Maternal genetic diversity and phylogeography of native Arabian goats

Article *in* Livestock Science · December 2017

DOI: 10.1016/j.livsci.2017.09.017

15 authors, including:

Nasser Ali Al-Araimi
CIBIO Research Center in Biodiversity and Genetic Resources
12 PUBLICATIONS **8** CITATIONS
SEE PROFILE

Raed Al-Atiyat
Mu'tah University
80 PUBLICATIONS **206** CITATIONS
SEE PROFILE

Osman Mahgoub
Sultan Qaboos University
158 PUBLICATIONS **2,259** CITATIONS
SEE PROFILE

Raquel Vasconcelos
University of Porto
59 PUBLICATIONS **414** CITATIONS
SEE PROFILE

Livestock Science 206 (2017) 88–94

Contents lists available at ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci

Maternal genetic diversity and phylogeography of native Arabian goats

Nasser Ali Al-Araimi[a,*], Raed Mahmoud Al-Atiyat[b], Osman Mahgoub Gaafar[c], Raquel Vasconcelos[a,d], Agusto Luzuriaga-Neira[a], Mohamed Osman Eisa[e], Nadir Amir[f], Mohammed Hocine Benaissa[g], Abdulbari Abbas Alfaris[h], Riyadh Saleh Aljumaah[i], Sayed M. Elnakhla[j], Mohamed M.I. Salem[k], Ibrahim A. Ishag[l], Mohammed El Khasmi[m], Albano Beja-Pereira[a]

[a] Research Center in Biodiversity and Genetic Resources (CIBIO), InBIO, University of Porto, R. Padre Armando Quintas 7, Vairão, 4485-661 Porto, Portugal
[b] Department of Animal Production, Faculty of Agriculture, Mutah University, Al-Karak 61710, Jordan
[c] Department of Animal & Veterinary Sciences, College of Agricultural & Marine Sciences, Sultan Qaboos University, P.O. Box 34, Al-Khod 123, Oman
[d] IBE, Institute of Evolutionary Biology (CSIC-UPF), Barcelona, Spain
[e] Department of Animal Production, Faculty of Agriculture, Omdurman Islamic University, P.O. Box 382, Khartoum 14415, Sudan
[f] Laboratoire de Biochimie Appliquée, Faculté des Sciences de la Nature et de la Vie, Université de Bejaia, Bejaia 06000, Algeria
[g] Scientific and Technical Research Center for Arid Areas (CRSTRA), Biophysical Station, PB 30240, Nezla, Touggourt, Algeria
[h] Department of Surgery and Obstetrics, College of Veterinary Medicine, University of Basra, Basra, Iraq
[i] Animal Production Department, College of Food and Agriculture Sciences, King Saud University, P.O. Box 2460, Riyadh 11451, Saudi Arabia
[j] Public Authority for Agriculture and Fish Resources (PAAFR), Animal Production Department, P.O. Box 21422 Safat Rabia, Kuwait 13075, Kuwait
[k] Animal and Fish Production Department, Faculty of Agriculture, Alexandria University, Alexandria 21545, Egypt
[l] Department of Zoology, Faculty of Science, University of Tobruk, Tobruk, Libya
[m] Department of Biology, Laboratory of Physiopathology and Molecular Genetics, Faculty of Sciences Ben M'Sik, University Hassan II of Casablanca, Casablanca, Morocco

ARTICLE INFO

Keywords:
Capra hircus
Arabian Peninsula
Native goat population
Haplogroup G
Genetic diversity
Conservation

