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The current state on characterisation of indigenous breeds of sheep and goats in Ethiopia

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Introduction

From the beginning of domestication, the transportation of domestic animals resulted in genetic and demographic processes that explain their present-day global distribution, genetic diversity and structure. Animal genetic resources (AnGR) encompass all animal species, breeds, strains and varieties that have been utilised in the past and present and have potential to be used in the future for food production and agriculture (Assefa 2019). Maintaining sufficient diversity in AnGR is necessary to retain adaptation potential in times of uncertainty (Boettcher et al. 2015). Livestock are critical for global food security and livelihoods. Around 1.3 billion people, majority of who comprise the rural poor rely directly on livestock for their livelihoods (World Bank 2021). Many countries have indigenous animal breeds that could potentially contribute far more to food and agricultural production than they currently do, meeting much wider household and market needs. Genetic characterization involves generating knowledge on genetic variation and it is the initial step in the sustainable management of AnGR. In the absence of appropriate characterization, breed attributes and genes with potential for future benefit may be lost through, for example breed replacement and extinction. Efficient utilization of AnGR based on proper phenotypic and genetic characterisation, is a prerequisite to harness the opportunities presented by AnGR to meet the future demand for animal source foods and improve livelihoods of the poor (ILRI 2006).

The ability of goats (Capra hircus) and sheep (Ovis aries), to adapt to a range of climatic and dietary extremes, combined with their specialized production traits and ease of transportation, has made these two ruminant livestock species the most adaptable, versatile and valuable domestic animals to humankind. The importance of sheep and goats (shoats), and their breeding for production and consumption, are diverse. Since domestication, shoats have been a source of animal proteins (milk and meat), a source of products of industrial significance (wool, mohair and skin), and as a source of products of agricultural significance (manure). Since the beginning of animal agriculture, shoats have played important socio-cultural roles in many human societies with no religious taboos being associated with the species. Shoats have also provided an efficient biological resource for utilising marginal environments, with poor potential for arable agriculture, through pastoralism/agropastoralism for the benefit of humankind.

The Ethiopian livestock sector constitutes a substantial component of the country's economy and sustains most farm and non-farm family's (Shapiro et al. 2017). In 2021, there were approximately 42.9 and 52.5 million sheep and goats, respectively in Ethiopia (CSA 2021). The majority of sheep (99.56%) and goats (99.88%) are of indigenous genotypes (DAD-IS, 2021; http://dad.fao.org/; accessed June 2021). The shoat sector accounts for approximately 19% of the country's GDP (equivalent to 35% of the agricultural GDP) and generates 16% of the Ethiopia's foreign exchange earnings (MoA 2012). The annual estimate of the number of sheep and goats slaughtered in Ethiopia is approximately 10,272,026 and 11,321,888 heads, respectively (FAOSTAT, 2019). Shoats have been the target of community-based breeding programs (CBBP) in Ethiopia (Haile et al. 2019) due to their affordability to subsistence farmers, their tendency to be cared for by women, youth and children and their greater adaptation to marginal environments. The CBBP have been shown to have resulted in substantial improvement in animal performance and thus in the standard of living of resource poor farmers (Haile et al. 2020) and they currently being advocated as the go-to strategy for improving the performance of indigenous livestock.

To take advantage of locally adapted indigenous breeds of livestock the generation, documentation and dissemination of information on a country's livestock resources is important. Such knowledge can inform the development and design of selection criteria and breeding programs. Here, we present a digest of the most recent findings on the genetic characterisation of shoats in Ethiopia. Because of the country's strategic location within a geographic region that has been critical in the initial introduction of domesticates into Africa (Boivin and Fuller 2009; Fuller et al. 2011), its indigenous shoats could be sharing a common historical and genetic legacy with other African breeds of shoats. We first provide an overview of the origin, introduction and dispersal of shoats into Africa and into Ethiopia evidenced from zoo-archeological and molecular findings. We then provide a brief summary of their phenotypic characterisation followed by an in-depth documentation of their genetic characterisation based on the analysis of a diverse set of genetic marker loci. We have excluded a documentation of the classification and description of shoats in Ethiopia as these have been well synthesized and documented by other authors (FARM-Africa 1996; Gizaw et al. 2008; Gizaw 2008a, 2008b) From the beginning of domestication, the transportation of domestic animals resulted in genetic and demographic processes that explain their present-day global distribution, genetic diversity and structure. Animal genetic resources (AnGR) encompass all animal species, breeds, strains and varieties that have been utilised in the past and present and have potential to be used in the future for food production and agriculture (Assefa 2019). Maintaining sufficient diversity in AnGR is necessary to retain adaptation potential in times of uncertainty (Boettcher et al. 2015). Livestock are critical for global food security and livelihoods. Around 1.3 billion people, majority of who comprise the rural poor rely directly on livestock for their livelihoods (World Bank 2021). Many countries have indigenous animal breeds that could potentially contribute far more to food and agricultural production than they currently do, meeting much wider household and market needs. Genetic characterization involves generating knowledge on genetic variation and it is the initial step in the sustainable management of AnGR. In the absence of appropriate characterization, breed attributes and genes with potential for future benefit may be lost through, for example breed replacement and extinction. Efficient utilization of AnGR based on proper phenotypic and genetic characterisation, is a prerequisite to harness the opportunities presented by AnGR to meet the future demand for animal source foods and improve livelihoods of the poor (ILRI 2006).

