

# African Sheep Breeds

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The African continent is home to more than 400 million heads of sheep, the majority of which are classified as indigenous and raised primarily for subsistence. They live and thrive well in a wide range of climatic and production conditions, ranging from unfavorable to favorable environments.

Keywords: genetic diversity ; haplotypes

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## 1. Introduction

Domestic animal agriculture plays a crucial role in maintaining food security, as envisioned in sustainable development goal two ("End hunger, achieve food security and improved nutrition and promote sustainable agriculture") <sup>[1]</sup>. At present, the estimated global sheep, goat and cattle populations are 1.2, 1.1, and 1.5 billion heads, respectively <sup>[2]</sup>. The African sheep population is estimated to be above 400 million heads. To enhance production, diversity and adaptation under the current climate change challenges <sup>[3]</sup> in recent decades, researchers have extensively studied the origin, history, phylogenetic relationships and diversity of domestic animals within species and among populations such as in sheep <sup>[4][5]</sup> <sup>[6][7]</sup>, goats <sup>[8][9][10]</sup>, and cattle <sup>[11]</sup>. Information on the diversity and history of the species and/or breed provides the foundation on which conservation and breeding programs are made <sup>[12]</sup>.

Archeological evidence suggests that sheep were among the first animals to be domesticated approximately more than 10,000 years ago in present Iran, some Arabic countries and Turkey, formerly referred to as the fertile crescent at the Zagros Mountains of Iran <sup>[9][13]</sup>. It is hypothesized that at least two independent domestication events took place, leading to the raise of haplogroup B and A which are globally most frequent <sup>[4][14]</sup>. According to studies, haplotypes belonging to haplogroup B are descendants of European mouflon (*Ovis aries musimon*) and are more frequent in Europe <sup>[4][6][14]</sup>, while haplogroup A descends from Asiatic mouflon (*Ovis orientalis*) which is mainly present in Asian breeds <sup>[4][15]</sup>. Other authors, however, aver that European mouflon, a native to Sardinia and Corsica Islands in the Mediterranean Sea are pre-domesticated forms (feral) of Asian Mouflon <sup>[14][15]</sup>. Further studies have identified the existence of other sheep clades from C to E <sup>[4]</sup>. These could have risen from post domestication selection leading to the emergence of varied phenotypes, for instance, meat production traits, wool characteristics, coat color, presence or absence of horns, body sizes and tail size <sup>[15]</sup>. Studies indicate that haplogroup C is present in China <sup>[4]</sup>, whereas clades D and E are very rare although spotted in near East sheep <sup>[14]</sup>.

The history of domestic sheep in Africa is still inconclusive and thus it is an area calling for further investigation. This could be due to inadequate mtDNA CR studies done on African sheep breeds to explore their matrilineal lineages. However, the available inferences suggest that sheep spread throughout Africa with the pastoral communities after being introduced from the Near East <sup>[4]</sup>. The role of the East African region in the spread of sheep in the African continent is largely unknown, although, it is thought it was vital to the introduction of sheep from Southern Asia or the Arabian Peninsula and/diffusion southwards African continent <sup>[4][16]</sup>.

## 2. Meta-Analysis of Mitochondrial DNA Control Region Diversity to Shed Light on Phylogenetic Relationship and Demographic History of African Sheep (*Ovis aries*) Breeds

Autochthonous sheep breeds are vital to the economy and subsistence of many farm families and pastoralists over the African continent. They thrive well in ecologically marginal zones like mountains, arid and semi-arid areas (ASALS) where other domestic animals can not economically thrive <sup>[17]</sup>, and are thought to harbor novel genomic variants that enable them to be resilient to stressful environmental conditions. However, their existence is threatened by the emergence of superior performance breeds. Thus, they are neglected, breeding without directional selection and hence encouraging high levels of inbreeding, which could lead to a loss of genetic diversity. Although their performance is low, these breeds could be crucial in the future, especially when the world is faced with climate change challenges <sup>[3]</sup>.

Understanding the history and phylogenetic relationships of native sheep breeds in Africa is fundamental for the development of breeding and conservation strategies. Several archaeological studies are in concurrence that sheep were among the first animals to be domesticated [16]. Further, population geneticists concur that the present African sheep breeds are mainly descendants of two main ancestors, as inferred by the widespread of two major haplogroups (A and B) [4][18][19]. However, the general genetic history of African continent sheep populations and the relationship among them is not well addressed. The scope of the present meta-analysis was to elucidate their mtDNA CR diversity and phylogenetic relationships as well as the demographic history of African sheep breeds clustered in four regions.

A high level of mtDNA CR diversity was observed in all studied populations. Results observed in the present study are comparable to findings observed in other research works in different livestock species. For example, Revelo et al. [7] observed a  $H_d$  and  $p_i$  of 0.920 and 0.010 respectively in the Colombian Creole sheep. Likewise, a  $H_d$  of 0.998 and  $p_i$  of 0.250 were observed in Egyptian sheep [20], Moroccan sheep [21], and Arabian goats [9], while Tibetan sheep [18] and Nigerian cattle [22] also exhibited similar results of high diversity among populations. Global organizations also recognize the crucial role of maintaining high biodiversity levels. Genetic diversity as one of the components of biodiversity has been addressed in several international conferences, e.g., [23].

