



ORIGINAL ARTICLE

Mitogenome revealed multiple postdomestication genetic mixtures of West African sheep

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Summary

Notable diversity observed within African ovine breeds makes them of great interests, but limited studies on genetic origins and domestications remain poorly understood. Here, we investigate the evolutionary status of West African native breeds, Djallonke and Sahelian sheep using mitogenome sequencing. Compared with other ovine mitogenome sequences, West African sheep were revealed a Eurasian origin, and the initially tamed sheep breeds in West Africa have been genetically mixed with each other and mixed with European breeds. Worldwide domestic sheep is deemed the Eurasian origin and migrated west to Europe and Africa and east to the Far East, in which dispersed and received selection for acclimation to autochthonic environment independently and ultimately evolved into different native breeds, respectively. Our results contribute to the comprehensive understanding of the domestic sheep origin and reveal multiple postdomestication genetic amelioration processes.

Introduction

Modern domestic sheep (*Ovis aries*) are thought to be descended from the wild mouflon in Europe and Asia (Bruford & Townsend 2006; Meadows *et al.* 2011). Sheep domestication began in the upper parts of Tigris and Euphrates rivers at the central Fertile Crescent in the 7th millennium BC (Lev-Yadun *et al.* 2000; Zeder 2011), and its dispersion occurred with human migrations (Pereira *et al.* 2006; Chessa *et al.* 2009). Archaeological studies indicated that African domestic sheep originated from Sinai Peninsula, proceeded through the Nile Delta, the eastern Sahara and the Red Sea hills approximately 7500–7000 BP and entered the African continent around 3700 BP (Breunig *et al.* 1996). However, the absence of phylogenetic analyses of African domestic sheep keeps the mysterious status of mondial ovine domestication and origination.

African sheep have been largely described based on their appearance features (Birteeb *et al.* 2013; Doko *et al.* 2013), but the genetic studies are poorly investigated. Djallonke and Sahelian sheep are commonly used in West Africa and are considered as ancestrally different genetic entities (Alvarez *et al.* 2009). Djallonke sheep, also named West African Dwarf sheep, Forest Dwarf sheep and Grassland Dwarf sheep, are characterized by a small body size (25–30 kg) and have resistance to trypanotolerant performance (Goossens *et al.* 2001; Gbangboche *et al.* 2005). Djallonke sheep inhabit under humid climates of the sub-Saharan area including the coastal region of the West and Central Africa. Sahelian sheep are also named Sahel, Fulani, Peul, Bali-Bali, Maure, Tuareg, Guinea Long-legged and West African long-legged sheep, which are characterized of a larger body size (45–80 kg) and sensitive to trypanosomiasis (Gbangboche *et al.* 2005). Sahelian sheep is encountered

mostly in arid areas of the northern part of West African countries and south of the Sahel. The morphology and the geographic repartition of Djallonke and Sahelian sheep are illustrated in Figure 1.

In this study, we sequenced the complete mtDNA coding regions of the two popular sheep breeds in West Africa, Djallonke Sheep and Sahelian Sheep, and along with small-tailed Han sheep, a typical local breed in China for phylogenetic analysis. Mitogenome-coding sequences were compared with available existing homologues from worldwide domestic sheep and wild sheep. The purpose of this study was to determine the maternal origin and phylogenetic status of West African sheep.

Materials and methods

Animals and sample collection

The sheep used in this work were maintained under standard management conditions. The guidelines for the experimental animal management of China Agricultural University (CAU) were followed throughout the study, and the related experimental protocols were approved by the Experimental Animal Care and Use Committee of CAU.

A total of 173 blood samples were collected from three sheep breeds for this study, including 98 Djallonke sheep (DJ) and 21 Sahelian sheep (SS) from a local urban farm in Cotonou, Benin (West Africa) and 54 small-tailed Han sheep (ST) from Hebei Liansheng Mutton Sheep Breeding Farm in Hebei Province, China.

DNA extraction and mitochondrial genome sequencing

The genomic DNA was extracted using standard phenol–chloroform method. Primer pairs described in the previous study (Hiendleder *et al.* 1998) were used for mitogenome sequencing. The PCR was performed in a 25 μ l volume containing 2.5 μ l of 10 \times buffer (with MgCl₂), 0.5 mM dNTPs, 0.5 μ M each primer, 2 U Taq DNA polymerase and 50 ng genomic DNA pool. The reaction began with an initial denaturation at 95°C for 5 min, followed by 35 cycles of denaturation at 95°C for 20 s, annealing at gradients 50–65°C for 30 s and extension at 72°C for 40 s. The final extension was given at 72°C for 7 min. The PCR products were resolved in 1–1.5% agarose gel, and gel was then exacted and purified for sequencing. Sequencing was carried out on an ABI 3730XL automated DNA sequencer (Applied Biosystems, USA) using the ABI Prism Big Dye Terminator v3.1 Cycle Sequencing kit. Sequences were edited using the DNASTAR software (DNASTAR Inc. Madison, WI, USA).