ABSTRACT

The ability to adapt to harsh environments and thrive with minimal food and water input, places goats among the most popular livestock species in Arab countries. However, little is known about the historical and contemporary genetics of most Arabian goat breeds and populations. In this study, we genetically analyzed 617 individuals (126 from this study and 491 from published sources) representing 18 Arabian goat populations by evaluating variation in the mitochondrial DNA control region (D-loop). Our data were also combined and compared with those from 339 Asian, African, European and Canarian populations. We found 186 different polymorphic sites, which allowed us to identify 453 different haplotypes belonging to three maternal haplogroups: A, B and G. Haplogroup A is the most represented among Arabian goats and highly widespread among Arab countries, whereas B group is rare. Haplogroup G is the second most frequent haplogroup and also the most diverse among Arabian goats. Measurements of nucleotide and haplotype diversity and the mean number of pairwise differences in the 18 populations yielded values of 0.025, 0.998 and 10.586, respectively. These results show that the diversity of native Arabian goat populations is high and similar to that of populations at the center of origin. Based on estimated population structures, comparison of pairwise F_{ST} and AMOVA values between Arabian populations indicated low genetic differentiation. In addition, median-joining network analysis results provide very little evidence of a previous connection between Arabian goats and regions of historical Arab influence were once installed (Iberian Peninsula and Southern Europe). Finally, the same thin evidence was also found between extant Arabian and Canarian goats, which might have partially originated due to commercial trade or during the migratory movements of ancient humans.

1. Introduction

Archaeozoological findings have suggested that the earliest detectable domestication of animals occurred in the Near East during the middle of the 11th millennium BC in the Pre-Pottery Neolithic A (PPNB) period (Vigne, 2011). This includes the domestication of goats (*Capra hircus*), which are thought to have been one of the first livestock species to be domesticated much later (10,000 years ago) in the Zagros

* Corresponding author.
E-mail address: nsralaraimi@cibio.up.pt (N.A. Al-Araimi).

http://dx.doi.org/10.1016/j.livsci.2017.09.017
Received 23 April 2017; Received in revised form 12 September 2017; Accepted 14 September 2017