Generally, the larger number of haplotypes observed coupled with a higher number of unique haplotypes suggests that a high level of mtDNA CR differences exist among studied individuals and populations. None of the studied regional populations exhibited significantly negative or positive Tajima's  $D$  tests. However, Fu's  $FS$  test returned significant negatives for both the North and West African populations, which could be a suggestive indicator of an expanding population. Mismatch distribution produced a multi-modal pattern for North Africa (Figure S1A) and a unimodal for West Africa (Figure S1B), agreeing with Fu's  $FS$  test results. However, the East African (Figure S1C) population produced an irregular multi-modal pattern contrary to the neutrality test results. In this case, our interpretation suggests that East African sheep could be undergoing selective pressure mainly driven by adaptation to unfavorable production environments. A similar mismatch distribution pattern was also observed for all sequences pulled together (Figure S1E). Hence, we can conclude that in general, African sheep populations have undergone selective signatures for adaptation concurring with the study of the world's sheep breeds which detected genomic regions under selection [24]. It is important to note that processes leading to environmental adaptation could also impact the phenotypic characteristics of an animal and this hypothesis could explain the variation of phenotypes among sheep breeds. The unimodal with a slight skewness pattern of West Africa supported by a significant negative Fu's  $FS$  suggests a recent expansion from a relatively small population, concurring with a narrative that West African populations dispersed further to the Canary Islands and the Caribbean region [25]. The North African sheep population could also have undergone a series of population expansions owing to the archeological history of the role of Egypt in sheep arrival to Africa. For instance, studies indicate that sheep and goats first arrived in Egypt via the Sinai peninsula, the Red Sea and the Mediterranean seacoast, then dispersed Southwards towards Sudan and Ethiopia through the Nile basin [26]. This could explain the haplotypes observed being shared between North and East African sheep populations. Tarekegn et al. [26] also observed shared haplotypes between Ethiopian, Kenyan and Egyptian goats, suggesting a common maternal history.

The median-joining network of haplotypes formed three haplogroups (A, B and C) lacking phylogeographic clustering. Haplogroup B (B1, B3 and B3) was the most common comprising sequences from all studied regions. However, haplogroup A had breeds only from Egypt while haplogroup C consisted of sequences from all North African countries (Morocco, Algeria and Egypt). This observation suggested that studied sheep populations originated from a common matrilineal ancestor (European mouflon) and differentiated into different breeds adapting to local environmental conditions through natural and human selection. Populations in sub-haplogroup B1 are more specifically from West Africa and Sudan (most frequent in hap 233) seem to have displayed further dispersal characteristics compared to other populations in different haplogroups. On the other hand, Sudan played a crucial role in sheep dispersion, as discussed later in this section. Sub-haplogroup B3 formed by the present sequences exclusively included sheep from South Africa. This was expected, as the sequences were obtained from samples excavated from the second layer of the stone age, which is estimated to be more than 2700 years of age [27] and thus could not suggest a conclusive relationship between South African sheep breeds with breeds from other regions. Lack of phylogeographic clustering of small ruminant populations appears to be common; the phenomenon has been observed worldwide in sheep and goats [24][26][28].

The African continent is endowed with sheep breeds and varying phenotypes, among which is tail type. Recent research materials have indicated that the fat tail phenotype is an adaptation to hot and dry environments. In our phylogenetic network, sheep breeds characterized with thin tails mainly dominated haplogroup B1 e.g., Ouled Djella, Sardi, D'man and all the West African and Sudan sheep breeds. This could be an indication of a common historical background. According to Muigai [16], thin-tailed sheep could have been the first sheep to enter Africa between 7500 and 7000 before present (BP) through the Isthmus of Suez and/or the southern Sinai Peninsula, followed by fat-tailed sheep through the

Northeastern part and the Horn of Africa. The fat tail sheep breeds dominated sub-haplogroup B2 (the largest group). The present observations concur with assertions that fat-tailed sheep are widely distributed in Africa, and it is hypothesized that the phenotype developed from selection among thin-tailed sheep breeds [16]. Most of the cross-boundary shared haplotypes, together with the most frequent haplotype (233), were found in sub-haplogroup B1 supporting a narrative of possible Southward dispersion of sheep into Ethiopia and Sudan. The ease with which small ruminants can be transported, their use as items of trade and socio-cultural exchange, and their inherent ability to adapt to a diverse range of production and ecological environments could explain their lack of phylogeographic structure and high level of genetic diversity [26].

The higher variance (54.696%) among populations as compared to within populations (45.304%) suggested the existence of a possible geographical population structure, although this is weak. These results are comparable to other studies that registered similar findings e.g., [7][29][30]. In contrast, other studies observed higher within population variance than among the populations, e.g., [31][32][19]. On the other hand, the difference in haplotype frequencies could be explained by 98.43% within populations. This could be due to the high number of private haplotypes observed and even for shared haplotypes, a larger percentage was within populations. In domestic livestock genetic studies, it is advised to maintain a higher genetic variation within than between breeds [19] because it provides an opportunity for breed improvement to be initiated from within breed selection [30][33]. Higher variation within than among populations suggests a high female-mediated gene flow [19]. The overall  $F_{ST}$  value observed was also very high (0.547), indicating high levels of population differentiation. This could be due to the vast geographical representation and vast difference in production environments. Furthermore, the haplotype frequency  $F_{ST}$  observed was high (0.016), indicating that haplotype differentiation among populations has occurred but not as much. In general,  $F_{ST}$  is regarded as low when the value is below 0.050, moderate when it is between 0.050 and 0.150, high between 0.150 to 0.250, and very high when the value is above 0.250 [30]. Based on the present results, there may be a significant gene reserve in African sheep populations and thus, a need to enhance studies on these populations for a better understanding of their diversity, history, and phylogenetic relationships.

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