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REVIEW

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History and genetic diversity of African sheep: Contrasting phenotypic and genomic diversity

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Abstract

Domesticated sheep have adapted to contrasting and extreme environments and continue to play important roles in local community-based economies throughout Africa. Here we review the Neolithic migrations of thin-tailed sheep and the later introductions of fat-tailed sheep into eastern Africa. According to contemporary pictorial evidence, the latter occurred in Egypt not before the Ptolemaic period (305–25 BCE). We further describe the more recent history of sheep in Egypt, the Maghreb, west and central Africa, central-east Africa, and southern Africa. We also present a comprehensive molecular survey based on the analysis of 50K SNP genotypes for 59 African breeds contributed by several laboratories. We propose that gene flow and import of fat-tailed sheep have partially overwritten the diversity profile created by the initial migration. We found a genetic contrast between sheep north and south of the Sahara and a west–east contrast of thin- and fat-tailed sheep. There is no close relationship between African and central and east Asian fat-tailed breeds, whereas we observe within Africa only a modest effect of tail types on breed relationships.

KEYWORDS
adaptation, Africa, fat tail, history, phylogeography, sheep, thin tail

INTRODUCTION

The African continent presents a remarkable diversity of sheep attested by the wide variety of phenotypes encountered (Mason, 1967; Epstein, 1971; Ryder, 1984; Blench, 1999a; Hall, 2000; Bemji et al., 2023; Table S1, Figure 1, Figure S1). Traditionally, groupings have been as follows: thin-tailed breeds from the Mediterranean coast; thin-tailed hair sheep of the Sahel; thin-tailed trypanotolerant dwarf hair sheep of coastal west Africa, and fat-rumped and fat-tailed breeds in east Africa. Other traits distinguishing breeds have been tail length, the types of coat (hair or wool), dwarfism and adaptations to different climates, disease and parasites. As with other livestock, the distribution of these types at the continental level reflects human

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migration routes, adaptation to extreme eco-climates and infectious diseases, such as trypanosomosis (Ebhodaghe et al., 2018; Geerts et al., 2009) and ovine rinderpest (*peste des petits ruminants*, Kjekshus, 1977). Additionally, transhumance and permanent migrations may have been strategies to cope with environmental

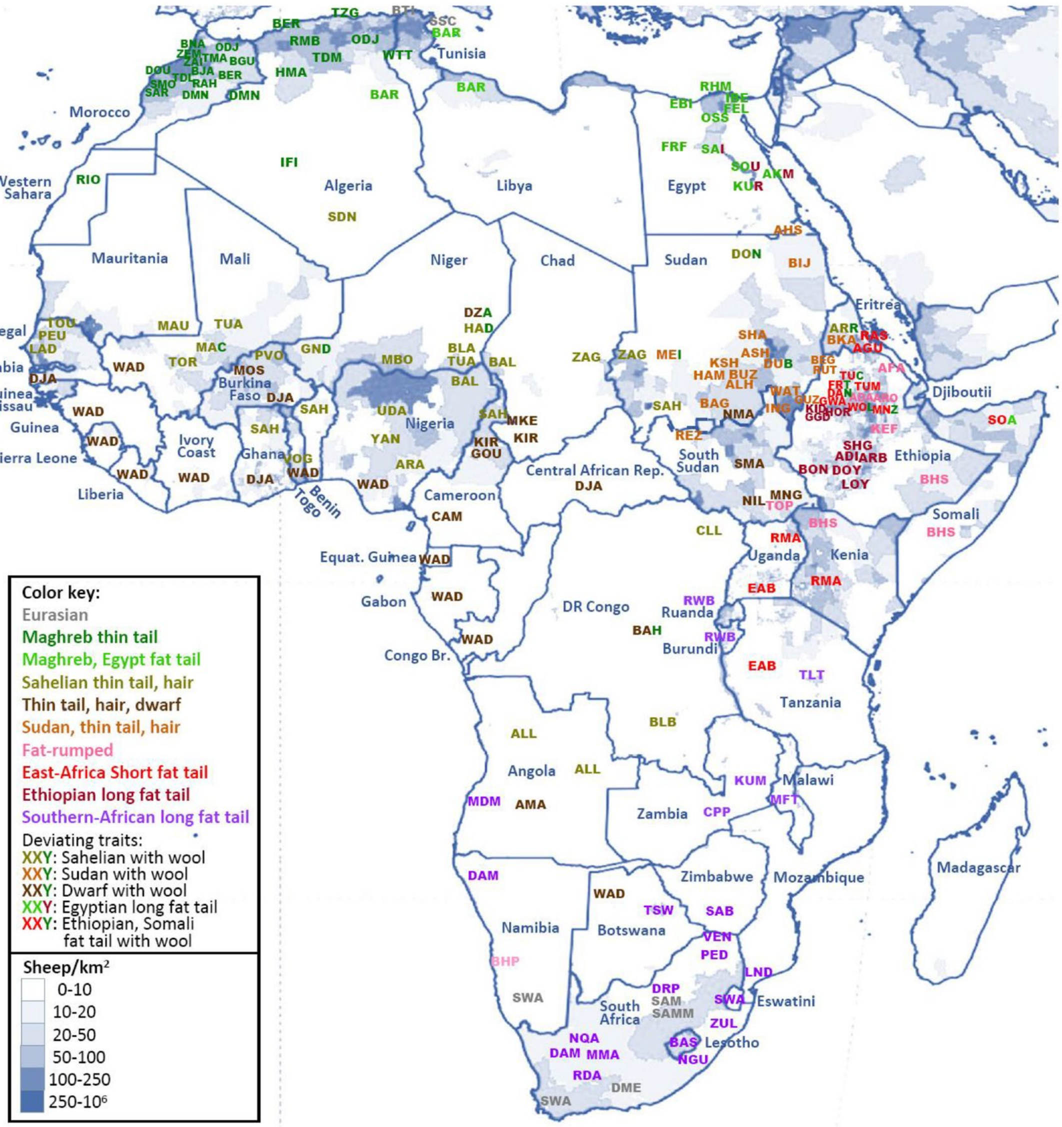

FIGURE 1 Current density of sheep (Gilbert et al., 2018) and approximate locations of continental African sheep breeds with colors indicating the types of sheep. See Table S1 for details and references. Breed codes: ADA, Adane; ADI, Adile; AFA, Afar; AGU, Akele Guzai; AHS, Abour-Halai-Shalat; AKM, Abudeleik Kanzi Maenit; ALH, Al Ahamda; ALL, Angola Long-legged; AMA, Angola Maned; ARA, Ara-Ara; ARB, Arsi Bale; ARO, Arabo; ARR, Arrit; ASH, Shugar; BAG, Bagarra; BAH, Bahu; BAL, Balami; BAR, Barbarine; BAS, Basotho; BBA, Bali-Bali; BEG, Begait; BER, Berber; BGU, Beni Guil; BHP, Black-headed Persian; BHS, Black-headed Somali; BIJ, Bija; BJA, Boujaad; BKA, Baraka; BLB, Baluba; BNA, Beni Ahsen; BON, Bonga; BTI, Black Thibar; BUZ, Buzee; CAM, Cameroon Dwarf; CLL, Congo Long-legged; CPP, Chi Pepo; DAM, Damara; DAN, Dangila; DJA, Djallonke; DME, Döhne Merino; DMN, D'man; DON, Dongola; DOU, Doukkala; DOY, Doyogena; DRP, Dorper; DUB, Dubasi; DZA, Dané Zaqla; EAB, East African Blackheaded; EBI, Barki; FEL, Fellahi; FRF, Farafra; FRT, Farta; GGD, Gumuz Gesses Dibate; GHI, Ghimi; GND, Goundoun; GOU, Gourane; GUZ, Gumz; GWA, Gafera Washera; HAD, Hadina; HAM, Hammari; HMA, Hamra; HOR, Horro; IBE, Ibeidi; IFI, Ifilène; ING, Ingessana; KD, Kido; KEF, Kefis; KIR, Kirdi; KSH, Kabashi; KUM, Kumumava; KUR, Kurassi; LAD, Ladoum; LND, Landim; LOY, Loya; MAC, Macina; MAU, Black Maure; MBO, Mbororo; MDM, Mondombe; MEI, Meidob; MFT, Malawi Fat-tailed; MKE, Mayo-Kebbi; MMA, Meatmaster; MNG, Mongalla; MNZ, Menz; MOS, Mossi; NGU, Nguni; NIL, Nilotic; NMA, Nuba Maned; NQA, Namaqua Afrikaner; ODF, ODJ, Ouled Djellal; OSS, Ossimi; PED, Pedi; PEU, Peul-Peul; PVO, Peul Voltaique; RAH, Rahalya; RAS, Rashaidi; RDA, Ronderib Afrikaner; REZ, Rezegat; RHM, Rahmani; RIO, Rio d'Oro; RMA, Red Maasai; RMB, Rembi; RWB, Rwanda-Burundi; SAB, Sabi; SAH, Sahelian; SAI, Saidi; SAM, South African Merino; SAMM, SouthAfrican Mutton Merino; SAR, Sardi; SDN, Sidaoun; SHA, Shanbali; SHG, Shubi Gemo; SMA, South Sudanese; SMO, South Moroccan; SOA, Somali Arab; SOU, Souhagi; SSC, SiciloSarde; SWA, Swakara; SWZ, Swazi; TDL, Tadla; TDM, Tadmit; TLT, Tanzania Long-tailed; TMA, Timahdite; TOP, Toposa; TOR, Toronké; TOU, Touabire; TSW, Tswana; TUA, Tuareg; TUC, Tucur; TZG, Tazegzawt; UDA, Uda; VEN, Venda; VOG, Vogan; WAD, West African Dwarf; WAT, Watish; WOL, Wollo; WKA, West Kanem; WOL, Wollo; WTT, Western Thin-tailed; YAN, Yankasa; ZAG, Zaghawa; ZAI, Zaian; ZEM, Zemmour.