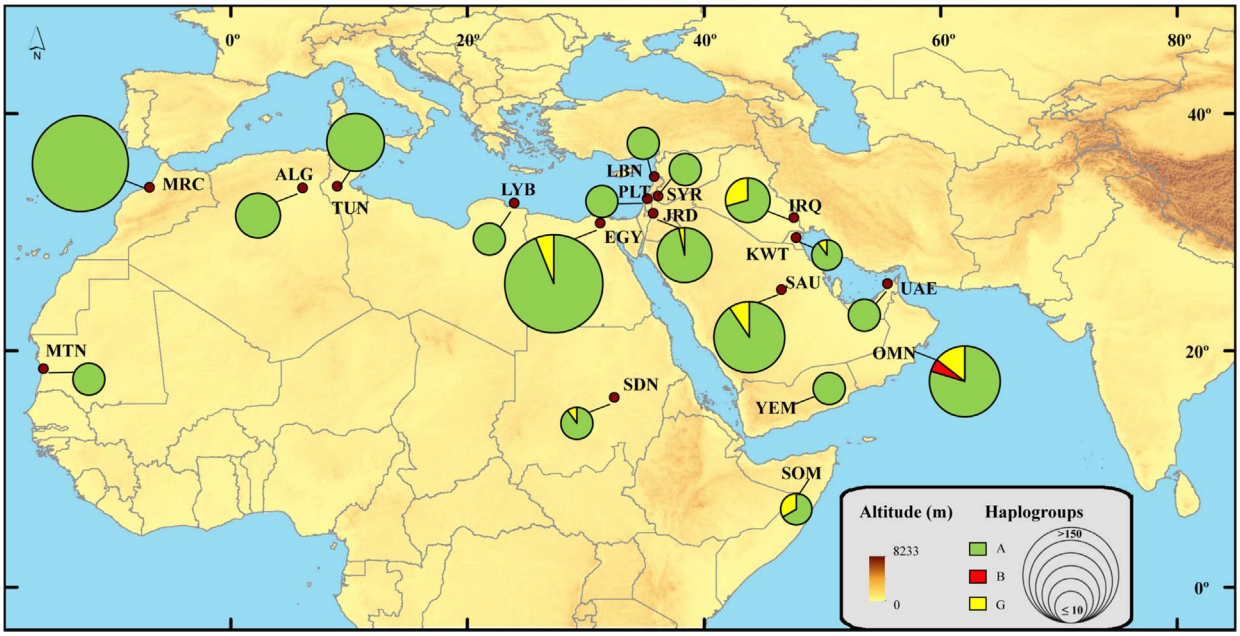

Fig. 1. Sampling sites and distribution of the three major mtDNA haplogroups (A, B and G) in Arabian goats. The sampling sites are indicated by dark brown dots. Each specific haplogroup is represented by one of three different colors and the sizes of the circles in the pie charts are proportional to the sample sizes. The abbreviations correspond to the analyzed populations and are provided in Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Mountains of modern Iran, near the region known as the Fertile Crescent (Zeder and Hesse, 2000). The Fertile Crescent includes regions of Iran, Turkey and many Arab countries. Arab countries are located in the Arabian Peninsula and North Africa and extend from the northwestern end of the Zagros Mountains of western Asia in Iraq to the shores of the Atlantic Ocean in western North Africa in Mauritania. The domestication of goats in the region spread throughout the world along terrestrial and maritime routes of migration and commerce (Naderi et al., 2007; Piras et al., 2012), playing an important role in human history. Over the last 10 millennia, the goat has been a good source of milk, meat, skin and fiber for human use.

Throughout history, Arab people have been intrinsically linked to the intercontinental trade of goods, animals and plants (e.g., frankincense, myrrh, spices and exotic animals) across Asia, Africa and Europe. Due to their activity as traders, Arabs were frequent travelers and also experienced massive demographic movements as a result of the destruction of the Marib Dam at the end of the 6th century BC and the spread of Islam during the 7th century AD. These movements displaced both people and their animals within the Arabian Peninsula and across the Mediterranean Basin, West and East Africa, the Central Asian Plateau and the Indian Ocean Rim, including the Indus Valley (Jawād, 1968; Martin, 1974; Brunner, 2000).

Perhaps due to their arid and semi-arid climates of origin, goats are important livestock in Arab countries, as evidenced by their numbers. Today, 103 million goats and 96 distinct native goat breeds or strains are present in Arab countries, representing a unique reservoir of genetic diversity (DAD-IS; http://www.fao.org/dad-is/). These native goats show high within-population phenotypic diversity in characteristics such as coat hair type, ear length and orientation, and horn morphology and patterns. Due to their high rusticity and adaptability to harsh environments, goats are the most economically important livestock species in Arab countries.

The knowledge of genetic diversity and population structures that results from phylogenetic analyses and haplogroup classifications is required to understand the role of past and current evolutionary processes in shaping the distribution of goat biodiversity observed today. The most widely used DNA marker is mitochondrial DNA (mtDNA); in particular, the control region (CR) has been used to investigate the history, phylogenic relationships and genetic diversity of animals (Luikart et al., 2001). Goats have been classified into six highly divergent maternal haplogroups (A, B, C, D, F and G) based on mtDNA analyses (Naderi et al., 2007). More than 90% of goats belong to haplogroup A, which is the most diverse and widely distributed haplogroup on all continents (Colli et al., 2015). The remaining haplogroups exhibit geographically distinct distribution patterns. Haplogroup B was previously found throughout most of Asia (the Indian subcontinent, Southeast Asia and Central/Eastern Asia), with a small proportion of these sequences deriving from Sub-Saharan African (South Africa) and European (Greece) goats (Naderi et al., 2007; Lin et al., 2013). Haplogroups C and D are primarily found in East Asia and Europe (Lin et al., 2013; Colli et al., 2015). Haplogroup F, which is rare among domestic goats, has been detected only on the island of Sicily in Mediterranean Europe (Sardina et al., 2006). Finally, Haplogroup G has only been observed in individuals from southwestern Asia and northern and eastern Africa (Naderi et al., 2007; Kibegwa et al., 2016; Ahmed et al., 2017).

