlapping Runs of Homozygosity (ROH) regions within populations.

2. Materials and methods

2.1. Materials

A total of 897 genotyped animals, sampled from 14 sheep breeds were included. Individuals of the Blackhead Persian (BHP), Damara (DAM), Dorper (DOR), nondescript Fat-tail (FTT), Karakul (KAR), Meatmaster (MMR), Merino (MER), Namakwa Afrikaner (NAM), Pedi (PED), White Dorper (WDOR) and Zulu (ZUL) breeds were genotyped at the Agricultural Research Council, Biotechnology Platform (ARC-BTP), using the Illumina® Ovine 50 K SNP BeadChip. Only secondary data was used. Additionally, genotypes for Ethiopian Menz (EMZ), Red Maasai (RMA) and Ronderib Afrikaner (RDA) were obtained from publicly available resources (WIDDE, http://widde.toulouse.inra.fr/widde/). The various phenotypes presenting in these populations are indicated in Fig. 1.

2.2. Methods

To compare and investigate the underlying genes associated with four distinct morphological traits (coat colour, fleece type, presence/absence of horns and tail type), the animals were classified and their genotypes merged according to the known breed phenotypes for these traits. The breeds, number of animals per population and phenotypic classification are indicated in Table 1.

Quality control (QC) was performed on the datasets per population using PLINK software (Purcell et al., 2007). Sample- and marker-based quality control were performed, in order to filter both non-informative SNPs and individuals from the dataset. Animals were removed according to missing genotype rates (using –mind), while SNPs were removed based on call rate (using –geno). The standard threshold levels used were mind 0.05, geno 0.05. LD-pruning was performed before Principal Component Analysis (PCA) and admixture analysis, but not included for the selection signature analyses.

After QC procedures, marker-based summary statistics indicating genetic diversity were estimated per breed using PLINK (Purcell et al., 2007), including mean expected and observed heterozygosity (He and Ho), inbreeding coefficient (Fis), minor allele frequency (MAF) and linkage disequilibrium (LD) estimates, calculated as r^2 over distances of 50 KB, 100 KB and 1 MB.

Common SNPs between datasets were extracted and datasets were merged. SNP-based genetic relatedness between individuals was calculated using GCTA version 1.24 (Genome-wide Complex Trait Analysis) (Yang et al., 2011). A genetic relationship matrix was created using the command –make-grm, followed by the estimation of eigenvalues and eigenvectors for the first three principal components using the command –pca 3. Microsoft Excel was used to visualise PCA plots by importing the eigenvectors file to Excel and constructing scatterplots of the principal components (values for principal component one on x-axis and principal component two on y-axis). The PCAs were constructed for the merged dataset of all breeds on all chromosomes, as well as for each trait class per selected chromosome.

ADMIXTURE 1.23 software (Alexander et al., 2009) was used to determine the genetic population structure of the animals through the maximum likelihood estimation of ancestry. The appropriate K-value for plot visualisation was determined based on the lowest cross-validation error estimate by adding the –cv command when running ADMIXTURE. The admixture plots were visualised using the BITEv2 R package (Milanesi et al., 2017).

The Hamming distance matrix between pairs of individuals was calculated for phylogenetic reconstruction using the –distance and –square functions in PLINK v1.09 (Purcell et al., 2007). The resulting matrices were converted to text (.txt) files and imported into R (R Core Team, 2022) for constructing a Neighbor-Joining (NJ) tree with the 'ape' package (Paradis and Schliep, 2019). The tree was subsequently converted to Newick format and uploaded to iTOL (Letunic and Bork, 2021) for graphical visualization.

For each classification group, chromosomes with known genes associated with the trait were analysed (coat colour: OAR 1, 2, 10, 13, 14, 23; fleece type: OAR 1, 2, 3, 6, 11, 14, 19, 25, 26; horns: OAR 2, 10, 22; tail type: OAR 2, 3, 4, 7, 8, 11, 13, 15, 17). Known genes for each morphometric trait included, as well as their location on the genome, are listed in Supplementary Table 1.

Supplementary 1: Known genes for each morphometric trait included in this study and their location in the genome.