Phylogenetic analysis

The complete mtDNA-coding sequences generated in this study and corresponding sequences downloaded from GenBank were aligned using algorithm MUSCLE (Edgar 2004) in the MEGA 5 software (Tamura *et al.* 2011). The online FaBox 1.41 toolbox was used to collapse the data set of aligned sequences into haplotypes (<http://users-birc.au.dk/biopv/php/fabox/>).

Haplotypes obtained in this study were used to evaluate the phylogenetic status of African sheep by

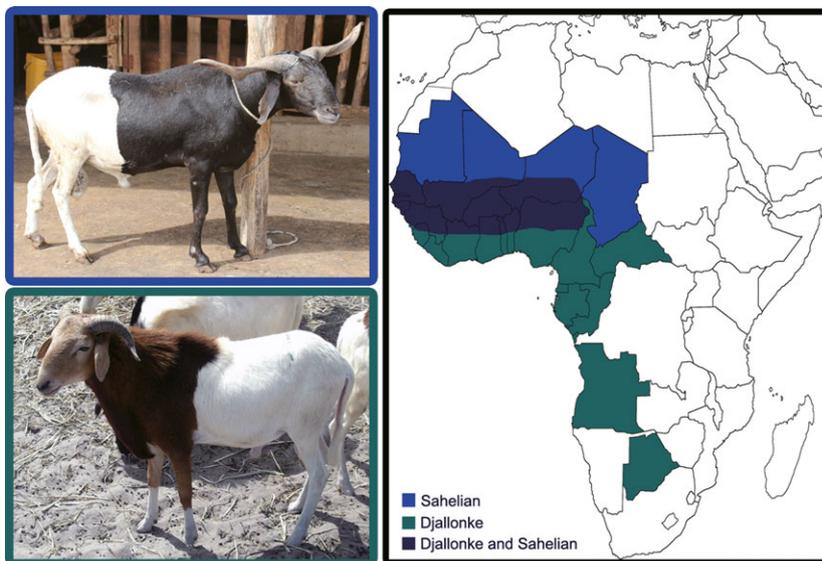


Figure 1 Morphology of the two West African sheep breeds investigated and their geographic repartition. Blue frame for Sahelian ram and green frame for Djallonke ram.

Bayesian calculation. The data set was converted into BEAST XML format by BEAUti 1.7.5 with the following parameter settings: A. selection the GTR+I model (general time reversible distances with invariant sites) as the best-fit model identified by MEGA 5; B. Yule process (a birth process based on the assumptions of independence and of a constant birth rate) for the tree prior superposition; C. the MCMC chain was set to 10 000 000. The calculation was carried out by the software of BEAST 1.7.5 (Drummond *et al.* 2012). TreeAnnotator 1.7.5 was used to summarize the results and find the best supporting phylogenetic tree by discarding the first 10% as burnin. The tree resulting was depicted (Figure 2) using FigTree 1.4.0 (<http://tree.bio.ed.ac.uk/software/figtree/>). Aligned mtDNA complete coding sequences were inserted in phylogenetic Network 4.611 software (<http://www.fluxus-engineering.com/>), and the median-joining method was used to examine the genetic relationship among different sheep breeds.

Geographic population genetic analysis

According to the geographic origin of the sheep breeds investigated in this study, the geographic distribution was defined as African Djallonke (DJ), African

Sahelian (SS), Chinese small-tailed Han (ST), European breeds (EU, including various sheep breeds from Scotland, France, Germany and Italy), Eurasian breed (EA, including various sheep breeds from Israel and Turkey) and Australian breeds (AU, including Merino sheep and Romney sheep from Australia).

The nucleotide diversity for the geographic definition for domestic breeds was calculated using DnaSP 5.10 (Librado & Rozas 2009). The polymorphisms in the analysed segments and the pairwise mismatch distribution between different geographic group classifications were obtained using the Arlequin 3.5 computer package (Excoffier & Lischer 2010).