The Arab region is one of the few geographical regions in which the genetic diversity and origin of goats have not been properly and fully analyzed, and studies in this region have been limited (Benjelloun et al., 2011; Othman and Mahfouz, 2016; Ahmed et al., 2017). Similar to other locations throughout the world, many of the natively adapted populations in Arab countries are starting to disappear due to breeding substitutions, indiscriminate cross-breeding with commercial strains and the absence of breeding development programs. Thus, the most well-adapted native breeds are at a risk of extinction before they are properly studied. Given that Arab countries are mostly localized in arid or semi-arid regions that are highly affected by water shortages, the disappearance of this well-adapted resource poses a paramount threat to the food security and self-sufficiency of this region; thus, immediate steps based on biodiversity and genetic conservation studies must be taken to conserve Arabian goats. In this context, it is highly significant to study the molecular genetic diversity and origin of the Arabian goats, which could contribute to understanding the origin, differentiation and genetic relationships of goat breeds and population resources of Arab countries.

2. Materials and methods

2.1. Sample collection

Biopsies of ear tissues from 126 individuals were collected from 15 Arabian native goat populations and used to investigate the origin, genetic relationships and diversity of these native populations. To select the animals for sampling, the knowledge of native experts in each country was utilized to distinguish pure native goats from exotics and crossed breeds. The details of the sampled goats are listed in Table S1 and Fig. 1. Genomic DNA was extracted from ear skin tissue using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocols.

2.2. PCR amplification and sequencing conditions

A fragment (598 base pairs, bp) of the mtDNA control region (D-loop) located between nucleotide positions 15,653 and 16,250 in the reference goat mitochondrial genome AF533441 (Parma et al., 2003) was amplified using two primers: CAP-F (5'-CGTGTATGCAAGTACAT-TAC-3') and CAP-R (5'-CTGATTAGTCATTAGTCCATC-3'). PCR amplifications were performed in a 20 μL reaction volume containing ≈20 ng genomic DNA, 1 X PCR buffer (10 mM Tris-HCl pH 8.3, 50 mM KCl, and 0.1% Triton X-100), 2.5 mM $MgCl_2$, 0.3 mM ddNTP mix, 0.25 U *Taq* DNA Polymerase (Applied Biosystems®, Foster City, California, USA), 0.3 μg/μL bovine serum albumin (BSA), 0.8 μM each primer, and ddH_2O to complete the final volume. The samples were amplified using a Dual 96-Well GeneAmp® PCR System 9700 thermocycler (Applied Biosystems®, Foster City, California, USA) according to the following conditions: initial denaturation at 94 °C for 10 min, followed by 40 cycles of 30 s at 94 °C, 30 s at 6 °C, and 30 s at 72 °C, with a final extension step of 10 min at 72 °C. The PCR products were evaluated in 2% agarose gels stained with GelRed™ (Biotium Inc., Hayward, CA, USA), and the amplicons were then PCR sequenced using an ABI3730XL capillary sequencer (Applied Biosystems®, Foster City, California, USA). The raw sequences were edited manually using SeqMan Pro v7.1 (DNASTAR, Lasergene Inc., Madison, WI, USA).

In addition to the mtDNA sequences obtained in this work, a set of 491 previous published sequences of goats from some Arab countries were obtained from GenBank and added to the dataset (accession numbers available in Table S2). To distinguish the genetic affinities of the studied population from native populations of other regions in Asia, Africa, Europe and the Canary Islands, 339 goat sequences were downloaded from GenBank and included in our analyses (accession numbers available in Table S2). Twenty-two goat reference sequences belonging to the six central and most common haplogroups: A, B, C, D, F and G (Naderi et al., 2007) were also selected from GenBank in this study to determine the possible origins of the Arabian goat populations.