Pairwise F_{ST} values were calculated within each trait class, using the

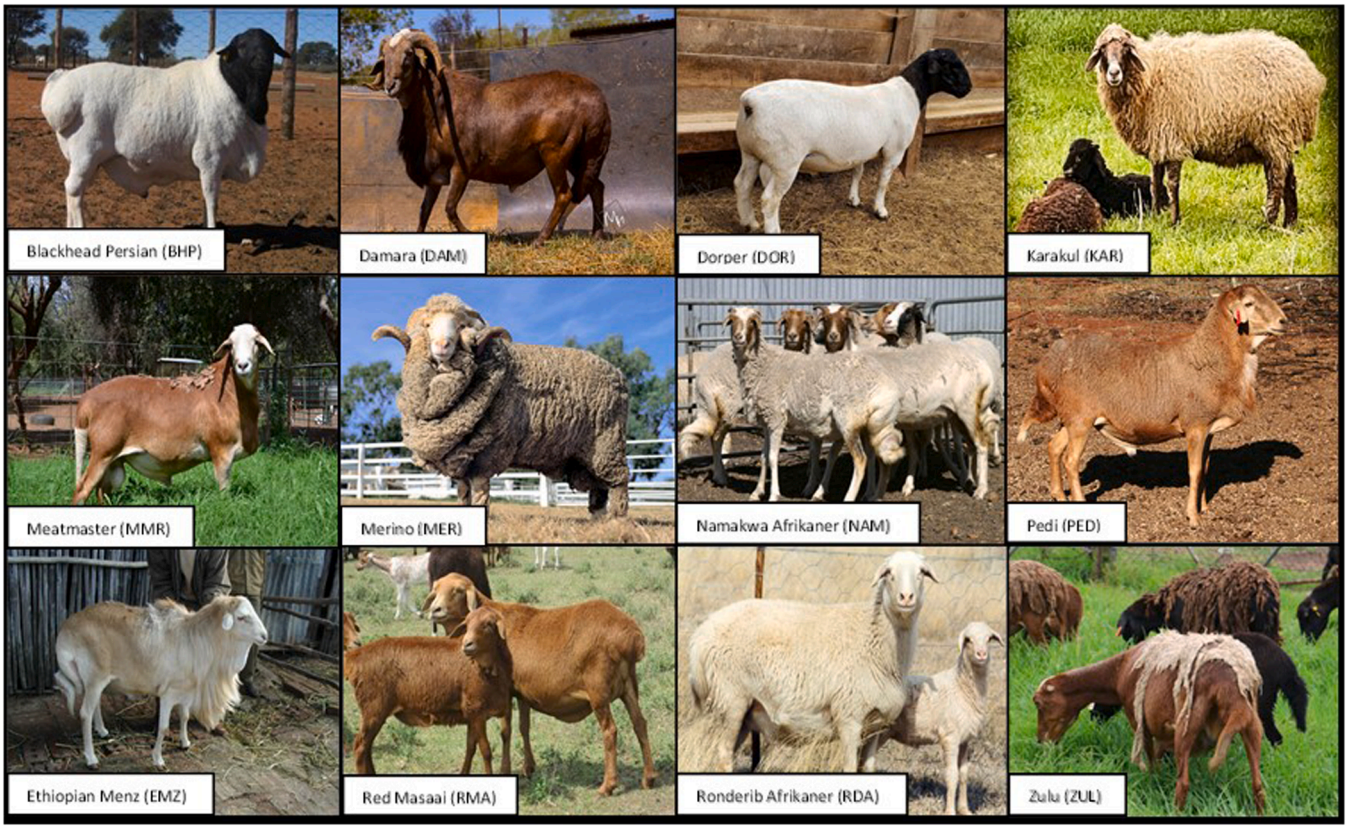

Fig. 1. Photos of 12 African sheep breeds included in this study (Source: Weblinks listed after references).

unbiased estimator proposed by Weir and Cockerham (1984) with PLINK v1.9 (Purcell et al., 2007). The top 1 % of F_{ST} values were considered as relevant regions indicating selection signatures for each pairwise comparison, where after the top F_{ST} values were compared to known gene locations for each trait, in a window of 50,000 base pairs below and 50,000 base pairs above the known gene locations, in order to identify possible selection signatures associated with the known genes.

ROH analysis was performed on the datasets grouped according to phenotype, using the sliding window approach in PLINK v1.9 (Purcell et al., 2007) and the –homozyg option. The minimum ROH length was set to 1 Mb. The minimum number of SNPs required to constitute a ROH (l) was estimated as proposed by Lencz et al. (2007):

$$l = \frac{\log_e \frac{\alpha}{n_s \cdot n_i}}{\log_e(1 - het)}$$

where n_s is the number of SNPs per individual, n_i is the number of individuals, α is the percentage of false positive ROH, set to 0.05 in this study, het is the mean SNP heterozygosity across all SNPs. Up to one possible heterozygous genotype was permitted per ROH window. The minimum SNP density per ROH was set to 1 SNP every 100 kb and the maximum gap permitted between consecutive homozygous SNPs was set to 700 kb.

ROH was identified per phenotype, on chromosomes previously indicated to contain regions with genes responsible for the specific phenotype. The ROH incidence was calculated as the percentage of individuals with a SNP that is within a ROH segment for a specific population. The top 10 % of ROH incidences were considered as relevant regions indicating selection signatures, whereafter the top ROH values were compared to known gene locations for each trait, in a window of 50,000 base pairs below and 50,000 base pairs above the known gene locations, in order to identify possible selection signatures associated with the known genes.

3. Results

After quality control (QC) was performed on each population, the number of remaining SNPs per breed ranged from 37320 for BHP to 52110 for RMA. The number of animals per population ranged from 7 for KAR, to 243 for DOR (Table 2).

3.1. Within population genetic diversity

Genomic heterozygosity levels were the lowest for the ZUL breeds (0.308) and highest for the MER (0.352) as indicated in Table 3. The MAF values indicated ascertainment bias in the BHP, with a low average MAF of 0.182. The highest MAF estimated was still in the low range at 0.266 for the DOR. Linkage Disequilibrium estimates decreased over longer distances for all populations, as expected (Table 3). Genomic inbreeding levels varied between low negative and low positive values, with no clear indication of inbreeding.

3.2. Genetic differentiation between populations

Based on genome-wide SNP information, most individuals clustered within their expected populations, although some overlapping between populations was observed (Fig. 2). The commercial MER population formed a distinct, separate cluster. The DOR and WDOR clustered together, as expected. Some of the non-descript FTT individuals clustered together with the NAM sheep, but this combined cluster formed a distinct grouping from the rest of the indigenous as well as exotic breed populations. The remaining indigenous South African populations formed loose within-population clusters in the same quadrant, with the KAR sheep forming a separate cluster.

In the PCA analyses resulting in Fig. 3, the populations were separated into phenotypic classes. The thin tail class (including MER, DOR and WDOR) separated from the fat-tailed classes, and while

Table 1
List of breeds genotyped, the sample size and phenotype classes included in this study.

Breed	Sample Size	Tail type	Horns	Colour	Fibre	Origin of data
BHP	30	Short fat-tailed	No	Black head	Hair	Western Cape
FTT	16	Short fat-tailed	Yes	Multi coloured	Hair	Beaufort West, Western Cape
PED	85	Short fat-tailed	Yes	Multi coloured	Hair	Oudtshoorn, Western Cape
EMZ	34	Short fat-tailed	Yes	Multi coloured	Hair	WIDDE
ZUL	59	Short fat-tailed	Yes	Multi coloured	Hair	University of Zululand, KwaZulu-Natal
KAR	7	Short fat-tailed	Yes	Black	Hair	Upington, Karakul Research Station, Northern Cape
RMA	45	Short fat-tailed	Yes	Red	Hair	WIDDE
RDA	17	Short fat-tailed	Yes	White	Hair	WIDDE
DAM	84	Long fat-tailed	Yes	Multi coloured	Hair	Ladismith, Hartenbos, Western Cape
MMR	142	Long fat-tailed	Yes	Multi coloured	Hair	Communal area Steinkopf, Northern Cape
NAM	102	Long fat-tailed	Yes	Red head	Hair	Nortier, Western Cape
DOR	326	Thin tailed	No	Black head	Hair	Nortier, Western Cape
WDOR	33	Thin tailed	No	White	Hair	Nortier, Western Cape
MER	132	Thin tailed	Yes	White	Wool	Western Cape

Table 2
Number of animals and SNPs before and after QC.