Results

Mitogenome sequencing

The complete mitochondrial genome sequence was obtained for each of the three local sheep breeds including West African Djallonke sheep and Sahelian Sheep, and small-tailed Han sheep. All the three sequences were submitted to GenBank (Accession nos: KF977845, KF977846 and KF977847). The complete mtDNA coding region (except for D-loop) for each individual was sequenced. Additionally, 44

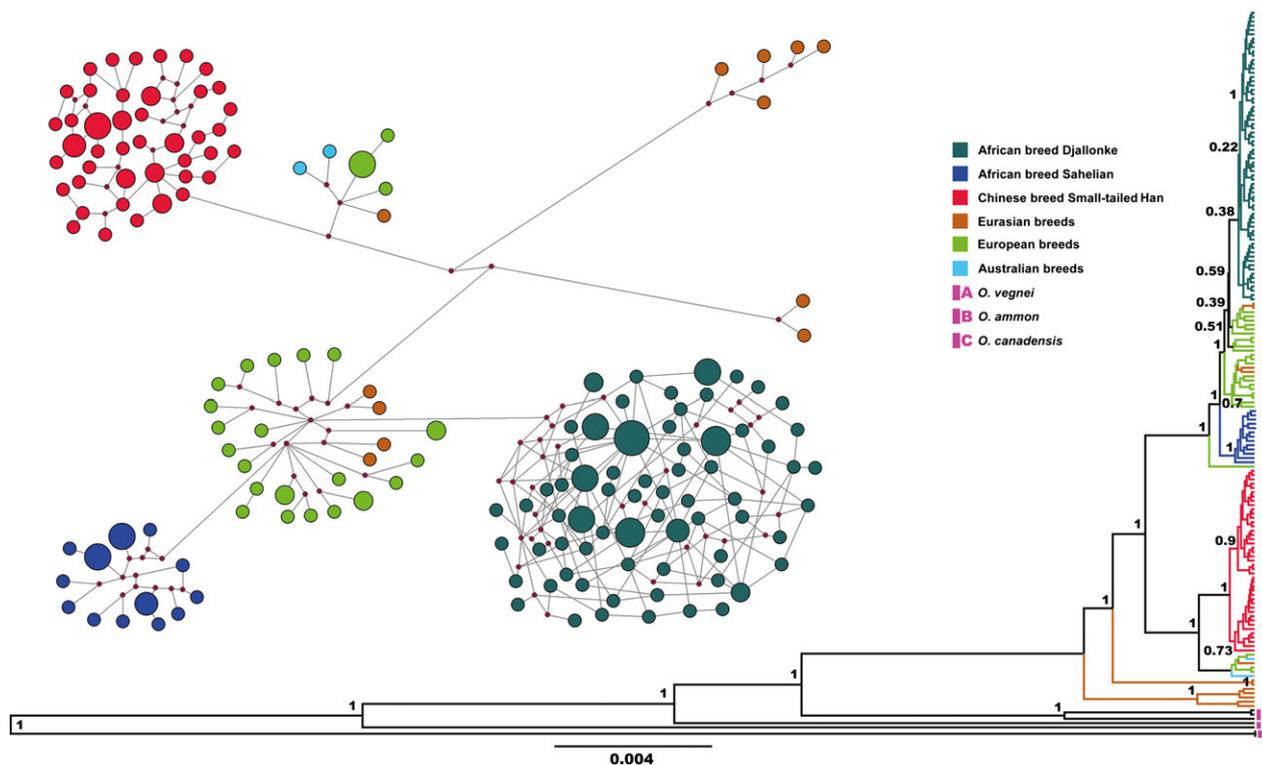


Figure 2 Consensus phylogenetic tree and median-joining network.

complete mtDNA coding sequences from sheep (*O. aries*) were obtained from GenBank, including various breeds from Europe, Eurasia and Australia, and nine wild sheep including Argalis (*O. ammon*) from Kazakhstan and Tibet (China), Urials (*O. vignei*) from Kazakhstan, Bighorn Sheep (*O. canadensis*) from Alberta (Canada) and Mouflons (*O. orientalis*/*O. musimon*) from Germany (Table S1).

The mtDNA polymorphic sites for Djallonke and Sahelian sheep were listed in Table S2. By analysing the genetic structure, the average number of difference (K) for Djallonke sheep and Sahelian sheep were 3.811 and 8.381, respectively. The K-score for each local breed was significantly lower than that of all domestic breeds ($p < 0.01$). Besides, the number of polymorphic/indel/missing sites (S), the haplotype diversity (Hd) and the nucleotide diversity (Pi) for Djallonke sheep and Sahelian sheep indicated all the two breeds were in a conservative status in the genetic dimension (Table 1).