challenges. Therefore. genetic variation of African sheep should be interpreted in historic and sociocultural contexts (Gifford-Gonzalez & Hanotte, 2011) as well as in terms of physical and adaptive characteristics. The same considerations apply to goats (Amills et al., 2017; Pereira & Amorim, 2010).

African sheep have evolved in both migrating pastoral and resident farming societies (Broodbank & Lucarini, 2019; Brower Stahl, 2005; Garcea, 2016; Gifford-Gonzalez, 2005; Marshall & Hildebrand, 2002) and now number over 400 million animals (FAOSTAT 2021, https://www.fao.org/faostat/en; data from 2015). In terms of agricultural production, sheep in Africa have been primarily a source of meat and much less important as milk and wool producers, than they are in Eurasia and Australasia. However, their value for meat production may have been less important than their social and ritual value (Russell, 2017). In several African regions, social status of owners has been indicated by the flock size, which may have created an environment where selection has been more based on survival than production traits. In traditional settled communities, sheep are kept by smallholders (McDermott et al., 2010; Udo et al., 2011) and their husbandry is becoming appreciated by policymakers as promoting the participation of women in the local microeconomy (Chanamuto & Hall, 2015; Haile et al., 2020).

An abundance of livestock images in rock art demonstrates ancient husbandry practices (Ben Nasr & Walsh, 2020; Muzzolini, 2000). Tantalizing evidence for the cultural or religious significance of sheep comes from these images, which include corkscrew-horned sheep in Libya and Sudan (Le Quellec, 2016, 2020), and 'radiant sheep' (*ovins solaires*) or rams with decorative headgear (*beliers ornés*) (Achrati, 2003; Bangsgaard, 2014; D'Huy, 2018; Roubet & Amara, 2015). However, these images are difficult to date and our understanding of the symbolic or cultural significance of the rock art is only partial (Holl, 1998a; Lenssen-Erz, 2012).

Here, we describe for different regions in Africa the immigrations of sheep and their later history: thin- and fat-tailed sheep in Egypt and the Maghreb; thin-tailed Sahelian, Sudanese sheep and West-African Dwarf sheep; and fat-tailed sheep in central-east and southern Africa. We then present a molecular-genetic analysis of African sheep breeds, which suggests that the diversity pattern created by the earlier migrations has been changed by more recent gene flows. Breed relationships also show that there is no consistent genetic contrast between thin- and fat-tailed sheep.

EGYPTIAN AND MAGHREB SHEEP

Wild *Ovis* species are acknowledged never to have occurred in Africa, refuting early notions of an African domestication (Epstein, 1971; McDonald, 1998). Sheep husbandry commenced during the Neolithic period with agriculture spreading from western Asia to Egypt between 6500 and 5000 BCE (Zeder, 2017). Egypt appears the most obvious entry point for livestock after their domestication in southwest Asia and it has generally been assumed that the first African sheep entered the continent via the Sinai Isthmus/Isthmus of Suez (Gautier, 2002). However, evidence of cattle and/or ovicaprines (Di Lernia, 2021; Figure 2) at several sites in North Africa of roughly the same date, indicate a rapid spread of livestock husbandry. This occurred faster than the longitudinal migrations in Eurasia and indicates maritime transportation of early Neolithic sheep, from both the eastern Mediterranean and the Iberian Peninsula to Tunisia and Morocco (Baazaoui et al., 2024; Fregel et al., 2018; Kandoussi et al., 2020; Linstädter et al., 2012; Myles et al., 2005; Simões et al., 2023; Zeder, 2018).

Many hunter–gathering and foraging societies apparently responded to the spread of herding by developing into forager–herder societies (Broodbank & Lucarini, 2019; Dunne et al., 2018; Martínez-Sánchez et al., 2018). Thus, in the Maghreb, the Capsian culture in eastern Algeria and Tunisia had acquired Neolithic features in a hunter–gatherer context by 6000 BCE and, from 5400 BCE, a Neolithic productive economy (Aouadi et al., 2014; Mulazzani et al., 2016). Subsequently, fully pastoral societies with dairying and intensive animal husbandry were established along, and south of, the Mediterranean littoral (Smith, 1992; Hassan et al., 2000; Gautier, 2002; Barich, 2014, 2016, 2019; Cruz-Folch & Valenzuela-Lamas, 2018; Dunne et al., 2018; Rowland et al., 2021; Figure 2).

In the Nile Delta, Neolithic sites are difficult to access because of continuous silting (Smith, 1992), but microfossils have shown that animal husbandry had started by 4700 BCE. Ovicaprine bones, some of which are undoubtedly from sheep and dated at around 6500 BCE have been found in Egyptian archaeological sites (Holdaway & Wendrich, 2016; Linseele, 2016, 2021; Linseele et al., 2014; Shirai, 2020). These findings indicate a mobile lifestyle, without proof of cultivation of crops. The transition of a hunter-gatherer to a pastoral society in the Nile Valley since 6000 BCE was probably a locally differentiated process (Salvatori & Usai, 2019), which may in Egypt and other north African regions have lasted around 1000 years (Dunne et al., 2018).

Artistic representations of sheep in Ancient Egypt allow us to describe the types of sheep during successive periods. Egyptian sheep from 3000 BCE to 200 CE show characteristic horizontal corkscrew horns, long legs and thin tails of medium length (Figure S2B). These sheep have sometimes been known as *Ovis longipes palaeoaegyptiacus*, but in response to current nomenclatural practice (Gentry et al., 2004), we propose the designation Ancient Egyptian corkscrew-horned (AEC). Sheep with such horns were already present during