Breed	Animals before QC	Animals after QC	SNPs before QC	SNPs after QC
BHP	30	13	54242	37320
DAM	84	84	51770	51282
DOR	245	243	46829	46547
EMZ	35	34	46820	46746
FTT	16	16	52047	45538
KAR	7	7	51680	51004
MER	132	37	52047	46742
MMR	92	55	51647	51535
NAM	98	65	46800	46705
PED	85	74	52110	51282
RDA	17	17	46819	46676
RMA	45	45	46819	46752
SAMM	36	36	54242	44528
WDOR	34	34	46817	34821
ZUL	59	55	51680	50810

differentiation can be seen between long fat tail and short fat tailed types, some overlap was observed (A). The horn and no horn classes (B) separated into relatively distinct clusters, with the polled class including the DOR types, as well as BHP. The red head class (consisting only of NAM individuals) formed a distinct cluster, while the white class formed three separate groups (C), consisting of the MER, DOR and RDA respectively. No overlap between the three white coated populations was observed. Hair and wool (MER) classes formed two distinctly separate clusters (D).

Table 3
Genomic diversity parameters for the 14 sheep populations included in the study.

Population	Fis	H_o	H_e	MAF	LD 50 KB	LD 100 KB	LD 1 MB
BHP	−0.076	0.350	0.326	0.182	0.351	0.309	0.235
DAM	0.075	0.296	0.320	0.226	0.178	0.145	0.094
DOR	0.019	0.347	0.354	0.266	0.183	0.145	0.091
EMZ	−0.001	0.345	0.345	0.243	0.185	0.138	0.069
FTT	0.025	0.326	0.334	0.217	0.288	0.248	0.190
KAR	−0.025	0.360	0.351	0.204	0.373	0.339	0.287
MER	−0.012	0.356	0.352	0.246	0.233	0.194	0.140
MMR	−0.015	0.354	0.349	0.254	0.173	0.143	0.098
NAM	0.026	0.310	0.318	0.200	0.307	0.264	0.196
PED	0.032	0.314	0.324	0.228	0.214	0.179	0.129
RDA	−0.079	0.364	0.338	0.220	0.286	0.246	0.186
RMA	−0.015	0.338	0.334	0.241	0.167	0.122	0.059
WDOR	0.019	0.335	0.341	0.246	0.248	0.213	0.162
ZUL	−0.045	0.322	0.308	0.200	0.254	0.210	0.144

Fis- Fixation index, Ho- Observed heterozygosity, He- expected heterozygosity, MAF- Minor allele frequency, LD 50 KB- Linkage disequilibrium over 50 kg base pair windows, LD 100 KB- Linkage disequilibrium over 100 kg base pair windows, LD 1 MB- Linkage disequilibrium over 1 mega base pair windows.

To visualize the extent of genetic differentiation, the phylogenetic tree in Fig. 4 was generated. It shows two main branches, one including the DAM, PED and ZUL populations and another main branch included all other populations. Interestingly, the main branches closely mimicked the main tail phenotypes. The thin-tailed MER, DOR and WDOR types branched off together, although the KAR (short fat tailed) also shared a node with MER. The other short fat tailed populations formed a separate cluster. This node also included the MMR, that is subjected to phenotypic diversity with regards to its tail type, due to a high level of admixture in its breed formation. The DAM (short fat tailed), however, surprisingly shared a node with the long fat tailed populations (PED and DAM), while the NAM (long fat tailed) formed a separate cluster. Some admixture could be observed as individuals from various populations (e.g. BHP, DOR and FTT) were interspersed in various branches / clusters.

The circular admixture plot (Fig. 5), indicates a high level of variation admixture in most of the populations. At K= 22, the DOR, MMR, NAM and PED populations all showed two distinct subpopulations within the populations. The lowest levels of admixture could be seen in the EMZ, RDA and RMA populations.

3.3. Selection signature analyses

Pairwise F_{ST} analysis was performed between the various phenotypic classes per trait. The top 1 % of F_{ST} values were considered as significant regions indicating selection for each trait comparison. The top F_{ST} results were compared with the locations of known genes for each phenotype.

Runs of Homozygosity (ROH) analysis was performed within population per trait. The top 10 % of ROH incidence for results from the analysis of overlapping ROH regions were compared to regions known to contain genes identified for each phenotype.

The largest percentage of ROH for all phenotypic classes (Fig. 6A), except the black colour phenotype was found in the shortest category (0 to 1 Mb). For the black colour phenotype, the largest percentage of ROH was found in the 4 to 8 Mb, and 8 to 12 Mb categories.

The highest total number of ROH (Fig. 6B) was observed for the hair phenotype, and most of these were found in the 0 to 1 Mb category. For all phenotypes, the highest number of ROH was observed in the shortest length (0 to 1 Mb) category.