All sequences were aligned using the default parameters of the ClustalW algorithm implemented in the MEGA 6 software package (Tamura et al., 2013). The final dataset consisted of sequences of a 423 bp fragment corresponding to positions 15,764 to 16,187 bp in the *C. hircus* mtDNA reference sequence. The 126 sequences reported in this paper have been deposited in the GenBank database under accession numbers KY815106 - KY815231.

2.3. Statistical analysis

Genetic variation at this mtDNA region was used to estimate haplotype diversity (Hd), nucleotide diversity (π), the mean number of pairwise differences (*k*), the corresponding standard deviations (SD), mismatch analysis and Fu's *Fs* values, using Arlequin ver. 3.5.1.2 (Excoffier and Lischer, 2010). In addition, the differentiation of Arabian goat populations was evaluated through pairwise comparisons (F_{ST}) and analysis of molecular variance (AMOVA) using Arlequin ver. 3.5.1.2 (Excoffier and Lischer, 2010).

An analysis of sequence variants was conducted for all sequences using the neighbor-joining algorithm based on the Kimura two-parameter model with 1000 replications in the program MEGA6 (Tamura et al., 2013) to identify the possible haplogroups in each individual based on the reference sequences (Naderi et al., 2007). The haplogroup frequency proportions within each Arabian goat population were also estimated. Finally, to further demonstrate the relationships between the haplotypes found in Arabian goat populations and those observed in Asia, Africa, Europe and the Canary Islands, two median joining networks were generated using PopART ver. 1.7 (http://popart.otago.ac.nz/index.shtml).

3. Results

The comparison of 617 sequences (126 from this study and 491 from published sources) from 18 different Arabian goat populations revealed a high rate of polymorphism, including 453 different haplotypes and 186 polymorphic nucleotide sites, which accounted for 43.97% of the sequenced 423 bp fragment. Among these variable polymorphic sites, there were 149 transitions, 13 transversions (a transition/transversion ratio of 11.46) and 49 insertion–deletion (indel) mutations. Among the detected 453 haplotypes, 18 haplotypes were found to be shared between Arabian goat populations. Haplotype Hap 25 was found to be the most frequently shared haplotype, occurring in 12 individuals from seven goat populations (Fig. 2A). The remaining haplotypes occurred at low frequencies, and some of those were specific to particular countries.

The haplotype diversity (Hd) and nucleotide diversity (π) were calculated separately for each Arabian goat population (Table 1) and were estimated to be 0.998 and 0.025, respectively. The values for the two parameters (Hd and π) ranged from 0.889 to 1.000 and from 0.015 to 0.036, respectively. The highest value of Hd was found in eight populations from Yemen, Lebanon, Syria, Algeria, Libya, Mauritania, Sudan and Somalia (1.000), and the highest value of π was observed in Somalian goats (0.036). The lowest Hd and π values were recorded in two populations from Palestinian (0.889) and Libyan (0.015), respectively. Additionally, the mean number of pairwise differences (*k*) ranged from 6.381 to 15.400 and was higher in Somalian goats than those of all other populations (Table 1). The pairwise F_{ST} values revealed low genetic differentiation between the goats of different Arab countries (Table S3) with the exception of Palestinian goats (PLT), which generally displayed highly significant genetic differentiation ($P < 0.01$) from all other Arabian goats. Similarly, the AMOVA results supported the existence low differentiation between the populations (3.26%; $P < 0.001$; Table S4).