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Origin, and dispersal of shoats to Africa

As access to the past and current ranges of wild relatives of livestock increases, archaeological and genetic studies have continued to combine in an effort to elucidate the complex history of livestock domestication and subsequent dispersal from the centers of domestication. More recently, genetic evidence following maternally (mitochondrial), paternally (Y-chromosomal) and autosomal (whole genome sequence and single nucleotide polymorphisms (SNP)) inherited data has been used to elucidate the process of domestication and dispersal. Such information has complimented findings from zooarchaeological research. The mitochondrial DNA (mtDNA) has in particular been widely used as the marker of choice in studying the maternal phylogeny of domestic species. Because it is variable and structured enough across geographic ranges, and evolves at a constant rate, the control region (also known as the D-loop or hypervariable region) of the mtDNA has been especially useful in describing the genetic polymorphism of livestock species. Moreover, it has allowed maternal lineages to be followed and is less sensitive to introgression from wild species than nuclear DNA. On the other hand, studies based on the analysis of nuclear genes and autosomal markers have provided information on gene flow and selection processes that have greatly influenced the evolutionary history of livestock species.

Goats

Goats (*Capra hircus*) are one of the earliest ruminant livestock to be domesticated from the Bezoar ibex, *Capra aegagrus* (Manceau et al. 1999; Naderi et al. 2008) around 10,000 years ago in the Fertile Crescent (south-eastern Anatolia and the Iranian Zagros Mountains) (Porter 1996; Pringle 1998; Zeder and Hesse 2000; Zeder et al. 2006). A recent study based on whole genome sequence data (Zheng et al. 2020) has shown that all domestic goats form a monophyletic lineage to Bezoars, confirming that modern domestic goats descend from Bezoar-like ancestors. The other four wild Capra species (*C. Ibex*, *C. Sibirica*, *C. Falconeri*, and *C. Caucasica*), referred to as “Ibex-like” species, fall exclusively in a separate clade that is divergent from the Bezoar-goat. One wild Capra species, the Walia ibex (*C. walie*), is endemic to the northern escarpment of Ethiopia’s Simien Mountains. There is however no archaeological and genetic evidence implicating its domestication or hybridization with, or contribution to, the domestic variant. Following their domestication, goats spread globally and played an important role in the revolution of Neolithic agriculture and advance in human civilization. Modern-day domestic goats occur on all continents except Antarctica and they can also be found on many peripheral and remote islands.

Numerous detailed molecular phylogeographic studies have been carried out to clarify the dispersal routes of goats (Naderi et al. 2007; Naderi et al. 2008; Amills et al. 2009) based on the analysis of the hypervariable region of mtDNA. The analyses have revealed six major monophyletic mtDNA haplogroups (A, B (B1 and B2), C, D, F, G) in modern goats (Naderi et al. 2007 and references therein). Haplogroup A has a global distribution which may be responsible for the weak phylogeographic structure in modern goats and the extensive intercontinental translocation of the species (Luikart et al. 2001; Naderi et al. 2008; Amills et al. 2009). The B haplogroup has been found in the whole of Asia, and in a few individuals in sub-Saharan Africa and in Greece. Individuals with the B2 sub-haplogroup are restricted to China and Mongolia. Goats of the C haplogroup are found across Asia and Europe and the D haplogroup is present in the whole of Asia and Northern Europe. The F haplogroup is found in Sicily and the G haplogroup is present in the Middle East and northern Africa, near the Fertile Crescent. Two recent studies (Daly et al. 2018; Zheng et al. 2020) that analysed whole-genome sequences have shown that multiple divergent ancient wild goat sources may have been domesticated in a dispersed process in the Fertile Crescent resulting in genetically and geographically distinct Neolithic goat populations. These early goat populations contributed differently to the genetic makeup of modern goats in Asia, Africa, and Europe. Daly et al. (2018) also detected evidence implicating early selection for pigmentation, stature, reproduction, milking and response to dietary change, thus providing 8,000-year-old evidence for possible deliberate human efforts at moulding genome variation in goats. Zheng et al. (2020) provided evidence of an ancient introgression event from a West Caucasian tur-like species to the ancestor of domestic goats. One of the introgressed locus showed a strong signature of selection around the *MUC6* gene, which encodes a gastrointestinally secreted mucin and confers enhanced immune resistance to gastrointestinal pathogens. Another introgressed locus had a strong signal of selection that spanned the *STIM1-RRM1* gene that may be related to behavior. Time calibrations show that the selected alleles at these two loci emerged in domestic goats at least 7,200 and 8,100 years ago, respectively, and increased in frequency concurrent with the expansion of mtDNA haplogroup A. Results by Zheng et al. (2020) also show that Asian goats are genetically distinct from European and African goats and the Asian goats split into two geographic subgroups: southwest Asia-south Asia and east Asia. This agrees with the scenario that the ancestors of present-day domestic goats followed distinct dispersal routes along the east-west axis of Afro-Eurasia.

Archaeological findings indicate that domestic goats were first introduced to Africa via the Mediterranean Sea coast, the Red Sea Hills region, and the Sinai Peninsula and Nile River basin about 7,000 years ago (Hassan 2000; Gifford-Gonzalez and Hanotte 2011). Similar findings also suggest sheep and goats dispersed rapidly from the Near East into central Sahara and Ethiopian highlands between 6,500 and 5,000 BC (Clutton-Brock 2000) prior to spreading south of the continent. Radiocarbon dating of goat and sheep bones from archaeological sites in northern Africa dating to around 6,000 BC (Grotte Capeletti in Algeria) and 6,800 BC (Haua Fteah in Cyrenaica, Libya) are close to those of bones excavated in eastern Sahara, suggesting a very rapid dispersal of sheep and goats from southwest Asia into north Africa between 7,000 and 6,000 BC (Hassan 2000). A joint analysis of mtDNA and Y-chromosome sequence data have provided support for the Mediterranean route and the terrestrial dispersal of goats across northern Africa (Pereira et al. 2009).