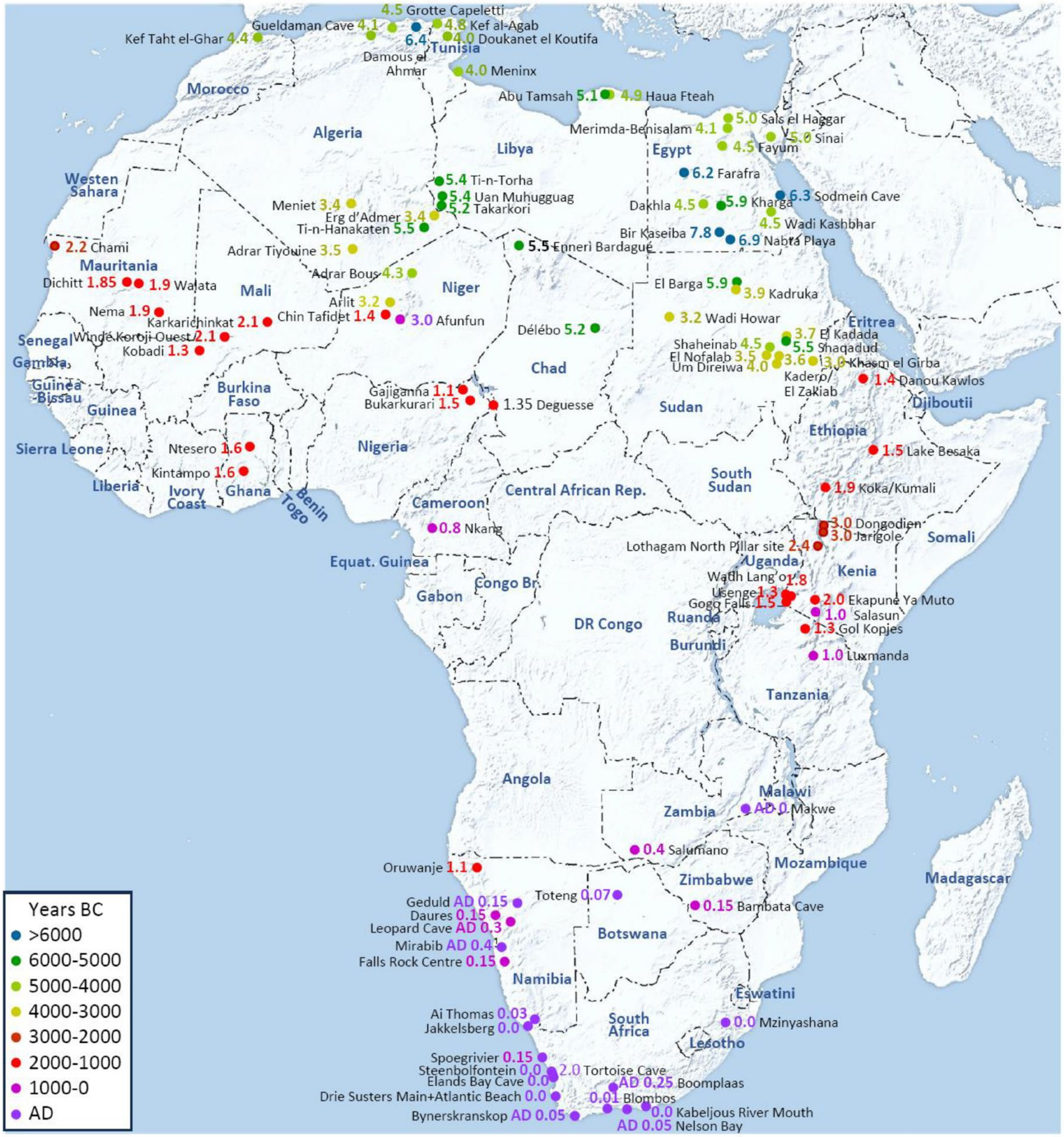

FIGURE 2 Archeological sites with ovine remains (Table S4). Datings may be based on the analysis of animal remains, food remains, or on the age of the site and are shown in 1000 years BCE or, if indicated, 1000 years CE. Per site and per region, only the oldest reported date is shown.

the 6th millennium BCE in Çatal Hüyük (Anatolia, Epstein, 1971; Figure S2B). Egyptian AEC sheep were depicted as black, white, and piebald. During the Middle Kingdom (2040–1782 BCE), AEC sheep were gradually replaced by sheep with coiled horns resembling those of a wild relative, the argali *Ovis ammon*, and the symbol of the god Amon. We have designated these sheep as the Ancient Egyptian Ammon-horned sheep (AEA, formerly *Ovis platyura aegyptiaca*; see Figure S2A,B). The AEC disappeared at the end of the Middle Kingdom period (Epstein, 1971; Ryder, 1983) but continued to be depicted as a symbol of the Khnum deity with adaptations to the contemporary morphology of sheep (Bickel, 1992): the addition of coiled horns during the reign of Ramses III (1194–1163 BCE) and with ears pointing backwards during the reign of Ptolemy III (246–222 BCE).

Several reviews (Clutton-Brock, 1993; Epstein, 1971; Muigai & Hanotte, 2013; Ryder, 1959, 1987) state that AEA sheep were fat-tailed, like contemporary sheep in southwest Asia and the Arabian Peninsula. All these sources derive from two French texts (Lortet & Gaillard, 1905, 1907), that indeed mention that AEA had fat tails, but without any evidence (see the supplemental text for more details). In fact, contemporary depictions show that, despite the designation *platyura* (=broad-tailed), AEA was thin-tailed during the 2nd millennium BCE (Boessneck, 1988; Gootwine, 2018; Figures S2C). An image from the period 1938–1756 BCE (Figure S2C) suggests that AEC and AEA were herded together, which would indicate that AEC and AEA are horn variants within one population. Plausibly, the Ammon horn trait originated from more western populations, which Yoyotte (2005), together with the thin-tailed AEA, classified as *Ovis aries palaeoatlanticus* (*Bélier du Fezzan*, *Fezzanschaf*; Fezzan is southwest Libya).

Egyptian sheep depicted during or after the Ptolemaic period (305–25 BCE; Boessneck, 1988; Gootwine, 2018; Figure S2D) show modest fat tails, while contemporary sheep in Anatolia already had developed much larger fat tails (Herodotus 430 BCE). This may be explained by the widespread keeping of pigs in ancient Egypt, so sheep were not needed as a source of animal fat. In contrast, fat-tailed sheep would have been a viable alternative to pigs in the dry climates of southwest Asia and in Jewish and Islamic societies (Simoons, 1978). Modern Egyptian sheep have large fat-tails and were possibly introduced during the Islamic conquest.

Rock art in Libya shows an AEC-like individual (Figure S2B, Le Quellec, 2020), suggesting a westward expansion of Egyptian thin-tailed sheep, which, just as in Egypt, was replaced by fat-tailed sheep. A depiction in the Atlas Mountains in Tunisia (Ben Nasr & Walsh, 2020; Figure S2A) that could be dated to 6200–4000 BCE shows sheep with normal coiled horns, which may very well have been the ancestors of the present-day Magreb thin-tailed sheep. However, the major indigenous breed in Libya is the fat-tailed Barbarine, which in east Algeria and Tunisia are kept together with thin-tailed sheep populations. The alternative designation 'Barbary' for the Maghreb fat-tailed sheep is unfortunately confusing and should be reserved for the wild aoudad or *Ammotragus lervia* from the same region.

The ancestors of the Barbarine sheep were considered to have been imported from Phoenicia to Carthage (Sagne, 1950; Sarson, 1971). From the 3rd century CE, Barbarine sheep in Tunisia were replaced by thin-tailed sheep (Sarson, 1973) and it has been proposed that this trend was reversed in the 9th century CE (Sarson, 1973), although supporting pictorial evidence has only been shown for the first event. Just like the Berber sheep (see above), the Barbarine sheep are now endangered because of absorption or replacement by the thin-tailed Ouled-Djellal sheep of the Arab type because of a reduced preference for fat tails (Belabdi et al., 2019; Jemaa et al., 2019).

Today, the Maghreb thin-tailed breeds are essentially reduced to the large and fast-growing Arab type, and the small and primitive Berber sheep on the poor pastures of the Rif and Kabylia Mountains (Table S1; Mason, 1967; Epstein, 1971). By 1000 BCE the northern Maghreb was inhabited by the Berber people with an economy based on intensive cereal production and the husbandry of cattle, pigs, goats, and sheep. The Berber sheep have been associated with a nomadic Berber subtribe, the Zenete, who between the Roman occupation and the Arab conquest spread over the plateau regions of the Maghreb (Sagne, 1950). The Roman period saw the development of a wool industry in the Maghreb and Egypt (Azaza & Colominas Barberà, 2019; Johannesen, 1954; Keenan, 1989; Trixl et al., 2020; Wilson, 2004). This may very well have stimulated the importation of high-quality wool breeds such as the Tarentine sheep (Ryder, 1959).

After the fall of the Roman Empire, wool production was discontinued. Later, a process of Arabization of the Berber sheep may have led to the emergence of an Arab type (Mason, 1967; Porter et al., 2016). This was accelerated by a strictly supervised pastoral policy during the colonial period, when the Berber and Barbarine types were judged to be of poor quality or even 'abnormal' (Cambon, 1893; Couput, 1900; Viger, 1982). However, some isolated populations, generally located in the mountains, persisted. Today, the Arab type extends from the plains of Western Tunisia through the Algerian steppes to the borders of Morocco. The most popular breed, the Ouled-Djellal, also called *Queue Fine de l'Ouest* in Tunisia (Bedhiaf-Romdhani et al., 2020; Jemaa et al., 2019) is widely used by breeders who crossbreed their animals to improve productivity. This anarchic crossbreeding is intensifying and may already have contributed to the genetic homogeneity of the Tunisian, Algerian, and Moroccan sheep breeds (Baazaoui et al., 2024; Belabdi et al., 2019; Gaouar et al., 2017; Kandoussi et al., 2021). Brisebarre (2009) reported massive and unregulated inflows (200 000 to 500 000 head per year) of Algerian Ouled-Djellal into Morocco. The Sidaoun thin-tailed hair sheep in the desert environment in Algeria are of the Tuareg type (Ayantunde et al., 2007) belonging to the Sahelian sheep.