Phylogenetic analysis

A consensus Bayesian phylogenetic tree considering both wild sheep and domestic breeds using 170 haplotypes was constructed. The wild sheep and domestic breeds were distinct two embranchments, and all wild sheep strongly rooted the consensus tree. For the domestic breeds, Eurasian breeds clustered at the root segment, which mean the ancestry of modern sheep. The other ovine breeds including European breeds, Australian breeds, West African Djallonke sheep and Sahelian sheep, and Chinese small-tailed Han sheep clustered into two obvious mix groups; one consisted of small-tailed Han sheep, Australian breeds and several European breeds, and the other group included Djallonke sheep, Sahelian sheep and the majorities of European breeds (Figure 2; Table S1).

The network analysis for domestic sheep revealed analogous phylogenetic relationship among various breeds (Figure 2). Djallonke sheep was found to be the tangled population without any dominant

maternal type, and African breeds and European breeds illustrated close relations with relevant haplotypes. On the other hand, small-tailed Han sheep, European breeds and Australian breeds shared similar genetic background. The Eurasian breeds appeared as intermediate genetic types by the network analysis.

Phylogeographic analysis

The average number of nucleotide difference (K) and the average number of nucleotide substitutions per site (D_{xy}) between every two geographic definition groups were calculated (Table 2). The lower K and D_{xy} values indicated that the relationships across Djallonke sheep, Sahelian sheep and European breeds were closer and more divergent from other regional ovine breeds (Figure 3 a,b). small-tailed Han sheep was found to be closer to Australian breeds than other regional breeds (Figure 3c), while Australian breeds had another closer partner of European breeds (Figure 3c). Therefore, a perspective from the centre position of westward and eastward geographic spread hinted that Eurasian breeds could be the ancestry of worldwide ovine breeds.

Discussion

The root position of Eurasian sheep is demonstrated in the phylogenetic tree (Figure 2); meanwhile, the intermediate genetic position of the Eurasian breeds revealed by the mitogenome network analysis corroborates the ancestral status among modern ovine breeds. The results are consistent with the widely accepted assertion that Eurasian sheep was the ancestry of sheep worldwide with domestication occurring in Eurasia (Tapio *et al.* 2006; Ajmone-Marsan *et al.* 2010; Muigai & Hanotte 2013). Moreover, the bis-offshoot emerged both in the Bayesian consensus tree and in the median-joining network brings the scenery of simultaneously westward and eastward spreading after sheep domestication in the Fertile Crescent.

Table 1 Genetic structure of Djallonke sheep and Sahelian sheep

Breed	N	Length (bp)	S	h	K	Hd±SD	Pi ± SD
DJ	98	15 437	15	68	3.811	0.985 ± 0.005	0.00025 ± 0.00001
SS	21	15 431	21	13	8.381	0.929 ± 0.036	0.00054 ± 0.00004
^a Total breeds	217	15 446	428	162	47.742	0.994 ± 0.002	0.00310 ± 0.00017

N, Number of sequences; S, Number of polymorphic/indel/missing sites; h, Number of haplotypes; K, Average number of differences; Hd, Haplotype diversity; Pi, Nucleotide diversity; SD, Standard deviation.

^aTotal breeds-All sheep breeds investigated in this study; DJ-Djallonke, SS-Sahelian.

Table 2 Geographic population genetic divergence among different ovine breeds

	DJ	EU	SS	AU	EA	ST
DJ		0.00159	0.00169	0.00445	0.00531	0.00540
EU	24.496		0.00252	0.00369	0.00545	0.00477
SS	26.037	38.857		0.00536	0.00622	0.00631
AU	68.653	56.900	82.690		0.00572	0.00210
EA	81.884	84.061	95.917	88.250		0.00675
ST	83.375	73.615	97.431	32.352	104.145	

DJ, Djallonke; EU, European; SS, Sahelian; AU, Australian; EA, Eurasian; ST, small-tailed Han.

The lower triangular matrix shows the average number of nucleotide difference (K) between every two geographic definition groups, and the upper part shows the average number of nucleotide substitutions per site (Dxy).