Only one study (Tarekegn et al. 2018) has so far investigated variation at the complete hypervariable region of mtDNA in Ethiopian indigenous goats. The authors analysed 13 breeds (Abergelle, Gondar, Ambo, Western highland/Agew, Western lowland/Gumez, Keffa, Woyto-Guji, Arsi-Bale, Afar, Hararghe highland, Short-eared Somali, Long-eared Somali, Nubian) and observed only haplogroups A and G. In concordance with other studies (Naderi et al. 2007, 2008), haplogroup A is the most diverse and has the widest geographic distribution in Ethiopia. Naderi et al. (2007, 2008) suggested that haplogroup A originated from eastern Anatolia and haplogroup G from Iran (northern and central Zagros). Both haplogroups (A and G) have been observed in Egypt (Naderi et al. 2007) and Kenya (Kibegwa et al. 2015) suggesting likely common maternal history of goats found in northern and eastern Africa.

Sheep

Zooarchaeological records suggest sheep was managed and domesticated during the Neolithic transition in the northern Levant (a large area of the Middle East including modern Israel, Lebanon, Syria and Turkey) *circa* 10,000-8,000 years before common era (BCE) (Rezaei 2007; Maher et al. 2012; Asouti et al. 2013; Arbuckle et al. 2014; Zeder 2008, 2017). The wild ancestor is thought to have been the Asian mouflon (*O. orientalis*), which was, by early Holocene, distributed from west Anatolia to east Zagros. Zooarchaeological (Arbuckle et al. 2014) and genetic evidence (Kijas et al. 2012; Deng et al. 2020) imply a complex demographic history of domestic sheep with a notable pattern being high levels of genetic heterogeneity in the species. This includes multiple distinct mtDNA haplogroups in modern breeds (Meadows et al. 2007), and high nuclear genetic diversity compared to some other domesticates, such as cattle or dog (Kijas et al. 2012; Naval-Sanchez et al. 2018). High diversity would be consistent with scenarios where domestication involved multiple centers and/or a large and heterogeneous wild population. A non-exclusive scenario would be major introgression from wild sheep into domestic flocks, a notion supported by zooarchaeological evidence.

Neolithic farmers are thought to be responsible for the dispersal of sheep north to Europe by approximately 7000 BCE, while demographic profiling of fossil records has dated the expansion south into Africa at 6000 BCE and east into Asia at 3000 BCE (Dwyer 2008; Gifford-Gonzalez and Hanotte 2011). The earliest remains of domestic sheep found so far in Africa date to between 7500 and 7000 BCE, deriving from the Nile River basin, the eastern Sahara and the Red Sea Hills (Gautier 1987; Close 1992; Vermeersch et al. 1996). From their domestication in the Fertile Crescent, sheep now span the diverse terrains of each inhabited continent (Dwyer 2008).

More recently, genetic data focused on Y-chromosome sequences suggest two patrilines in domestic sheep, one with a possible European origin and the other with a less restricted distribution (Meadows and Kijas 2009). The female mediated picture from mitogenome data has revealed five matrilineages (haplogroups A, B, C, D, E) (Wood and Phua 1996; Hiendleder et al. 1998; Guo et al. 2005; Pedrosa et al. 2005; Tapio et al. 2006; Meadows et al. 2007) that diverged before domestication (Meadows et al. 2011). Haplogroup A is of Asian origin, B is of European origin, C is encountered in South Asia, and D and E, which are rare, are encountered in Eurasia (Hiendleder et al. 1998; Guo et al. 2005; Pedrosa et al. 2005; Tapio et al. 2006; Meadows et al. 2007). Each of these five matrilines is present in modern domestic sheep from the Near East, but the frequency with which they occur together decreases with distance away from the center of domestication (Meadows et al. 2011). Global analyses of modern domestic sheep have shown matrilineages A, B, and C are the commonest.

Autosomal data paired with zoo-archaeological findings have been used to suggest two distinct entry points for thin- and fat-tailed sheep into Africa. Thin-tailed sheep are thought to have arrived first, entering overland from the Levant and spreading west (tomb paintings, 3100–2613 BCE). Fat-tailed sheep appeared later in recorded history and dispersed south past the horn of Africa to the continental cape (first depicted 1991–633 BCE) (Gifford-Gonzalez and Hanotte 2011). Autosomal data (endogenous retroviruses) has also revealed and support the finding that the global colonization of sheep occurred in waves (Chessa et al. 2009).

MtDNA analysis supports a common maternal ancestry for African sheep, while autosomal and Y chromosome DNA analysis indicates a distinct genetic history for African thin-tailed and sub-Saharan African fat-tailed sheep (Muigai and Hanotte 2013). Bruford and Townsend (2006) studied the mtDNA D-loop diversity of eight populations of fat-tailed sheep from east and southern African and identified haplogroup A only. Gornas et al. (2011) found haplogroup A and B only in Sudanese sheep with B predominating. A recent meta-analysis of mtDNA D-loop sequences of African sheep (Wanjala et al. 2021) confirmed the presence of haplogroups A, B and C in the continent. Haplogroup B is the most predominant and is represented by three sub-haplogroups (B1, B2, B3). Sub-haplogroup B1 comprise all sheep from western Africa and some from eastern and northern Africa but not southern Africa. Sub-haplogroup B2 is observed in sheep populations from northern (Morocco, Egypt and Algeria) and eastern (mainly Kenya) Africa. Sub-haplogroup B3 is made up exclusively of sequences of ancient breeds of South Africa. The fact that a mixture of haplotypes is observed across geographic regions suggest significant exchange of haplotypes over time (Wanjala et al. 2021). In spite the wide use of mtDNA data to understand the demographic and population history of domestic livestock species, similar datasets are lacking for Ethiopian indigenous sheep breeds.