SAHELIAN AND SUDANESE LONG-LEGGED HAIR SHEEP

By 5500 BCE, what is now the Sahara Desert was acquiring a savannah-like climate (Cremaschi et al., 2014; Dunne et al., 2018), which allowed gradual movements westwards and southwards of people dependent on pastoralism and/or cultivation (Gifford-Gonzalez, 2000). Sheep were present in the northern part of the Sahara as far back as 5500 BCE (Figure 2) and development of the Sahara Desert was essentially complete by 4000 BCE. Between 4000 and 3000 BCE, the southwards spread of husbandry into the Sahel region was relatively slow (Di Lernia, 2021; Hildebrand & Grillo, 2012; Smith, 1992). The migrations of sheep and other livestock species were at least partially in response to climate changes (Chritz et al., 2019; Phelps et al., 2020). The absence of any animal remains in the western Sahara suggests that sheep did not reach west Africa by a coastal route but migrated via an inland route (Holl, 1998b). An increase in aridity after 3000 BCE (Holl, 1998b; MacDonald et al., 2017) stimulated a shift from hunter–gatherer strategies to livestock. Thus, the earliest sites for cattle, sheep, and goat settlements in the Sahel are dated to 2000–2500 BCE (Holl, 1998b).

Further to the south in the humid coastal regions, the diffusion of sheep and other livestock is believed to have been impeded by parasitic disease pressures, and especially by moisture-related diseases such as trypanosomosis (Gifford-Gonzalez, 2017; Mitchell, 2018).

Modern Sahelian sheep are of the thin-tailed hairy African long-legged type, with the exception of the Macina wool sheep in Mali and Niger (Meyer, 2023), while the Sudan Desert type of long-legged sheep is found between Darfur (west Sudan) and the Red Sea (Adamu, 2005). This is an ancient type of sheep as testified by skeletons found in southeast Egypt (Wadi Khasbhar, 5000–4000 BCE; Osypiński et al., 2021) and in lower and upper Nubia (1500–2400 BCE, Chaix & Grant, 1987; Bangsgaard, 2014). As the ancestors of the Sahelian sheep arrived from Asia, northeast Africa and/or Europe before the development of wool sheep the hair phenotype probably is the ancestral trait. A common ancestry with the long-legged AEC is an obvious possibility (Epstein, 1971; Yoyotte, 2005, see above). Interestingly, the ancient horizontal Egyptian corkscrew horns now occur in the Uda sheep, a subtype of the Sahelian Fulani sheep. Similar horns but pointing upwards at an angle of 45° are carried by the Hungarian Racka sheep (Bodo, 1994; Porter et al., 2016).

Inhabitants of the Sahel area include many pastoral Fulani (also called Peul or Fulɓe) tribes composed of both nomadic herders and sedentary farmers. The Fulani may have originated from eastern Africa (Čížková et al., 2017) and migrated to the Futa Toro region in the lower and middle valley of the Senegal River (Skutsch, 2004). From the 15th century, they expanded from Senegal, southwards and especially eastwards in search of pasture in response to internal and external political challenges. More recently, they have become mainly concentrated in the western part of Africa and keep Sahelian breeds such as Fulani, Yankasa, and Uda. Some Fulani groups are scattered as far east as the Blue Nile region in Sudan and keep Sudan Desert sheep (Delmet, 2000; Stenning, 1957). In Nigeria, Uda sheep (Ayantunde et al., 2007; Blench, 1999a) gave their name to a Fulani clan, the Uda'en, who herd large flocks of this breed in northern Nigeria. The Balami are favored for stall-feeding by Muslims throughout the Middle Belt of Nigeria and are kept as a pastoral animal further north. Yankasa sheep are kept throughout Nigeria. The transboundary Touabire (or 'White Maure') breed is one of the major African sheep breeds and is kept by the Moor tribes in southern Mauritania, northern Senegal, and northern Mali.

Sudan Desert sheep are considered to be distinct from other Sahelian sheep (Gornas et al., 2011; Abied et al., 2021; Mufarrih, 1991; Salim, 2023), which is supported by SNP genotypes (see below). The Sahelian type is also found as the Zaïre long-legged sheep in the Kibali-Itaur district in northeastern Democratic Republic of Congo and as Angola long-legged in Angola (Figure 1, Figure S1).

THE WEST-AFRICAN DWARF IN THE HUMID ZONE OF WEST AND CENTRAL AFRICA

South of the Sahel, the humid zones include the west coast and central Africa where trypanosomosis, spread by the tsetse fly (Glossina spp), seriously handicaps livestock production (Ebhodaghe et al., 2018; Geerts et al., 2009). Human immigration with the introduction of livestock probably dates from 3000 to 2000 BCE following major and favorable environmental changes (Smith, 1992). Currently most sheep are of indigenous trypano-tolerant West African Dwarf (or *Djallonké*) type, which are assumed (Epstein, 1971) to have originated in the Fouta Djallon region of Guinea. This is the heartland of the Fulani and it is conjectured that, from about 1000 years ago these sheep accompanied the Fulani on their diaspora, through the humid forests, sub-humid zones and savannas now ranging from Senegal, through Chad, Central African Republic, South Sudan, Gabon, and Cameroon to the Republic of the Congo (Blench, 1999b). However, the current populations cannot be subdivided based on appearance (Devendra & McLeroy, 1983). The Cameroon Blackbelly is a distinct West African dwarf variant (Wiener et al., 2023; Woolley et al., 2023) and is the ancestor of American blackbelly sheep breeds.

Like the long-legged Sahelian sheep (see above), the dwarf sheep is an ancient type that already existed in the first millennium BCE in NKang, Cameroon (Mbida et al., 2000; Van Neer, 2000). In contrast to the proportionally miniaturized West African dwarf goat, the small size of the West-African Dwarf sheep appears to be a neotenous form with body proportions similar to those of an immature sheep (Hall, 1991, 2000). The distribution of coat fiber diameters is suggestive of a reduction of skin sweat glands and a possible accentuation of sebaceous glands (Hall et al., 1996).

The proposal that fat-tailed sheep migrated into central-east Africa via maritime transport to the Horn of Africa (Muigai & Hanotte, 2013), is not yet supported by archaeological or molecular evidence, although it does appear that from the Horn of Africa, the fat-tailed trait moved southwards reaching South Africa only around 1 CE (Pereira & Amorim, 2010; Sadr, 2019).

Remarkably, from 300 BCE to 350 CE the Meroitic kingdom around the confluence of the White and Blue

Nile knew a tradition of wool production, comparable to other isolated wool-producing regions in Mali, Sudan, and Ethiopia (Yvanez, 2018) (Figure 1).

CENTRAL-EAST AFRICAN FAT-RUMPED AND FAT-TAILED SHEEP

The earliest archaeological remains of a pastoral society in the Great Rift Valley near Lake Turkana date to 3000–2300 BCE (Ambrose, 1998; Hildebrand et al., 2018; Wright, 2011). Human genetics provides insights into the processes of pastoral spread in central-east Africa from 3000 BCE to 800 CE (Arthur et al., 2019; Grillo et al., 2020; Prendergast et al., 2019) with ancient human DNA indicating a mixing of early pastoralists with central-east Africans around 2000 BCE (Vicente & Schlebusch, 2020). The earliest datings for Neolithic sheep are from 2000 BCE (Figure 2, Table S4). Sheep skeletons dating from 1000 BCE to 1000 CE were found in Khasm al Girba and Mahal Taglinos, both in East Sudan (Gautier & Van Neer, 2006), or in Bieta Gyorgis (Aksum, Ethiopian Tigray region; Chaix, 2013). There were medium-sized sheep with withers heights of 50–75 cm. It is not clear if these were thin- or fat-tailed sheep, but undated rock art in Ethiopia shows fat-tailed sheep (Figure S2E; Tekle, 2011). As in ancient Egypt, the fat-tailed sheep were as source of fat in semi-nomadic husbandry better suited than pigs, which anyway were banned in Islamic regions.