The analyses of the genetic divergence reveal that Djallonke and Sahelian sheep are much closer to European Breeds than to Asian and Australian breeds, suggesting a westward dispatching route to Africa and Europe. Actually, previous studies have revealed that West African sheep and European sheep have similar mtDNA compositions (Ferencakovic *et al.* 2013), suggesting that they share common maternal genetic background (Alvarez *et al.* 2013). Following the sheep entrance into the African continent through the Nile Delta, an overland dispersal route is presumed westward bordering the coast to attain West Africa. However, the close genetic relationships between African and European sheep may also conclude subsequent introgressions by European sheep through Mediterranean maritime trading, which is thought to be alternative route for the sheep dispersal along the northern African coastline (Figure 3d) (Pereira *et al.* 2006). This situation is quite similar to that in domestic cattle’s spreading in the continent (Loftus *et al.*

1994; Yarwood & Evans 1998; Ajmone-Marsan *et al.* 2010).

small-tailed Han sheep was found genetically different with the investigated breeds, suggesting an independent maternal origin of Eurasian sheep, from which presented the result of eastward dispersal. Australian breeds are showed to be genetically related to small-tailed Han sheep, which indicate neighbourhood exchanges considering their close geographic distance and historical culture exchanges. The close relationships between Australian breeds and European breeds are supposed by the introduction of European sheep in Australia for improving the productivity during colonization period (Figure 3d).

High level of genetic admixture was revealed in all domestic sheep, which were compatible with a single large ancestral genetic pool (Kijas *et al.* 2012). Furthermore, microsatellite analyses reported the close relationships and genetic admixture among West African sheep populations from a same geographic

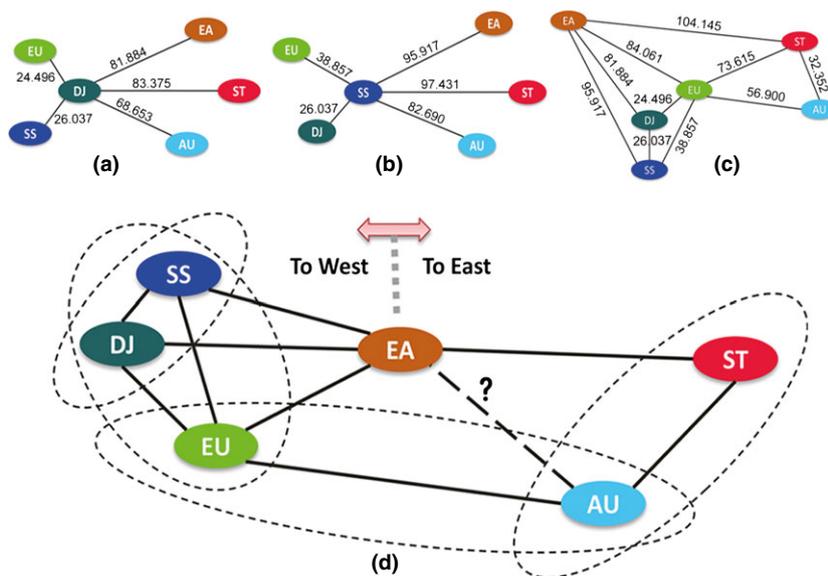


Figure 3 Schematic of geographic population divergence. (a–c) shows the genetic distance between the sheep breed clusters studied, and (d) indicates the probable sheep geolocalization and migration direction of the sheep breed clusters studied.

area (Muigai *et al.* 2009; Agaviezor *et al.* 2012; Soma *et al.* 2012). In the present study, each genetic cluster was constituted by an individual breed or region-specific breeds. The findings of the genetically tangled character of Djallonke sheep also echoed a previous report which deemed Djallonke sheep was a lack of selection breed (Wafula *et al.* 2005). The speculations that West African sheep breeds, Djallonke and Sahelian, were genetically closer within a maternal lineage were supported by a previous study by microsatellites (Alvarez *et al.* 2009).

In conclusion, by mitogenome sequence analyses, the worldwide domestic sheep is originated from the ancestral sheep in Eurasian regions, and after initial domestication at the Fertile Crescent, domestic sheep migrated west to Europe and Africa and east to the Far East, in which dispersed and received selection for acclimation to autochthonic environment independently and ultimately evolved into different native breeds, respectively. West African sheep (Djallonke and Sahelian sheep) were revealed a Eurasian origin, and the initially tamed sheep breeds in West Africa have been genetically mixed with each other and mixed with European breeds.

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Conflict of interests

The authors have no conflict of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Sheep investigated in this study and their haplotype.

Table S2. The mtDNA polymorphic sites for Djallonke and Sahelian Sheep.