Modern domestic sheep comprise three broad types: thin-tailed, fat-tailed and fat-rumped (Porter, 2020). Thin-tailed sheep are the most ancient in Africa, and two types are recognized, the long-legged (Sahelian) and the tropical Dwarf (Djallonké) sheep. The Sahelian is confined to hot arid marginal environments in eastern, western and northern Africa, and the Djallonke is well adapted to sub-humid and humid tropics of western and central Africa. In spite of both being thin-tailed, their mitochondrial genomes are divergent implicating separate maternal ancestries (Brahi et al. 2015). Genetic and archaeological information suggests separate introduction and dispersion histories for the African thin-tailed and fat-tailed sheep (Muigai 2003; Aswani 2007; Muigai and Hanotte, 2013). Thin-tailed sheep arrived in the continent via Egypt and their fat-tailed counterparts entered Africa in two waves, one wave arrived through northern and north-eastern Africa and the other via the Horn of Africa (Gifford-Gonzalez and Hanotte 2011). The fat-tailed sheep are the most widely distributed, being found in a large part of northern Africa (from Egypt to Algeria), and in eastern and southern Africa (from Eritrea to South Africa). They also show wide variation in the size and shape of the fat-tail depot structures. The thin-tailed sheep occur in northern Africa, western Africa, Sudan and Ethiopia.

Phenotypic characterisation and classification of Ethiopian shoats

As indicated earlier, a large body of work has provided excellent documentation on phenotypic descriptions, characterisation and classification of Ethiopian indigenous goats (FARM-Africa 1996; Gizaw 2008b) and sheep (Gizaw et al. 2008; 2008a). To the best of our knowledge the descriptions provided in these manuscripts are still valid and reflect the current inherent diversity in Ethiopian indigenous sheep and goats. We thus refer readers to these publications rather than duplicate the same information in this synthesis. However, a summary of the classification of Ethiopian sheep and goat are provided in tables 1 and 2, respectively. Appendix 1 and 2 provide a summary of the phenotypic description of Ethiopian sheep and goat breeds, respectively.

Table 1. Major groups, breeds and sheep types of sheep in Ethiopia.

Major group	Breed	Sheep types	Tail type/shape	Fiber type
Short-fat-tailed	Simien	Simien	Fatty and short	Wool/fleece
	Short fat-tailed	Sekota, Farta, Tikur, Wollo, Menz	Fatty and short	Wool/fleece
	Washera	Washera	Fatty and short	Short hair
Long-fat-tailed	Horro	Horro	Fatty and long	Short hair
	Arsi-Bale	Arsi-Bale, Adilo	Fatty and long	Short hair
	Bonga	Bonga	Fatty and long	Short hair
Fat-rumped sheep	Afar	Afar	Fat rump with fat tail	Short hair
	Black head Somali	Black head Somali	Fat rump/tiny tail	Short hair
Thin-tailed sheep	Gumz	Gumz	Thin and long	Short hair

Source: extracted from Gizaw (2008a)

Table 2.Goat families and breeds of Ethiopia

Family name	Breed name	Other local names
Nubian family	Nubian	
Rift valley family	Afar	Adal, Danakil
	Abergelle	
	Arsi-Bale	Gishe, Sidama
	Woito-Guji	Woyto, Guji, Konso
Somali family	Hararghe Highland	
	Short-eared Somali	Denghier or Deghiyer
	Long-eared Somali	Large white Somali, Degheir, Digodi, Melebo
Small East African family	Central Highland	Brown goat
	Western Highland	
	Western Lowland	Gumz
	Keffa	

Source: extracted from Gizaw (2008b)

Molecular characterization of Ethiopian indigenous goats and sheep

Characterizing genetic diversity and understanding genetic structure is a key component of developing sustainable breed improvement strategies (Groeneveld et al. 2010) and understanding adaptation to extreme environments (Ai et al. 2014). The molecular characterisation of Ethiopian indigenous shoats had previously been based on the analysis of variation at protein (blood and milk) polymorphism and microsatellite markers. With the advent of next generation sequencing, associated technologies and statistical computation, the analysis of genome-wide SNP and whole genome sequence datasets has permitted high resolution mapping of genetic diversity and structure, while providing a deeper understanding of the genome dynamics of Ethiopian indigenous shoats.

Goats

The diversity and structure in Ethiopian indigenous goats were first investigated with protein polymorphism markers (Abera et al. 2002). The study analysed variation in four indigenous goat breeds (Afar, Hararghe Highland, Western Highland and Western Lowland), two exotic breeds (Toggenburg and Anglo-Nubian) and four crossbreds (Toggenburg*Hararghe Highland, Toggenburg*Somali goats, Anglo-Nubian*Hararghe Highland, Anglo-Nubian*Somali goat). The study reported high genetic variation between-breeds and close genetic relationship within-breeds. Following this study, Tesfaye (2004) analysed variation at 15 microsatellite markers genotyped in 11 indigenous breeds from across the country. The analysis grouped the 11 breeds into nine genetic clusters comprising Arsi-Bale, Gumuz, Keffa, Woyto-Guji, Abergelle, Afar, Highland, Eastern and South-eastern goat breeds. The study also showed that four breeds, Afar (24.32%), Abergelle (19.22%), Gumuz (16.59%) and Keffa (12.99%)

explained 75% of the total Ethiopian caprine genetic variation. Chenyambuga et al. (2004) who genotyped 19 microsatellite markers in 10 breeds of sub-Saharan African (SSA) goats included two breeds (North-west Highland and Arsi-Bale) from Ethiopia in their study. Their analysis showed that the diversity in the two Ethiopian breeds did not differ from that observed in the other SSA goats. However, the phylogenetic analysis revealed four genetic clusters, one of which was specific to the two Ethiopian breeds. A study by Halima et al. (2012b) analysed 15 microsatellites in six breeds (Agew, Gumuz, Bati, Abergelle, Central Abergelle, Begia-Medir) found in northern and north-western regions of Ethiopia. The six breeds had medium to high genetic diversity with a mean observed and expected heterozygosity of above 56%. Begia-Medir and Central Abergelle had the closest genetic relationship supported by a genetic distance of 0.039 between them and the most divergent breeds were Gumuz and Abergelle that were separated by a genetic distance of 0.169. The phylogenetic analysis clustered the six breeds into two genetic groups, Abergelle in one group and Agew, Gumuz, Bati, Begia-Medir and Central Abergelle in the other. The findings by Tesfaye (2004) and Halima et al. (2012b) were not in concordance due most likely to the differences in the microsatellite loci used, differences in microsatellite allele scoring and the breeds analysed.