The import of Arabian sheep does not seem to have influenced the Sudanese type of thin-tailed sheep in northern Eritrea and Ethiopia along the Sudanese border, but has resulted in four ecotypes of fat-tailed sheep in the Horn of Africa (Figure 1, Gizaw et al., 2007, 2013; Deribe et al., 2021; Amane et al., 2023). These are: (i) the hairy fat rump type in Eritrea, Somalia, the eastern dry lowland areas of Ethiopia on the border with Somalia, South Sudan (Toposa) and northern Kenya; (ii) the short coarse wool fat-tail type, which is only found in the sub-Alpine parts of Ethiopia and east of Eritrea; (iii) the hairy short fat-tail type, also found in sub-Alpine Ethiopia and further along the Great Rift Valley in Kenya, Uganda and Tanzania; and (iv) the hairy long fat tail in mid- to high-altitude environments of Ethiopia, also present in the eastern part of DR Congo, Uganda, Rwanda, Burundi, Tanzania, Zimbabwe, southern Africa and along the Atlantic coast of Angola and Namibia (Figure 1, Figure S1).

In Ethiopia, local breeds such as the Menz and the Wollo are being upgraded by crossing with Southwest Asian Awassi, which can be monitored by genome-wide SNP analysis (Marshall et al., 2019). Other exotic breeds that are crossed with central-east African sheep are the South-African Dorper (see below) and the Spanish Merino.

The present-day hairy short fat-tailed Red Maasai in Kenya and the short-tailed sheep of Tanzania are raised by Maasai tribes. Originating north of Lake Turkana, the Maasai occupied by the mid-19th century, almost the entire Great Rift Valley and adjacent lands (Huntingford, 1969), but under British rule lost 60% of the original size of their territory (Waller, 1976), illustrating how colonization destabilized pastoralism in several African countries (Chacha, 1999; Lwanga-Lunyiigo, 1987; Masefield, 1962). Due to crossing since 1970 of Maasai with Dorper sheep, purebred Maasai have become rare (Zonabend König et al., 2016).

In coastal central-east Africa, the original hunter–gatherer lifestyle coexisted for at least 2000 years with farming and pastoralism, which were introduced since the Iron age (Culley et al., 2021; Wright, 2011).

SOUTHERN AFRICA SHEEP

The migration of sheep to South Africa is most likely to have accompanied the Bantu expansion (Bostoen, 2018; Clutton-Brock, 2000). This is thought to have started during the early Iron Age around 300 BCE in the Nok region of modern Nigeria, continued eastward and southward and reached South Africa 500 CE. This expansion overlaps with the transition to the Iron Age from 1000 BCE to 1500 CE (Kay & Kaplan, 2015) and was possibly in response to forest disturbances (2000–500 BCE) due to climatic changes or human activities (Bostoen et al., 2015; Clutton-Brock, 2000; Grollemund et al., 2015; Kay et al., 2019; Marchant et al., 2018). However, the introduction of agriculture in Central Africa post-dates the arrival of the Bantu (Bostoen, 2018).

Undated rock paintings in Zimbabwe show both thin- and fat-tailed sheep (Figure S2E; Manhire et al., 1986). Presumably, the thin-tailed sheep represent ancestors of remnant populations of thin-tailed sheep in Zimbabwe (Epstein, 1971; Table S1; see below). South African rock art only depicts fat-tailed sheep (Jerardino, 1999).

Fat-tailed sheep spread southwards from central Africa by both demic expansion and acculturation (Isern & Fort, 2019). Bantu people kept fat-tailed sheep as well as Sanga cattle, which indicates that they acquired pastoralism via contact with the east-African Cushitic or Nilotic speaking tribes. The primary non-Bantu speaking people in South Africa before the advent of the Bantu were the Khoekoen people (Khoi-Khoi, belonging to the Khoisans), (Guldemann, 2008; Mitchell, 2010; Sadr, 2008; Smith, 2016; Wright, 2017). Remains of sheep kept by Khoekoen in Toteng (Botswana) have been dated at 1 CE, a few hundred years before the introduction of iron technology by Bantu-speaking people (Blench, 2009; Robbins et al., 2005, 2008) and again illustrating the adoption of pastoralism by acculturation. Khoi-khoi pastoralists also kept cattle, but these were taurines unlike the taurindicines kept by the Bantus

(Blench, 2009). Pastoralism was also acquired by the related pre-Bantu Kwepe people from southern Angola (Guldemann, 2008).

The timing of the arrival of sheep in southern Africa is supported by palaeontological findings from several sites and by historical, iconographic, and linguistic evidence (Badenhorst, 2010; Coutu et al., 2000; Denbow, 1986; Guillemard, 2020; Henshilwood, 1996; Jerardino et al., 2014; Kinahan, 2016; Lander & Russell, 2018; Le Meillour et al., 2020; Mitchell & Whitelaw, 2005; Smith, 2009; Walker, 1983; Webley, 2007; Figure 2). Schools of thought differ on the mode of transition from foragers to herders (Russell & Lander, 2015; Smith, 2016). Cultural diffusion is supported by a northwest-to-southeast dispersal rate of >2 km/year (Jerardino et al., 2014), which is twice as fast as observed for Neolithic livestock in Europe (Ammerman & Cavalli-Sforza, 1971). An analysis of the compositions of stone toolkits (Sadr, 2015, 2019) lends support to the proposal (Muigai & Hanotte, 2013; Smith, 1992) of two South-African migration routes.

The migration of fat-tailed sheep converged in Angola and Namibia with a migration of thin-tailed breed, also southward but more to the west. This led in these countries to a coexistence of four types of sheep: thin-tailed Sahelian, thin-tailed West-African Dwarf, fat-rumped, and southern African long fat-tailed sheep. These breeds are distributed as isolated patches, testifying to the turbulent history of pastoral tribes in these regions. After inter-ethnic wars and the slave trade, the Portuguese and German colonization led to expropriation of land, livestock rustling, and the massacres of the Herero (Bantu group), Nama (Khoisan group), and Mucubal (Bantu group) pastoral peoples (Campos, 2021; Cumberland, 2018).

In South Africa, most of the indigenous breeds of southern African sheep (Ngcobo et al., 2022; Van Marle-Köster et al., 2021) are hairy and long fat-tailed and can be divided depending on their eco-climatic environment (Molotsi et al., 2020; Ngcobo et al., 2022; Van Marle-Köster et al., 2021). In the wet climate of Eswatini and Kwazulu-Natal near the eastern coast, relatively small-framed sheep were introduced by the Nguni tribes, who moved to the east coast of southern Africa during the Iron Age (1000–500 BCE). Although classified as long fat-tailed, Nguni sheep often have long thin tails with little fat (Molotsi et al., 2020), which is possibly an adaptation to the extremely hot and humid climate of the east South-African coast. Nguni sheep can be divided into four breeds (Kunene et al., 2009), with the Imvu as a local variety in Kwazulu-Natal (Van Zyl & Imvu, 2015), Swazi, Pedi (in the northeast of South Africa), and Landim (Mozambique).

In contrast, sheep from the western regions of South Africa are larger-bodied: Damara (Namibia and Northern Cape), Namaqua Afrikaner (originally kept by the Bantu Nama tribe), Ronderib Afrikaner (in Namibia and in the northern and central parts of Cape province), and Sabi (Zimbabwe). Mitochondrial DNA of the first three, at least, is of indigenous rather than exotic origin (Horsburgh et al., 2022). Damara was originally associated with the Himba tribe (related to the Herrero) in northern Namibia but is now an internationally successful breed (Almeida, 2011).

Exotic sheep breeds were already kept in South Africa in the 18th century. Merino sheep were imported in 1789 and are still popular for the production of wool and mutton (Dzomba et al., 2020; Van Marle-Köster et al., 2021). In spite of its name, the fat-rumped Black-headed Persian sheep originate from the Horn of Africa and descend from a few founder sheep imported in 1869 (Porter et al., 2016). Crossing with the English Dorset Horn in the 1930s resulted in the highly internationally recognized Dorper breed (Ojango et al., 2023). The Swakara sheep have been derived from Asian long fat-tailed Karakul sheep and are used for the production of lambskin.

MOLECULAR GENETIC SURVEY

Since the comprehensive review of molecular genetic studies of African sheep by Gifford-Gonzalez and Hanotte (2011), genomic technologies have become considerably more powerful. Published genome-wide studies on molecular diversity in African sheep breeds using the 50 K SNP panel (Kijas et al., 2012) have focused on northwest Africa, Egypt, west Africa, Ethiopia, or South Africa, respectively (Table 1). African fat-tailed sheep have been proposed to be of Asian origin (see above) but so far, there has been no detailed comparison of the fat-tailed breeds from different regions or continents.