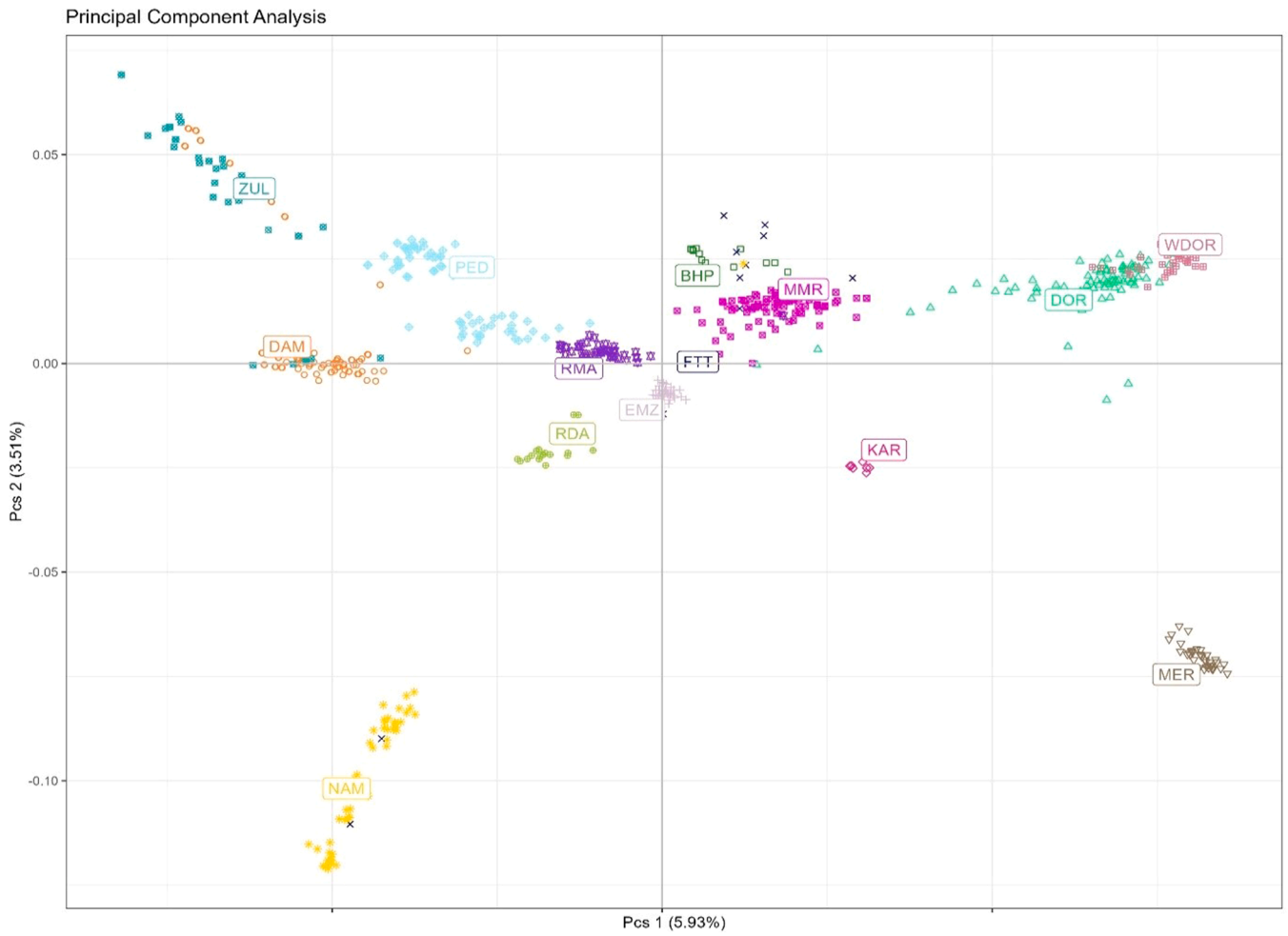

Fig. 2. The genetic relationships among the 14 sheep populations as seen when plotting the first and second principal components against each other.

Six genes that have previously been identified as affecting coat colour were found close to regions identified with the highest F_{ST} values, including the agouti signalling protein (*ASIP)*, melanocortin 1 receptor (*MC1R)* and tyrosinase-related protein 1 (*TYRP1)* genes (Table 4).

As indicated in Table 5, within the horned phenotype population, an overlapping region of ROH was found near the homeobox D1 (*HOXD1)* gene, known for influencing horn development in sheep. Two keratin-associated protein genes, keratin-associated protein 6–1 (*KRTAP6–1)* and keratin-associated protein 7–1-like (*LOC101104027)*, was identified in overlapping ROH regions in the hair phenotype population, together with fibroblast growth factor 5 (*FGF5*) which is involved in the regulation of the hair cycle, while the distal-less 3 (*DLX3)* gene, associated with wool quality was observed within the wool phenotype population. In a comparison between the hair vs. wool phenotypes through F_{ST} analysis, SNPs close to the *HR* gene (associated with hairlessness) was identified with a high F_{ST} value.

Overlapping ROH analysis of the short fat-tailed phenotype identified five genes associated with tail growth in sheep, including the platelet derived growth factor D (*PDGFD)* gene, which was also identified through F_{ST} analysis of long fat-tailed vs. short fat-tailed phenotype. Comparison of the long fat-tailed and thin-tailed phenotypes showed high differentiation at the bone morphogenetic protein 2 (*BMP2)* gene, which has been indicated to influence sheep tail fat deposition (Table 5).

4. Discussion

This study aimed to investigate the genetics underlying the various morphological features present in indigenous and locally developed South African sheep breeds. The sample populations included both commercially farmed breeds, as well indigenous breeds that are mainly kept in communal or subsistence farming systems. The different breeds' responses to both natural and artificial selection resulted in differentiated morphological changes, and thus the observed phenotypic and genetic diversity. Here we report for the first time on Southern African indigenous sheep breeds on the genetic basis of coat colour, tail, and horn phenotypes.

In the present study, we observed a marked loss of SNPs (19625 SNPs) in the BHP. The indigenous RMA, DAM and PED populations retained the highest numbers of SNPs, with no indication of ascertainment bias. The RMA was used in the development of the SNP array, and a high average MAF was thus expected for this breed, but not for the other indigenous populations. Although the BHP had the lowest average MAF of 0.182, its observed heterozygosity was moderate at 0.350. Indigenous breeds had both the lowest (0.296, DAM) and highest (0.364, RDA) levels of observed heterozygosity. The DAM samples in this study were sourced from stud breeders in the Western Cape region and this could explain the low observed heterozygosity. The high observed heterozygosity in other indigenous breeds such as the RDA, ZUL, WDOR, EMZ and KAR indicates that the general perception that communally farmed livestock are prone to inbreeding and decreased genetic diversity levels, is not always correct. It could also be explained by the tendency of communal farmers to crossbreed with exotic breeds which is evident in the admixture analysis from this study. In general, the diversity results correspond with those reported by Dzomba et al. (2020), van Marle-Koster et al., (2021) and Nel et al. (2022). Relatively small discrepancies can be attributed to differing thresholds used during