Apart from microsatellite markers which detect diversity at neutral portions of the genome, three studies have investigated variation at protein coding loci. Mestawet et al. (2013) investigated polymorphisms in the α_{S1}-casein gene in 10 Ethiopian goat breeds (Arsi-Bale, Somali, Weyto-Guji, Gumuz, Keffa, Afar, Abergele, Central-Highland, Nubian and Begaiti) and detected 37 novel SNPs (3 each in the exons and the 5′ UTR region, and 31 in introns). The first two exonic mutations resulted in a synonymous transitional substitution while the third gave rise to a non-synonymous transversion substitution. Although the effect of these mutations was not investigated, the authors hypothesised that they could affect the property of the mature protein in Ethiopian goats. Future work should therefore determine the effect of the exonic and the 5′ UTR SNPs on milk parameters. Tarekegn et al. (2016) analysed polymorphisms in exon 1 and 2 of the Kisspeptin 1 (*KISS1*) gene in two Ethiopian breeds (Gondar and Woyto-Guji) and detected five complete substitutions and 15 polymorphic sites in both exons with a transition-to-transversion ratio of 2:1. Four loci constituting 10 genotypes showed a significant contribution to litter size. Vitale et al. (2019) observed two novel amino acid substitutions and a high frequency of a scrapie protective variant, (p.(Asn146Ser)), in the prion protein (*PRNP*) gene in three Ethiopian breeds (Western Highland, Central Highland and Long eared Somali) indicating their lowered predisposition to scrapie infection. The occurrence of the p.(Asn146Ser) variant in Halep-Damascus, Ethiopian and Tanzanian native goats, but not in the Sicilian-Damascus breed, Algerian, Tunisian and Moroccan goats (Fantazi et al. 2018; Serrano et al. 2009), led Vitale et al. (2019) to suggest that following its emergence in the Middle East, the allele could have spread through central Sahara and Ethiopia and subsequently into southern Africa through a different route rather than through the Mediterranean and North African routes. In another study, Teferedegn et al. (2020) detected four non-synonymous novel polymorphisms (G67S, W68R, G69D, and R159H) in the first octapeptide repeat and in the highly conserved C-terminus globular domain of *PRNP* gene in Afar and Arsi-Bale breeds. The S146 genotype that is resistant to scrapie was detected in more than 50% of the study individuals (Teferedegn et al. 2020). *In silico* prediction showed that the R68 variant increased stability, while the S67, D69, and H159 variants decreased the stability of *PRNP* in the two Ethiopian breeds. The new variants occurring in the octapeptide repeat motif were predicted to decrease amyloidogenicity but the H159 variant increased the hotspot sequence amyloidogenic propensity. These novel variants could be the source of conformational flexibility that may trigger gain or loss of function of *PRNP* in Ethiopian breeds.

With the advent of next generation sequencing and its offshoot technologies such as SNP genotyping and statistical computations, several studies have taken advantage of these technologies to investigate the genetic diversity and structure, and genome-wide signatures of natural and artificial selection driving the evolution of domestic livestock. One such study (Tarekegn et al. 2016) used the caprine 50K SNP Chip and genotyped polymorphisms in 13 Ethiopian breeds (Abergelle, Gondar, Ambo, Western highland/Agew, Western lowland/Gumez, Keffa, Woyto-Guji, Arsi-Bale, Afar, Hararghe highland, Short-eared Somali, Long-eared Somali, Nubian). The analysis revealed differences in genome homozygosity, evolutionary history, and management among the 13 breeds, and phylogenetic analysis incorporating patterns of genetic differentiation and gene flow with ancestry modelling, highlighted past and recent intermixing and two deep ancient genome ancestries. The analysis of signatures of selection revealed four strong signatures that were specific to Arsi-Bale and Nubian. These overlapped with genomic regions harbouring genes associated with morphological, adaptation, reproduction and production traits and are most likely driven by selection under environmental constraints and/or human preferences. Interestingly the phylogeny and structure analysis did not support the FARM-Africa (1996) proposed classification of Ethiopian goats, and neither the results of Tesfaye (2004) and Halima et al. (2012b). It however differentiated the 13 populations into seven genetic clusters of which Keffa and Abergelle had the least admixed genomes. A recent study that analysed whole-genome sequence variation in five (Abergelle, Afar, Begait, Central highland and Meafure) breeds (Berihulay et al. 2019) reported closer genetic relationship between Abergelle and Central highland, and between Afar and Meafure, whereas Begait was genetically distinct. This result was supported by ADMIXTURE analysis which revealed a distinct genome profile for Begait but admixed genomes in the other four breeds. This clustering pattern was consistent with the geographic sampling location and genetic composition of the breeds. In their analysis of selection signatures, Berihulay et al. (2019) identified 108 and 205 outlier windows in Abergelle, and Begait goats, respectively which spanned candidate genes involved in reproduction, body weight, fatty acids, and disease related traits.

Sheep

Ethiopia hosts many indigenous sheep, with currently 14 breeds recognized and based on tail morphology, are subdivided into four broad groups: thin-tailed (4 breeds), short fat-tailed (6 breeds), long fat-tailed (3 breeds) and fat-rumped (one breed) (Gizaw et al. 2007).