We have collated 50-K and 600-K datasets of African as well as Eurasian breeds (Table 1). These genotypes were converted to a common format using the coordinates of the Ovine v4 reference genome assembly and merged into a single dataset. We applied quality controls (Ciani et al., 2020) and selected 18 858 from 28 210 SNPs by linkage-disequilibrium pruning (Plink indep-pairwise 100 10 0.05). As additional quality control we constructed neighbor-joining trees of individuals and after removal of duplicates and mislabeled or crossbred outliers kept 2818 individuals. We calculated Weir & Cockerham genetic distances between breeds by using the Plink 2.0 program (Chang et al., 2015), which were visualized by a NeighborNet Graph using the SplitsTree program (Huson, 1995). We reason that short genetic distances between breeds or groups of breeds that are not attached close to the center of the graph imply shared ancestry and origin, while the overall topology of a graph or tree indicates genetic clines. Plotted on a geographic map, these suggest migration routes and corresponding gene flows.

Starting with a few popular breeds known to have originated outside Africa, Figures S3A,B show subsets

TABLE 1 Sources of genome-wide 50K SNP profiles used for the NeighborNet plots. For the samples size per breed, see Table S1.

Country	Breeds	Source
Africa		
Africa	Australian Dorper, Barki, Menz, Namaque, Red Maasai, Ronderib Africaner	Kijas et al. (2012)
Algeria, Morocco	Algerian Berber, Barbarine, Algerian D'Man, Moroccan D'Man, Hamra, Beni-Guil, Algerian Ouled-Djellal, Moroccan Ouled-Djellal, Rembi, Sidaoun, Sardi, Timahdite, Tazegzawth	Belabdi et al. (2019)
Morocco	BeniGuil, Moroccan D'Man, Moroccan Ouled-Djellal, Boujaad, Moroccan, Rahalya, Sardi, Thimadite	Benjelloun (2015)
Senegal	Djallonke, Ladoum, Peulpeul, Touabire	Missohou et al. (2022)
Egypt	Abour–Halai–Shalat, Barki Souagi, Saidi, Farafra	Mwacharo et al. (2017)
	Ossimi	Ciani et al. (2020)
Nigeria	Nigerian Dwarf	Spangler et al. (2017)
Nigeria, Cameroon	Cameroon, Mbororo, Nigerian Dwarf, Uda, Yankasa	Cao et al. (2020)
Ethiopia	Adile, Arsi Bale, Blackheaded Somali, Horro, Menz	Edea et al. (2018)
Ethiopia	Farta, Horro, Wollo, Gafera. Washera	Amane et al. (2020)
Ethiopia	Adane, Arabo, Bonga, Doyogena, Gafera Washera, Gumuz Gesses, Kefis Dulecha, Kido, Loya, Menz, Shubi Gemo	Ahbara et al. (2019)
Sudan	Al Ahamda, Buzee, Hammari, Kabashi, Shanbali	Abied et al. (2021)
South Africa	Damara	Greyvenstein (2016)
South Africa	Blackheaded Persian, Meatmaster, Nguni, Swakara	Dzomba et al. (2020)
South Africa	Dorper, Namaque, Pedi, Sout African Mutton Merino, Zulu	Molotsi et al. (2017)
South Africa	Pedi, Zulu	A. Molotsi, unpublished data
Asia		Table 1:
Asia	Afshari, Awassi, Changtangi, Deccani, Karakas, Local. Moghani, Norduz, Qezel, Tibet	Kijas et al. (2012)
Saudi Arabia, Oman	Huri, Naimi, Najdi, Omani	Mastrangelo et al. (2019)
Iran	Zel, Lori Bakhtiari	Moradi et al. (2012)
China, Khazakstan	Altay, Baerchuke, Bashbay, Byinbuluke, Celei Black, Diqing, Duolang, Guangling Fat-tail, Guide Black Fur, Hanzhong, Hetian, Hu, Hulun Buir, Jingzhong, Kazak, Kirghiz, Lanping Black-bone, Lanzhou Large-tailed, Large-tailed Han, Lop, Luzhong Mountain, Minxian Black Fur, Ninglang Black, Shiping Gray, Sishui Fur, Small-tailed Han, Sunite, Taihang Fur, Tan, Tashkurgan, Tengchong, Tibetan, Tibetan, Tong, Turfan Black, Ujimqin, Wadi, Weining, Wuranke, Yecheng, Yuxi, Zhaotong	Zhao et al. (2017)
Europe, Siberia		
Europe	Comisana, Dorset-Horn, Rasa Aragonesa, Sardinian Ancestral Black	Kijas et al. (2012)
Balkan	Pramenka	Ciani et al. (2020)
Eurasia–Central Asia	Andean Black, Buubei, Edilbai, Kalmyk, Karachaev, Karakul, Kuchugur, Lezgin, Romanov, Tushin	Deniskova et al. (2018)
Italy	Laticauda, Pinzirita, Sardinian White, Valle del Belice	Ciani et al. (2013)
Italy	Barbaresca	Mastrangelo et al. (2017)
Spain	Manchega	Kijas et al. (2013)

of Mediterranean and South-African sheep, respectively. These patterns confirm the European origin of the Tunisian Black Thibar and Sicilo-Sarde (Jemaa et al., 2019; Bedhiaf-Romdhani et al., 2020), the Asian Karakul ancestry of the South-African Swakara and the Dorset × Black-headed Persian origin of the South-African Dorper, which has been confirmed by whole-genome sequencing (Qiao, 2022).

The NeighborNet graph of Figure 3 then focuses on 58 indigenous African breeds (Figure 3). This graph shows a clustering of breeds that correlates closely with their geographical origin with a clear separation of

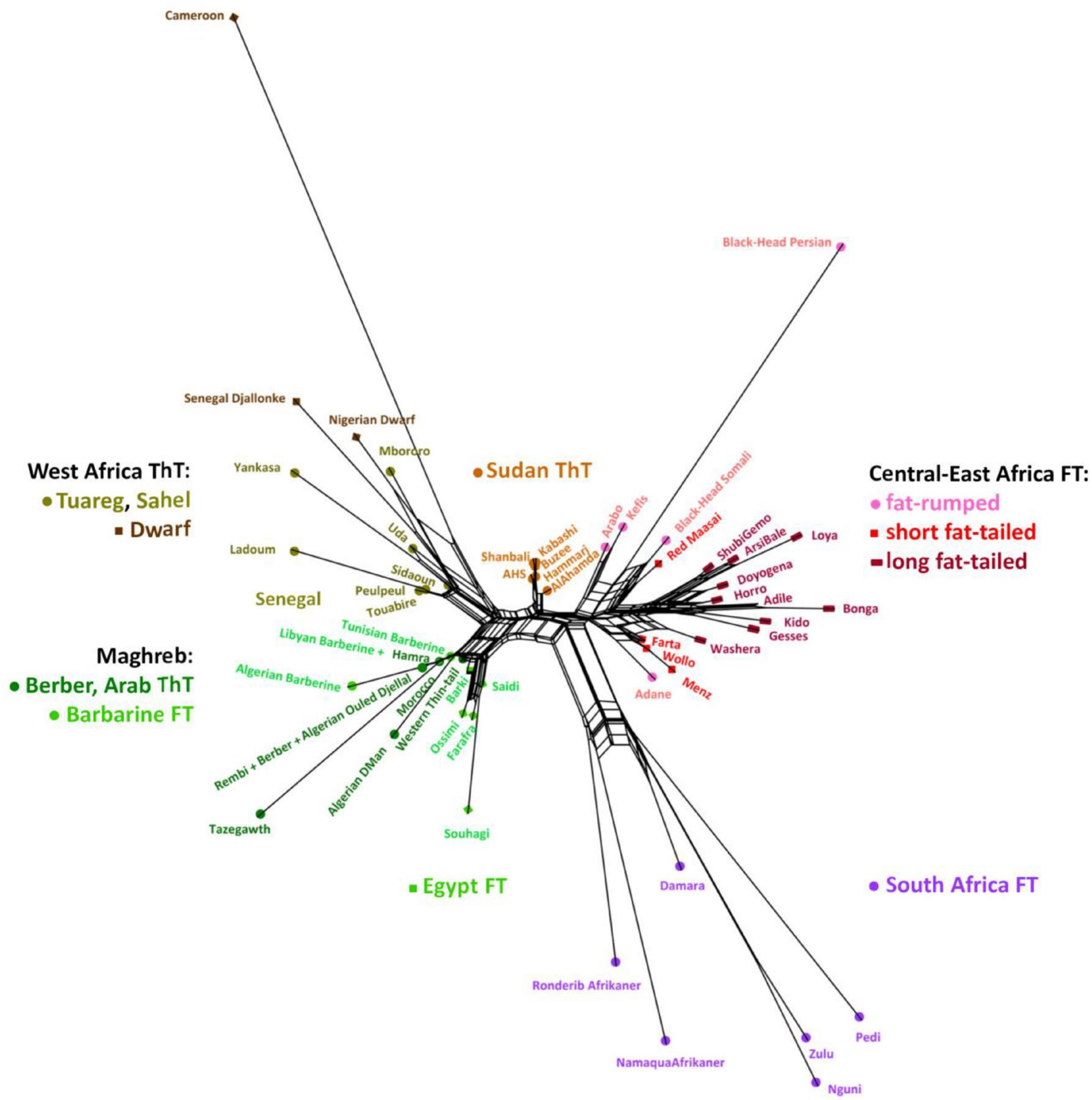

FIGURE 3 NeighborNet graph of F_{ST} distances between 57 indigenous African sheep breeds (984 individuals).