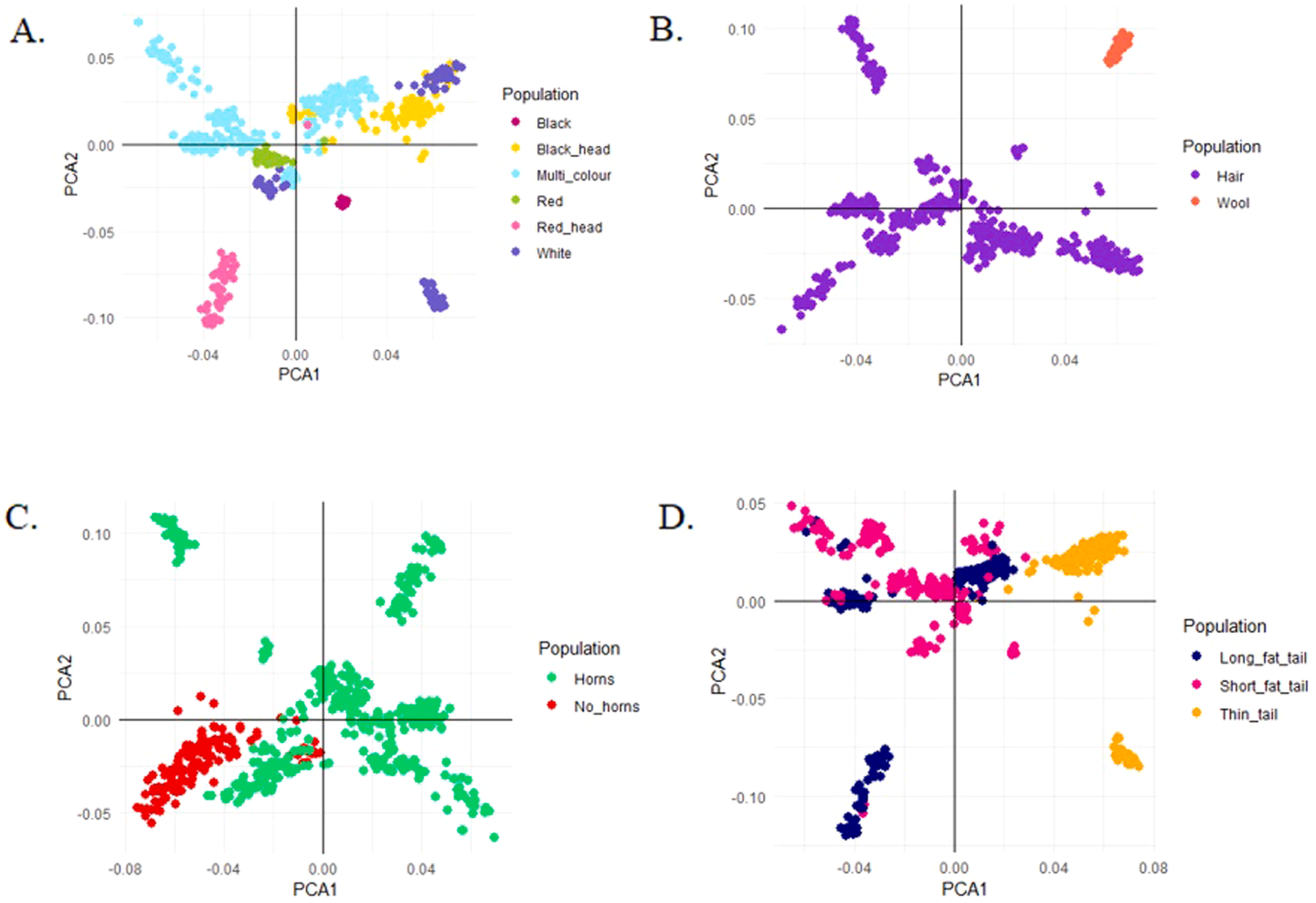

Fig. 3. The genetic relationships among the A: tail trait classes, B: horn trait classes, C: colour trait classes and D: fleece trait classes, as seen when plotting the first and second principal components against each other.

quality control and varying sample sizes. The moderate genetic diversity observed across the production types is encouraging, especially for numerically smaller indigenous breeds with no structured breeding or selection programs.

A number of genetic diversity studies have been performed on SA sheep breeds in the past, making use of either microsatellite markers or SNP genotyping. Soma et al. (2012) investigated 20 SA sheep breeds using 12 microsatellite markers. Observed heterozygosity levels ranged between 0.308 (Redhead Speckled Persian) to 0.641 (MER). Selepe et al. (2018) also reported moderate levels of genetic diversity, ranging between 0.57 (DOR) and 0.67 (MER) using a panel of 28 microsatellites. Other microsatellite-based studies reported similar values for various breeds, such as NAM (0.46–0.55, Qwabe et al., 2013) and ZUL (0.56–0.65, Kunene et al., 2014). Using eight RAPD markers, Gwala et al. (2015) found low diversity levels in a number of SA sheep breeds, ranging between 0.014 (ZUL) and 0.018 (DOR). The small number of markers used in the RAPD-based study however introduced bias and probably an underestimation of diversity levels.

SNP genotyping has mostly replaced the use of other DNA markers such as microsatellites. Sandenbergh et al. (2016) reported that the OvineSNP50 array could be successfully used in commercial SA sheep breeds, but that ascertainment bias might be a limitation in its application in indigenous breeds such as NAM with a high number of loci with a MAF lower than 0.1.

Based on PCA analyses, genetic relatedness between the different populations follow the same trend as in previous publications (Dzomba et al., 2020; Van Marle-Koster et al., 2021). The South African sheep population is a combination of exotic breeds, indigenous and locally developed composite breeds and thus contains a wide diversity of genetic resources. Clustering generally coincided with the production type of the sheep breed, with the highly selected commercial wool-mutton dual purpose MER and mutton-producing DOR (including WDOR) populations, forming two distinct clusters. The founder effect of the MER and DAM could be observed in the MMR, which is a composite breed developed from these two breeds, and which clustered between the two ancestral types. Some of the nondescript FTT clustered with the NAM, indicating a level of admixture. As the nondescript animals were sourced from communal producers, it is very likely that some of them were offspring of crosses with NAM animals. The loose dispersions of the indigenous populations are indicative of limited selection intensity, and thus more within-population genetic diversity.

The PCA analyses based on phenotypes produced phenotype-specific clusters for the various morphometric traits. The tail classes separated into two relatively distinct clusters, dividing thin and fat-tailed populations. The commercially farmed populations were selected to have thin tails, as fat tails have generally become undesirable for mainstream consumers and producers due to their influence on mating, walking ability, carcass traits and profit margins (Kalds et al., 2021). The differentiation between the tail types was thus expected, as the phenotype is linked to many underlying physiological differences between the types, as well as very diverse selection strategies. However, significant overlap was seen between long and short fat-tailed types, indicating less genetic differentiation.