Like goats, the molecular characterization of Ethiopian sheep breeds has also been undertaken with microsatellite markers (Gizaw et al. 2007) and next generation sequencing technologies (Edea et al. 2017, 2019; Ahbara et al. 2019; Amane et al. 2021; Wiener et al. 2021; Dolebo et al. 2019). From the analysis of 17 microsatellite markers and morphological traits in 14 breeds (Simien, Sekota, Farta, Tikur, Wollo, Menz, Gumz, Washera, Horro, Adilo, Arsi-Bale, Bonga, Afar, Black Head Somali), Gizaw et al. (2007) concluded that their population genetic structure is strongly associated with historical patterns of migration, geographic isolation and interbreeding, while morphological diversity follows ecological patterns. Based on F_{ST}, Bayesian clustering and morphological divergence analysis, Gizaw et al. (2007) amalgamated the 14 breeds they studied into nine breeds and six breed groups.

Studies by Edea et al. (2017) and Ahbara et al. (2019) evaluated population structure of Ethiopian indigenous sheep from the analysis of genotype data generated with ovine 600K (5 breeds; Adilo/Wolaita, Arsi-Bale, Horro, Black Head Somali, Menz) and 50K (13 breeds; Kefis, Adane, Arabo, Gafera/Washera, Menz, Bonga, Gesses, Kido, Doyogena, Shubi Gemo, Loya) SNP Chips, respectively. Both studies showed that Ethiopian breeds, in general, retain moderate to high levels of genetic diversity and admixed genomes. Structure analysis by Edea et al. (2017) clustered the five breeds according to tail phenotype and geographic origin i.e., short fat-tailed (very cool high-altitude), long fat-tailed (mid to high-altitude), and fat-rumped (arid low-altitude), with evidence of admixture between the long fat-tailed breeds. In contrast, the admixture analysis by Ahbara et al. (2019) clustered the 13 breeds into four genetic clusters independent of geographic sampling origin. The analysis by Ahbara et al. (2019) showed also a subdivision of long fat-tailed breeds into two sub-groups representing breeds from western and southern Ethiopia. Although they have the same tail phenotype, the two short fat-tailed breeds (Menz and Gafera) analysed by Ahbara et al. (2019) did not comprise a monophyletic group. The Menz clustered together with the fat-rumped breeds while Gafera clustered with the long fat-tailed breeds. This was attributed to close proximity of the sampling sites. With the aim of inferring genetic relationships of Ethiopian breeds at national, continental and global levels, Amane et al. (2020) generated 50K genotypes for four Ethiopian breeds (Washera, Farta and Wollo (short fat-tailed) and Horro (long fat-tailed)) and analysed them alongside genotypes of four other Ethiopian breeds (Adilo, Arsi-Bale, Menz, Black Head Somali) and east, north and south African, and Middle east and Asian goat breeds. Their population phylogeny and structure analysis returned four genetic clusters in the eight Ethiopian breeds and the four short fat-tailed breeds (Wollo, Menz, Farta, Washera) were not monophyletic. These results are consistent with those of Ahbara et al. (2019). Interestingly Amane et al. (2020) observed the Ethiopian fat-rumped sheep breeds shared a common genetic background with Kenyan fat-tailed breeds. This result is rather surprising given the physical geographic distance separating the two and their phenotypic differences. Amane et al. (2020) also observed that Ethiopian breeds had comparatively lower genetic diversity (average $H_E = 0.366$) than Middle east (Afshari; $H_E = 0.376$) and north African ($H_E = 0.401$) breeds. The higher level of genetic diversity in north African breeds may be because of their high degree of admixture resulting from deliberate mating between fat-tailed and thin-tailed breeds to reduce the fat-tail size in the former.

Ethiopia provides an ideal setting to investigate environmental adaptation in livestock due to its wide variation in geo-agro-eco-climatic characteristics and extensive genetic and phenotypic variation in its livestock. Based on the hypothesis that sheep in Ethiopia are adapted to diverse natural environments, Ahbara et al. (2019), Edea et al. (2019) and Wiener et al. (2021) assessed signatures of selection in Ethiopian sheep from the analysis of SNP genotype data and whole genome sequences. The analysis by Ahbara et al. (2019) identified eight candidate regions spanning genes influencing growth and skeleton development, phenotypic characteristics e.g., horn shape and size, fat metabolism and deposition and response to stress, pointing to possible outcomes of selection for adaptation and fat deposition. Edea et al. (2019) detected signatures of selection spanning regions overlapping genes known to be involved in biological processes and pathways of relevance to adaptation under extreme altitudes, including respiratory system development and smoothened signaling pathway in Menz and Long-fat tailed sheep. From the analysis of whole genome sequences generated in a set of 13 breeds, 12 from a range of environments and geographic regions across Ethiopia and one from Libya (LBR), all of which had been analysed previously by Ahbara et al. (2019), Wiener et al. (2021) identified over three million single nucleotide variants and applied landscape genomics approaches to investigate their association with environmental variables conferring adaptation. Although Wiener et al. (2021) found evidence of enrichment for genes associated with high-altitude adaptation, no strong association was identified with hypoxia-inducible-factor genes. In particular, their results showed that environmental adaptation for precipitation-related variables was stronger than that related to altitude or temperature, consistent with large-scale meta-analyses of selection pressure across species. Several altitude-associated genes showed evidence of adaptation with temperature, suggesting a relationship between responses to these environmental factors.

The investigation of the genetic basis of traits of economic importance has also been undertaken in Ethiopian sheep. Taking advantage of the observation of high prolificacy in the performance recorded Bonga breed, Dolebo et al. (2019) genotyped two classes of animals of high and low prolificacy. The former included animals that had given birth to twins, triplets and quadruplets, and the latter included animals that had given birth to singlets. These animals were genotyped with the Ovine 600K SNP BeadChip and by contrasting the two classes of animals, the authors identified two signals of selection, one on chromosome (OAR) X and the other on OAR5. The *BMP15* gene occured within the candidate region interval of the signal on OARX and *GDF9* occurred adjacent to the signal on OAR5. As the signal on OARX was the strongest, the authors hypothesised that *BMP15* could be the primary candidate gene for prolificacy in the Bonga breed while *GDF9* could be playing a secondary role.