breeds from the north and from the south of the Sahara, respectively. Most of the clusters comprise breeds that have been analyzed by different laboratories, which validates our merging procedure. Remarkably, breeds from Egypt are not closely related to the Sudan breed cluster, which includes the Abu Ramad–Halayeb–Shalateen sheep. This breed is named after the politically disputed Abu Ramad–Halayeb–Shalateen triangle on the eastern Egypt–Sudan border (Mwacharo et al., 2017). Genetic distances between fat-tailed sheep from Egypt and central-east Africa are even larger, which provides molecular support for two separate immigrations of fat-tailed sheep. Within central-east Africa, we see a clustering of breeds according to the tail type, which is in contrast to the close relationships of Maghreb thin- and fat-tailed breeds (Figure 3; Belabdi et al., 2019; Kandoussi et al., 2021).

To relate the African and Asian fat-tailed sheep on the basis of 50 K SNP data (Table 1), we first visualized F_{ST} distances between 70 Asian breeds. Figure S4 shows clear phylogeographic clusters, but several breeds are intermediate between the clusters. In addition, the Tibet, north China and central Asia-Xinjiang clusters contain breeds from different locations, presumably because of recent translocations. As in African sheep, there is only a partial correlation of genetic clusters with tail type.

Then, we show distances of fat-tailed breeds across the African-Asian contact zone. Figure S5 show similarities of Egyptian, north-African Barbarine and southeast Asian fat-tailed sheep, which are separate from the fat-tailed breeds from Ethiopia and the Arabian Peninsula. The links of Ethiopian fat-rumped sheep across the Red Sea and the Gulf of Aden with the Arabian Hiru and Najdi (see also Muigai & Hanotte, 2013) reflect the immigration of Asian fat-tailed sheep, but may also be explained by more recent export of Somalian sheep into the south-Arabian states (Boivin & Fuller, 2009; Muhumed & Yonis, 2018). The occurrence of the transboundary Rashaidi breed in both Eritrea and Yemen confirms the exchange of sheep between central-east Africa and the Arabian Peninsula.

Finally, Figure 4 shows a combined African–Eurasian NeighborNet pattern, which has been simplified by constructions of meta-populations comprising breeds from the same genetic cluster and having the same tail type without considering intermediate breeds and breeds with extremely long terminal branches (Table S3). This agrees with the more complicated network of breeds in Figures 3, S4, and S5, but allows a more effective visualization of genetic distances across continents (see also Ciani et al., 2020). The link between Italy and Spain and the Maghreb confirms gene flow across the Mediterranean Sea, which has been documented for the Roman Period (Ryder, 1959) and resulted in genetic distances that are shorter than between the Italian/Spanish sheep and their original ancestors from Southwest Asia. Similar gene flows between the Maghreb and south European breeds have been observed for goats (Manunza et al., 2016; Martínez et al., 2016).

The pattern of Figure 4 also emphasizes the contrast between Mediterranean African breeds and the breeds south of the Sahara. Archaeological evidence suggests that this corresponds to a divergence over the period of 4 millennia since the desertification of the Sahara. We observe a genetic continuum north as well as south of the Sahara and within the Maghreb a short genetic distance between the thin-tailed sheep and the Barbarine fat-tailed sheep (Figures 3 and 4; Baazaoui et al., 2024). Thus, the molecular data only partially reproduce the phenotypic contrast of thin-tailed breeds in the west and fat-tailed breeds in the east, whereas the fat-tailed breeds from central-east and southern Africa are well separated from the Asian breeds with the same tail type. For the Asian breeds, Figure 4 confirms a migration from central Asia to central and north China and then to Tibet and Yunnan (Zhao et al., 2017).

As shown in Figure 5, Neolithic migrations inferred from archeological dating (Table S4, Figure 2) are largely in agreement with the routes proposed by Muigai and Hanotte (2013). However, in agreement with Smith (1992) and Hildebrand and Grillo (2012), we propose a migration across the green Sahara rather than along the north-western African coast through regions where hardly any sheep are kept and no ovine remains have been found (Holl, 1998a). The available data suggest the following scenarios:

1. Most indigenous African sheep are very likely to be direct descendants of the original immigrants. Exceptions are the fat-tailed sheep in Egypt, north Africa, and the Horn of Africa, which were influenced by later immigration of fat-tailed sheep originating from Asia. For the Maghreb sheep, gene flow in combination with crossbreeding has led to a homogenization across breeds in spite of evident maintenance of phenotypic differences (Benjelloun, 2015; Belabdi et al., 2019; Bedhiaf-Romdhani et al., 2020; Figure 3). South of the Sahara, there is no clear genetic separation of the long-legged Sahelian and the West-African Dwarf breeds.

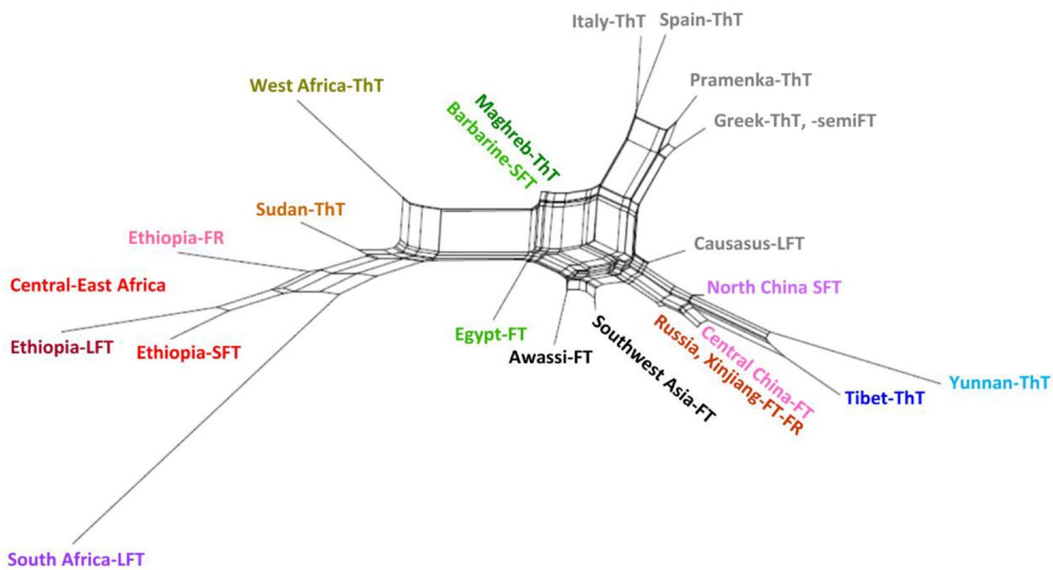

FIGURE 4 NeighborNet graph of F_{ST} distances between 21 European, Asian and African regional clusters (see Table S3) of closely related breeds of African and Asian sheep breeds, suggesting a relationship of Italian and Spanish breed with the Maghreb and Barbarine sheep and a partial separation of breeds according to the tail type. In this figure central-east African sheep are represented by Ethiopian sheep. Colors correspond to those in Figures 1 and S4.