The only populations included in the hornless class, was the Dorpertypes, as well as their foundation breed, the Blackhead Persian. This class formed a distinct cluster from the horned types. Indigenous breeds, which are often farmed in rural areas, still use horns for protection against predators, and as sexual weaponry (Kalds et al., 2022). As

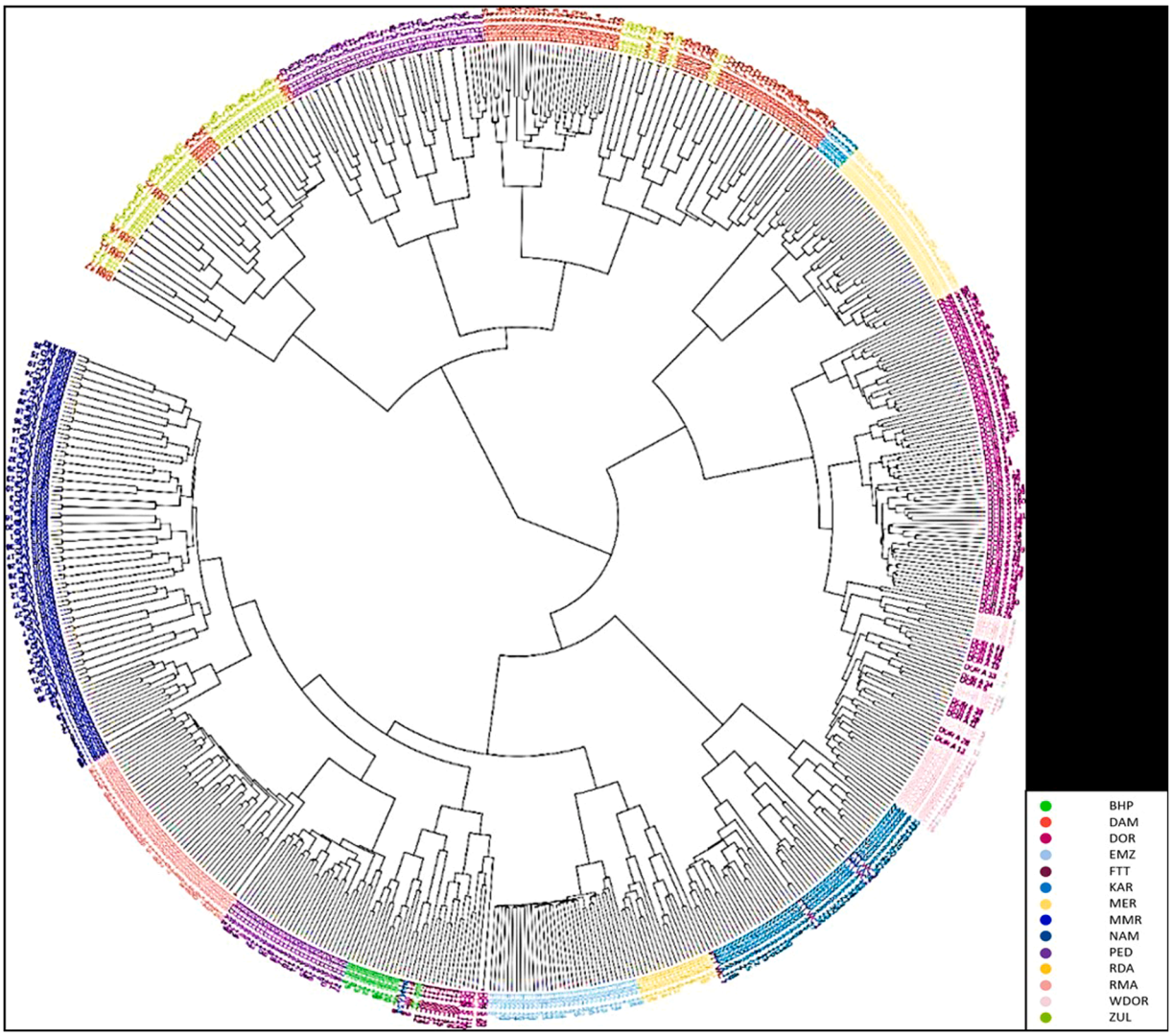

Fig. 4. Phylogenetic tree showing genetic relationships between individuals.

expected, distinct differentiation could be seen between the one wool-producing breed (MER) vs. the other hair-type populations. The Merino has been selected over time as a fine-wool producing breed (Jackson et al., 2020) and thus has completely different breeding and selection strategies as the other populations.

Lastly, some interesting clustering was observed between the various colour patterns. The white phenotype formed three distinct clusters. One of these consisted of the MER, in which a pure white wool fleece is a breed standard. The white Dorper produces kemp (a chalky, medullated hair type; Balasingam, 2005), but is selected for its large carcass and superior growth traits. On the other hand, the indigenous RDA is a white-haired population undergoing very little artificial selection pressure. Apart from the white, the only other clustering observed based on coat colour, was the red-headed NAM and black-headed DOR individuals.

Admixture based clustering indicated that the indigenous breeds could be uniquely separated from the mainstream commercial breeds. At K= 22, genetic variation could be observed within all populations, with some showing distinct within-population stratification. The DOR and MMR populations both divided into subpopulations, which was expected as they both are composite breeds with varied ancestral genotypes. The DOR was developed in the 1930s from crossing Dorset Horn males and Blackhead Persian ewes (https://dorpersa.co.za). The MMR is a much more recent addition to the South African population, as the Meatmaster Sheep Breeders Society was only formed in 2005. This breed was developed by crossing British and European breeds with fat-tailed indigenous sheep (https://meatmastersa.co.za). The divergence of the populations indicates their distinct genotypes and selection strategies. Treemix results support both the clustering-based analyses, as well as the Admixture results. The phylogenetic tree revealed differentiation that is associated with local adaptation in terms of both coat colour and other distinct phenotypic traits such as tail type.

The ROH analysis for colour phenotypes identified five genes (*ASIP*, *MC5R*, *MC1R*, *TYRP1*) which corroborates with literature. The *ASIP* and *MC1R* genes have been identified to play a role in the coat colour of Masesse sheep (Fontanesi et al., 2011). The *ASIP* gene is known to control where and when eumelanin and pheomelanin is produced in most mammals, and is known to interact with *MC1R* on an epistatic level (Koseniuk et al., 2018; Nazari-Ghadikolaei et al., 2018). Mutations in the *TYRP1* gene has been found to influence the darkness of coat colour (Kalds et al., 2022). Although *ASIP*, *MC1R*, and *TYRP1* have been identified in previous studies as influencing coat colours in sheep (Kalds et al., 2022), further research is still necessary to unravel the complexity of the expression and interaction between these genes.