Summary/Future directions

Shoats play a significant role in the macro- and micro-economy of Ethiopia. They have been part of the socio-cultural orientation of the communities associated with them for millennia. Here we provided an overview of genetic characterisation studies that have been undertaken in Ethiopian sheep and goats. Although different markers were used, a common underlying observation was that Ethiopian indigenous breeds of shoats have high genetic diversity but little genetic differentiation among them. The latter can be attributed to admixture between breeds due to socio-cultural and economic exchange of livestock to maintain societal and family bonds. Indeed, ADMIXTURE analysis did show that Ethiopian sheep and goats have admixed genomes. The analysis done by several studies also revealed signatures of environmental adaptation in Ethiopian breeds of shoats and the presence of variants that confer resistance to diseases such as scrapie and production such as prolificacy. In spite the pool of knowledge generated, the studies have been restricted in their scope in terms of geographic coverage and breeds. There is also little overlap in the breeds analysed between different studies thus the picture of the genomic composition of Ethiopian breeds of shoats remains incomplete and disjointed. There is thus a need to undertake a proper genetic characterisation that would sample all the breeds found in the country. The analysis would benefit by including breeds from across Africa, the Middle East and Europe, in the context of a meta-analysis, which will map the diversity in Ethiopian indigenous shoats to the global gene pool. The use of either high density SNP markers or whole genome sequences would particularly be useful in this regard due to the ease of integrating datasets from different studies. The analysis of whole genome sequences will also result in the identification of signatures of selection for adaptation to diverse environments and the likely causative variants. Furthermore, the implementation of community-based breeding programs targeting indigenous breeds across the country offers a unique opportunity to apply genomic techniques to investigate the genetic basis of the traits being recorded and under selection. It also provides an opportunity for the application of cutting-edge genomic technologies such as genomic evaluations, genomic selection and precision breeding under smallholder farmer conditions in tropical settings. In general, the results from the few studies summarised in here are providing the foundation to investigate further the genetic makeup and profiles of Ethiopian indigenous shoats.

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Annexes

Annex 3. Important distinguishing physical characteristics of sheep types in Ethiopia

Name	Other names	Important physical characteristics	
Menz	Legegora, Shoa, Abyssinian, Ethiopian Highland sheep	Short, fat tail turned-up at end; long fleece with coarse wool; small body size; short-legged; commonly black with white patches, white, brown, white with brown patches; straight-faced; horned males; short semi-pendulous ears with 12% rudimentary ears in the population.	
Sekota	Tigray Highland, Abergelle	Short, fat tail turned-up at end and fused with main part; hair coat (white animals have fine hair or woolly under-coat); medium-sized; predominantly plain brown or white coat, few blacks with brown belly; semi-pendulous or rudimentary ears in Wag Himra and Tigray, predominantly rudimentary in Tekeze valley. Reared by Agew, Tigray and Amhara communities.	
Semien		Short, fat tail; well developed woolly undercoat; largest of the highland wooled sheep; plain brown, plain white, brown/white with white/brown patches, plain black and black with brown belly; unique long laterally spiral horn in males and short horns in most females; Reared by Amhara communities.	
Tikur		Short fat tail; woolly undercoat; small body size; predominantly (60%) black coat; majority short semi pendulous ears, 24% rudimentary ears. Reared by Amhara communities	
Wollo		Short, fat tail with short twisted/coiled end, occasionally turned up at end; well developed woolly undercoat; small size; predominantly black, white or brown, either plain or with patches of white, black or brown; long hair with woolly undercoat; horned males. Reared by Amhara communities	

Farta		Short, fat tail; woolly under coat; medium size; commonly white (37.5%), brown (27.5%) and black with brown belly (15%), white/brown with brown/white patches; males are horned. Reared by Amhara communities	
Washera	Agew, Dangilla	Short, fat tail; short-haired; large body size; predominantly brown; both males and females are polled. Reared by Amhara and Agew communities	
Adilo	Wolaita	Long, fat tail reaching the hocks, broad at the base and upper third with long tapering end; short-haired; large size; males are short-horned and 18.4% of ewes are horned; predominantly brown (43%), brown with white patches (32%), black (16%), and black with brown patch (9%). Reared by southern communities	
Arsi-Bale		Long, fat tail with twisted end in some; hairy fibre, especially in adult ewes, males have minor wool growth in some parts of body; medium size; males and most females (52%) are horned; large size; brown coat (35.1%), brown with white patches (24.3%), black, white, and combinations of above colors. Reared by Oromo communities	
Horro		Long, fat tail extending below hock, either straight (51.4%) or coiled/twisted (48.6%) at the tapering end; prominent fat tail in males; short-haired; large size and leggy; dominant colors are brown and fawn, belly is lighter especially in adult ewes, less frequent are black, white, brown with white patches; both sexes are polled. Reared by Oromo, Benishangul and Gambella communities	

Bonga	Gesha Menit	Long, fat tail with straight tapering end (98.4%); hair sheep; large size; predominantly plain brown (57.9%) or with black (.9%) or white (5.3%) shade, plain white (10.5%) or with brown patches (10.5%), and black (2.6%); both sexes are polled. Reared by Keffa, Sheka and Bench communities	
Afar	Adal, Danakil	Rump, wide, fat tail, with some large fat tails reaching below the hock; hair fibre; medium size; characteristically uniform creamy white/ beige coat; rudimentary ear; polled; dewlap. Reared by Afar, Amhara, Tigray people	
BHS	Wanke, Ogaden, Berbera black	Short, fat rump with a stumpy appendage; short-haired; medium size; uniform white body and black head and neck; polled; convex face, especially in males; short, outward forward drooping ear; well developed dewlap. Reared by Somali and Oromo, Konso and south Omo communities	
Gumz		Long, thin tail reaching below the hocks; hair coat' somewhat dwarf; convex face profile; long pendulous ear; commonly plain brown or with patch (39.4%), white with brown or black patch (21%), black (15.8%), white, black with white patch, brown with black patch; polled. Reared by Gumz and Amhara communities.	