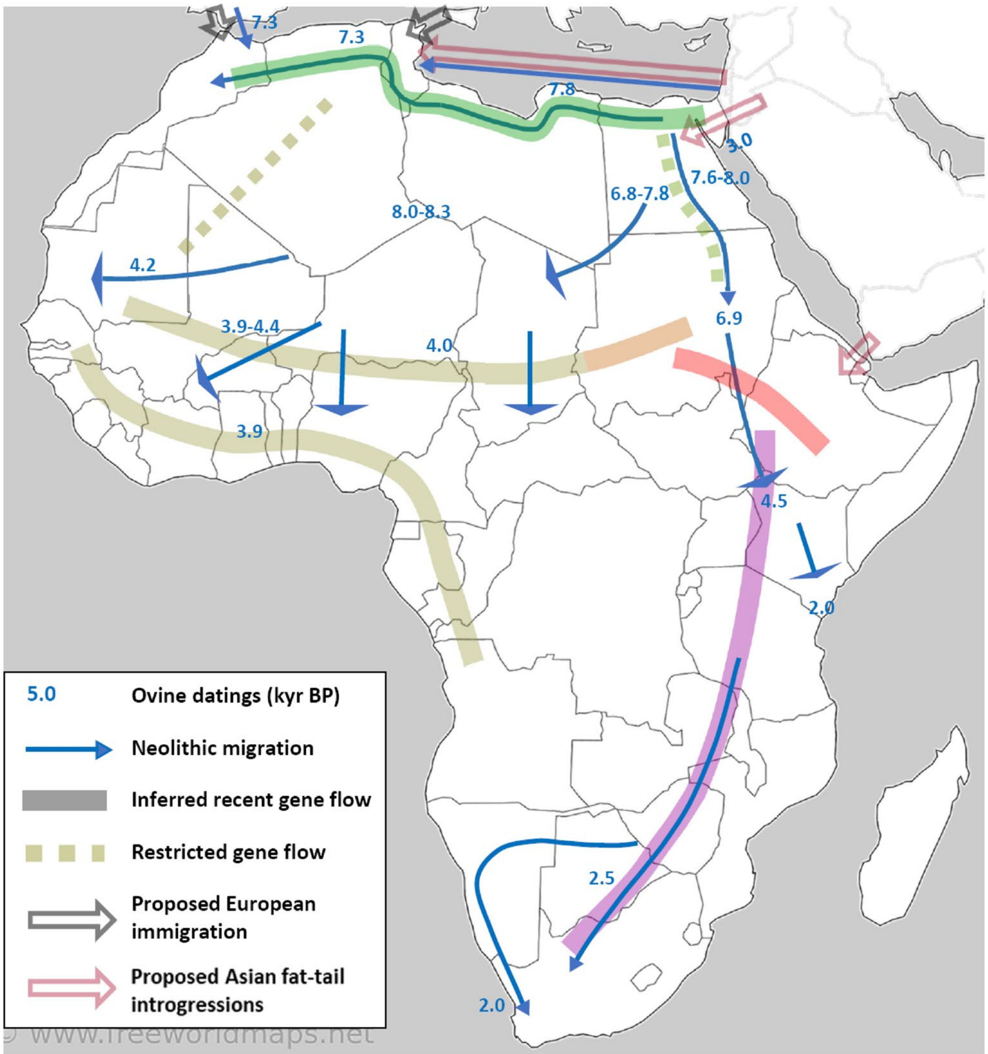

FIGURE 5 Blue arrows indicate Neolithic migrations in Africa inferred from datings of sheep remains. The broad lines with colors corresponding to those in Figure 1 indicate gene flow inferred from genetic distances between modern sheep breeds.

2. Long genetic distances between the Maghreb and the Sahelians and trypano-tolerant dwarf breeds and between Egyptian and Sudanese breeds indicate a restricted gene flow across the Sahara, which obscures the genetic relationships between the northern and Sahelian populations. Migration southwards along the Nile probably occurred, but the Sudanese sheep are genetically clearly separated from the Egyptian and have remained thin-tailed.
3. A more intense gene flow within the Sahelian climate zone created a cline of Sahelian breeds via Sudan towards Ethiopia, which turned southwards and eventually reached South Africa.
4. The genetic impact of the introgression of fat-tailed sheep tail traits is only modest. African and Asian fat-tailed sheep do not have any obvious similarity and each group resemble more the respective neighboring thin-tailed breeds. North African Maghreb thin-tailed and Barbarine fat-tailed breeds are intermingled, whereas in central-east Africa the introduction of the fat-tailed breeds does not interrupt the genetic cline from Sudan to southern Africa.

The observation that the difference in fat-tail types does not have a substantial effect on the genetic distances indicates that these traits are encoded by a small part of the genome (Baazaoui et al., 2021; Kalds et al., 2021, 2022; Lagler, 2022; Li et al., 2020, 2023; Yuan et al., 2016). We propose that the import into the Horn of Africa introduced the diverse fat-tail traits via a fast selective sweep of causative gene variants but without major effect on the rest of the genome. It will be interesting to analyze further the relationship of fat-tailed breeds of different continents, for instance by comparing haplotypes of candidate genes in Asian and African sheep. This may also answer the question of whether the fat-tailed phenotypes have a single origin.

There are a few interesting parallels of fat-tailed sheep and humped zebu (indicine) cattle. Both have a highly characteristic fat deposition – for sheep in or near the tails and for zebus between the shoulders. In both species, the fat-tail and hump are considered to be an adaptation to their environment, although fat-tailed sheep are not as restricted to tropical zones as zebus. Both originated in Asia and immigrated into Africa. However, the indicine genomes differ clearly from the taurine genomes and the two cattle subspecies also differ in their disease susceptibility. A degree of resistance to rinderpest allowed indicine cattle to replace their taurine counterparts in the Sahelian zones and to expand towards the Atlantic coast, whereas fat-tailed sheep remained restricted to eastern Africa.

In the near future, the origins of African livestock, their unique adaptations and selection landscapes may be studied in greater detail by whole-genome sequences of their constituent breeds. This has already been demonstrated by studies of Moroccan (Benjelloun, 2023; Ouhrouch et al., 2021), west-central Africa (Yaro et al., 2019) northeast African (Ahbara et al., 2022), Ethiopian sheep (Amane et al., 2022; Asmara et al., 2023; Wiener et al., 2021), South-African breeds (Dzomba et al., 2023), and African sheep in a global context (Li et al., 2023). The close genetic relationships between the Sahelian and West African Dwarf sheep may lead to localization of the genetic determinants of the West African Dwarf phenotype (Dolebo et al., 2019). Other traits that may be explored are the wool of Macina sheep and the corkscrew horns of Uda sheep, the latter are possibly due to variants in the *RXFP2* gene as found for other horn types (Cheng et al., 2023). A promise for the future may be an analysis of ancient sheep genomes allowing to trace the age of hair types, tail types and other relevant traits.

CONCLUSIONS AND PERSPECTIVES

African sheep represent a unique genetic resource. Their rich diversity reflects the history and husbandry practices of many ethnic groups and indigenous cultures and can contribute to sustainable microeconomic developments. We confirm that phenotypic variability has been modulated by introduction of the fat-tailed trait, which is most likely to be of Asian origin. However, this has not suppressed a genomic divergence, which is dominated by the contrast of breeds north and south of the Sahara. The information and datasets provided herein will be relevant for informing the management of African animal genetic resources. The commercial focus is still on agricultural performance of productive breeds, but it is the well-adapted local breeds that remain essential for supporting the micro- and macroeconomy in much of the continent.

AUTHOR CONTRIBUTIONS

Anne Da Silva: concept, data collection, writing – first draft, review and editing. **Abulgasim Ahbara:** data collection, writing – review and editing. **Imen Baazaoui:** data collection, writing – review and editing. **Yinhong Cao:** data collection, writing – review and editing. **Elena Ciani:** data collection, writing – review and editing. **Edgar Farai Dzomba:** data collection; **Linda Evans:** Egyptology, writing – review and editing. **Elisha Gootwine:** Egyptology. **Stephen J.G. Hall**: concept, timelines, writing – first draft, review and editing. **Olivier Hanotte:** writing – review and editing. **Laura Harris:** Egyptology, writing – review and editing. **Slim Ben Jemaa:** data collection, writing – review and editing. **Johannes A. Lenstra:** concept, molecular-genetic analysis, writing – draft, review and editing. **Salvatore Mastrangelo**: data collection, writing – review and editing. **Meng-Hua Li**: data collection. **Ayao Missohou:** data collection, writing – review and editing. **Annelin Molotsi:** data collection, unpublished data, writing – review and editing. **Farai C. Muchadeyi:** data collection. **Joram M. Mwacharo:** data collection, writing – review and editing. **Gaëlle Tallet:** Egyptology. **Pascal Vernus:** Egyptology.

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CONFLICT OF INTEREST STATEMENT

We declare no competing financial interests.

DATA AVAILABILITY STATEMENT

The combined dataset of 2818 African, European or Asian sheep genotyped for 28 210 SNPs is available via 10.6084/m9.figshare.26731378.v2.

ETHICS STATEMENT

All datasets have been previously published except those data for the Zulu and Pedi breeds, Their use in the present study has been approved by the Research Ethics Committee: Animal Care and Use of Stellenbosch University under number ACU-2019-10 914.

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SUPPORTING INFORMATION

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