The genes that were identified under selection for tail growth and fat deposition included *PDGFD, BMP2*, and T-box transcription factor T (*TBXT)* which concurred with those reported by Kalds et al. (2022) in a comprehensive review of genes influencing phenotypic traits. *PDGFD*

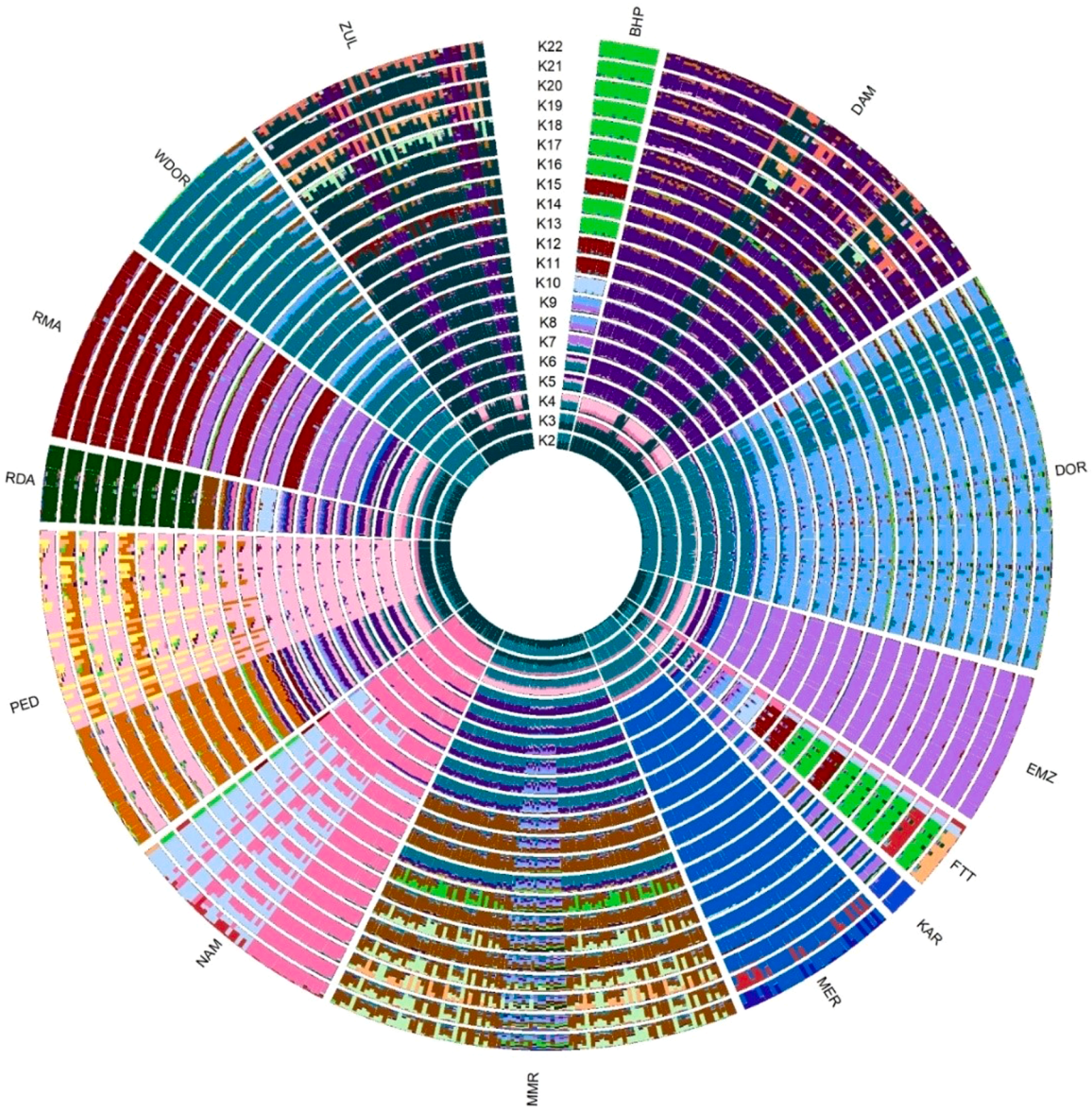

Fig. 5. Circle ADMIXTURE graph showing the proportional ancestry for each individual at K= 2 to 22. Optimal K= 22.

and *BMP2* have consistently been reported by various researchers to play a role in terms of fat deposition (fat vs. thin tailed breeds), with *PDGFD* playing a role in adipogenesis and the maintenance of mature adipocytes, while *TBXT* was associated with caudal vertebrae number (Kalds et al., 2021). Mutations of the *TBXT* gene has been shown to cause a reduction in sheep tail length. Li et al. (2022) also identified these two genes as crucial in sheep tail formation, and further suggested that tail morphology is probably governed by multiple genes, due to the high levels of variation observed between populations. Gene expression studies are necessary to elucidate the role of both fat deposition, and length and number of caudal vertebrae in terms of sheep tail phenotype.

For the wool phenotype the following genes were identified *KRTAP6–1*, and *LOC 101104027*. *KRTAP6–1* is known to influence fibre diameter-associated traits, while *LOC 101104027* is known to be associated with the wool fineness (Pu et al., 2024). The Merino breed included in this study has been intensely selected for wool quality and decrease in fibre diameter, and therefore it is expected for the keratin associated protein group to be under selection. This gene group has also been associated with other animal produced fibre (i.e. mohair) quality traits (Nazari-Ghadikolaei et al., 2018). Furthermore, *DLX3* has also been found to influence fleece type and quality in terms of wool crimp, as it is important in the development of the hair follicle, and for hair formation and regeneration (Rong et al., 2015; Kalds et al., 2022).

Although a number of genes, such as keratin genes (*KRT*) and *RXFP2* have been identified as consistently strong markers for horn development in sheep (Kalds et al., 2022), they were not identified in the current study. Alternatively, the *HOXD1* gene was found the be under selection in the horn phenotype analysis. Interestingly, this gene was also identified by Zhang et al. (2023) when investigating multi-horn development in the Sishui sheep breed. In their review, Kalds et al. (2022) refers to the *HOXD* cluster as a gene complex associated with polyceraty (multiple horns) in sheep. This result indicates that the indigenous sheep populations included in the current study might have a predisposition towards multi-horn phenotypes.