Extracted from Gizaw (2008a)

Annex 4. Key distinguishing physical characteristics and other important physical features of goat breeds

Name	Physical characteristics	
Nubian	**Key identifying features:** Tall (height at withers = 70.1 cm in females and 74.0 cm in males); markedly convex facial profile; long ears; hairy. **Other features:** 63% of the males have curved horns; 37% have straight horns; horns in males are pointed backwards; the main coat color is black (72%); with occasional white and red patches on a black background; ruff and beard are present; no wattles.	
Afar	**Key identifying features:** concave facial profile; narrow face; prick eared; leggy; long, thin upward-pointing horns; patchy coat color. **Other features:** fine, short hair coat; variable colors - white 48%, light brown 25%, black 27%, and flecks and patches are also common; ruff is present in 67% of the goats; beard is present in 79% of males; wattles are relatively common (19%).	
Abergelle	**Key identifying features:** Stocky build; mostly reddish-brown color; males have magnificent spiral horns directed backwards. **Other features:** straight (44%) to concave (56%) facial profile; plain coat color (56%), with 33% patchy and 11% spotted; hair is short and smooth; ruffs and beards are present; wattles are almost entirely absent (94%).	
Arsi-Bale	**Key identifying features:** Medium-large size; often hairy; coat colors are mostly in a combined patchy pattern. **Other features**: predominantly straight facial profile (98%); males have curved (47%) and straight (41%) horns mainly pointing backwards (58%) with some pointed straight upwards (28%); polled goats were 6% in both sexes; ruffs occurred in 33% of males with beards on 92% males and 52% of females; wattles are present in 14% of males and 11% of females.	
Woyto-Guji	**Key identifying features:** coat colors are brown, black or red often marked with black or brown stripes along the back, on the underside or on the front of the legs; short, shiny, smooth coat; small head with mainly straight facial profile. **Other features**: medium-sized; straight horns (71% of the males), curved (26%), polled (3%); horns point	

	backwards (75%), upward (21%) and laterally (2%); beard is present on 96% of all males, ruff present in 91% and wattles in 10%.	
Hararghe Highland	**Key identifying features:** Small; white, brown or black; commonly polled. **Other features**: straight (60%) or concave (40%) facial profile; horned goats have straight (32%) or curved horns (29%); short hair; colors are mainly plain (90%), 10% are spotted; beard present in 72% of males; no ruffs; wattles present in 14% of goats.	
Short-eared Somali	**Key identifying features:** Medium-sized (smaller than Long-eared Somali); mainly white coat; short smooth hair. **Other features**: straight facial profile; males bear straight horns (46%) or upward pointing (64%); females bear curved horns (50%) either pointing upwards (55%), backwards (27%) or laterally (12%); polled goats are found in 5% of males and 7% of females; low incidence (6%) of spiral horns; in both sexes; coat color white (76%), brown (9%), black (7%) and grey (7%) occasionally in spotted patterns (12%); no ruffs; beards present in 79% of males and 14% of females; wattles found in 5% of all goats.	
Long-eared Somali	**Key identifying features:** Large; white; short hair. **Other features**: predominantly straight face; horns are curved (41% in males, 46% in females), and pointed backwards in 38% of males and upwards in 48% females; 13% of horns in both sexes have a lateral orientation; polledness is 19% in males and 8% in females; color is plain white (92%), brown (4%), black (3%) and grey (1%); spotted coat pattern observed in 21% of males; ruffs occur in 21% of males but never in females; beards in 66% of males and 7% of females; wattles in 6% of males and 3% of females.	
Central Highland	**Key identifying features:** Medium-sized; broad-faced; thick horns; reddish-brown color. **Other features**: facial profile straight (71%) or concave (29%); males are horned, 82% straight and pointed backwards, 13% curved and 5% spiral horns; coat type is short and smooth with 51% plain color, 42% patchy and 7% spotted; predominant color is red-brown (41%), the rest being black, white and grey; beard is present in 82%; ruff in 99%; and wattles in 6% of males.	

Western Highland	**Key identifying features:** Tall; coarse hair; white and/or fawn color. **Other features:** concave facial profile (100%); coarse long coat (82%); 12% of the animals have hair on their thighs; color pattern is either plain (51%), patchy (42%), or spotted (7%); colors are white (42%) and fawn (42%), and combinations of these colors; polled (14%); horned goats have straight (76%) horns directed backwards (73%); ruff present	
Western Lowland	**Key identifying features:** Short, straight face, fawn or white patchy color. **Other features:** straight facial profile (100%); short smooth coat (81%) and coarser coat (16%); colors are white (42%), fawn (38%), black (9%) and grey (11%), occurring mainly in patches (73%). Most males have straight horns (85%) orientated backwards (77%); 12% of males are polled; ruff present in 96%, beard in 70% and wattle in 12% of males.	
Kaffa	**Key identifying features:** Small, red or black, short neck, short prick ears. **Other features:** straight facial profile 92%; most males (83%) have straight horns pointing backwards (80%), a small proportion (14%) have curved horns; low incidence of polledness (3%); most goats have a coarse (38%) to hairy (27%) coat type; some 16% have hair on the thighs; plain colors predominate (52%), with some patchy color patterns (45%); main colors are black (30%) or brown (31%); among males, 88% have beards, 97% have ruffs; wattles are present on 12% of all goats.	

Extracted from Gizaw (2008b)