5. Conclusion

This study reports on a number of indigenous and locally developed sheep breeds in South Africa – a group that is historically under researched with little focus on their unique phenotypes and adaptive characteristics. The results provide valuable baseline data and insights into the genomic architecture of both adaptation and morphological

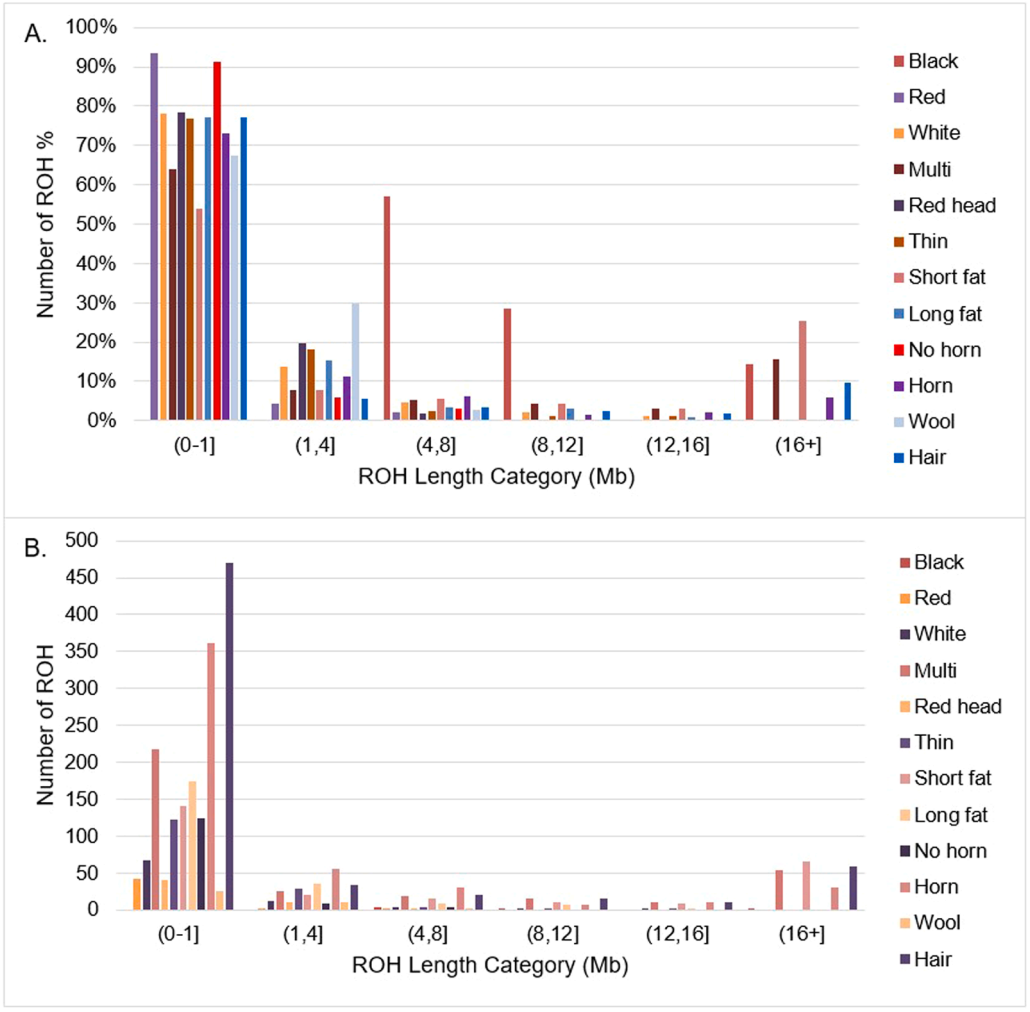

Fig. 6. The number of runs of homozygosity per population within the defined length categories. A: percentage of ROH within categories. B: number of ROH within categories.

Table 4
Known genes identified within the top 1 % of F_{ST} and the top 10 % ROH incidence estimates based on colour phenotypes.

Gene*	Colour Phenotype	F_{ST}	ROH incidence
ASIP	Black vs White	1	-
	White vs Multi	1	-
MC5R	Black vs White	1	-
	Black vs Red	0.794	-
	White vs Multi	1	-
	Multi vs Black head	0.536	-
MC1R	Black vs Black head	0.863	-
	White vs Black head	0.404	-
	Red vs Black head	0.702	-
TYRP1	Multi vs Red head	0.684	-
	Black head vs Red head	0.644	-
	Multi coloured	-	0.029
DCT	Black vs Red head	0.911	-
	Black vs Black head	0.739	-
	Multi vs Red head	0.615	-
MLPH	Black vs Red	0.782	-
	White vs Red head	0.657	-
	White vs Black head	0.377	-

traits in South African sheep. Using SNP genotypes, we clarified the phylogenetic relationships between various indigenous and locally developed sheep breeds. The majority of the genes identified for colour, horn development and thin vs fat-tailed in the indigenous breeds are similar to what was found in Asian related breeds, thus supporting the suggested gene flow from wild relative to domestic populations, as well as confirming highly conserved areas of the ovine genome. Further research needs to be done to verify these genes under selection in our South African breeds using real-time PCR which can be used to assist in the development of marker-tests, which farmers can used to aid in their genetic selection programs.

CRediT authorship contribution statement

C. Visser conceptualized and drafted the manuscript. A. Retief performed the statistical analyses. All authors (C. Visser, A. Retief and A.H. Molotsi) contributed to interpretation of data, writing, and revising the manuscript.

Ethical approval

Ethical approval for the use of the data in this study was obtained from the Ethics Committee of the Faculty of Natural and Agricultural Sciences at the University of Pretoria (NAS394/2019), as well as from Stellenbosch University, Research Ethics Committee: Animal Care and Use (ACU-2019–10914).

Table 5
Known genes found within the top 1 % of F_{ST} and top 10 % ROH incidence selection signatures estimates based on horn, fleece and tail type phenotypes.

Trait	Phenotype/comparison	Known genes found	F_{ST} value	ROH incidence value
Horn presence	Horned	*HOXD1*	-	0.015
Fleece type	Hair	*KRTAP6−1*	-	0.01
		LOC101104027	-	0.01
		FGF5	-	0.02
	Wool	*DLX3*	-	0.135
	Hair vs Wool	*HR*	1	-
Tail type	Short fat-tailed	*HOXA11*	-	0.096
		SP3	-	0.038
		SP9	-	0.008
		PDGFD	-	0.019
		PPP1CC	-	0.012
	Long fat-tailed vs Short fat-tailed	*WDR92*	0.271	-
		TBXT	0.224	-
		PROKR1	0.202	-
		PDGFD	0.283	-
	Long fat-tailed vs Thin-tailed	*BMP2*	0.553	-

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Declaration of Competing Interest

The authors wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.smallrumres.2025.107499.

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