Phylogenetic relationship analysis of the obtained sequences (neighbor-joining tree; data not shown) grouped all Arabian goat sequences into three haplogroups: A, B and G (Table 1 and Fig. 1). Haplogroup A was observed in all goat populations, with an average frequency of 94%. Moreover, haplogroup B, and more specifically, subhaplogroup B1, was very rare (0.65%) in Arabian domestic goats and was detected in only four individual goats from the Oman population on the southern Arabian Peninsula (Table 1 and Fig. 1), indicating a distinct population. The second largest haplogroup among the Arabian goats, haplogroup G, was present in eight populations (Table 1 and Fig. 1). Haplogroup G represented 5.35% of the total samples and was predominant (22/33) in the Arabian Peninsula region. Among the investigated populations, the goats from Oman exhibited the highest frequency of haplogroup G (30.30%, 10 individuals), followed by the populations from Egypt (24.24%, 8 individuals), Iraq and Saudi Arabia (15.15%, 5 individuals), whereas haplogroup G occurred at low frequencies in a few individuals in the other Arabian goat populations (Table 1 and Fig. 1). We also estimated the genetic diversity of haplogroups A and G, whereas estimation for haplogroup B was not performed because it was represented by a single haplotype. Haplogroup A had the highest haplotype and nucleotide diversity values of 0.998 and

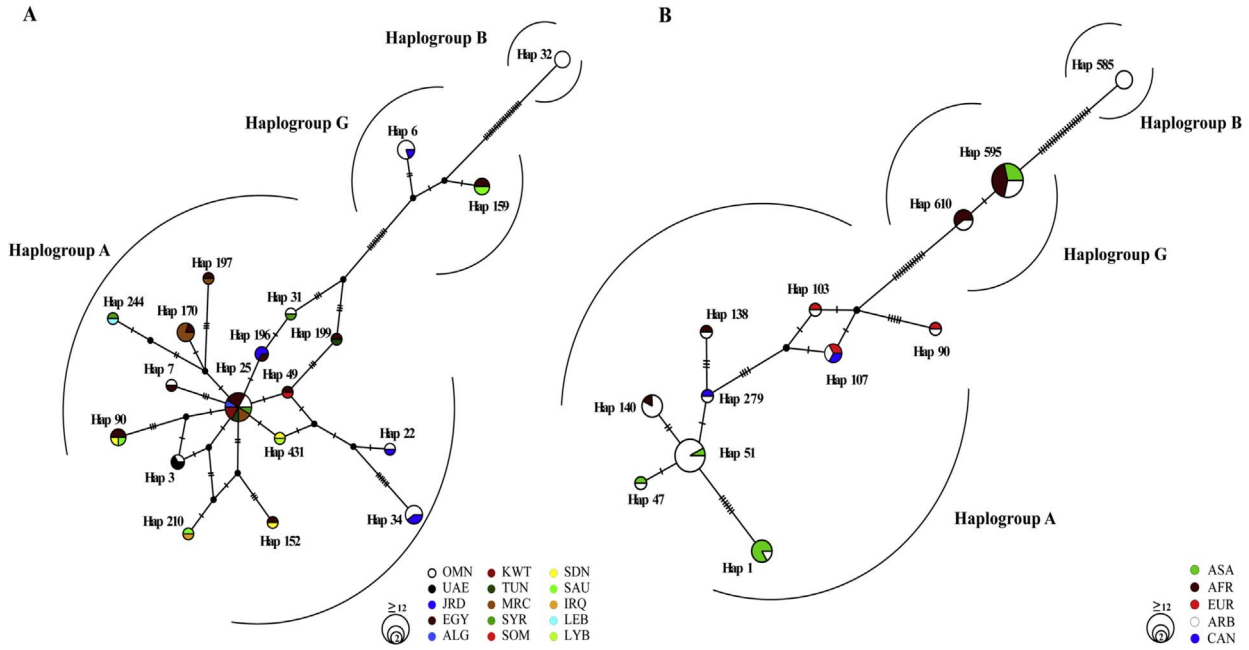

Fig. 2. Median-joining networks depicting the relationships between the shared haplotypes obtained from a set of Arabian goat samples (A) and among Arabian, African, Asian, European and Canarian islands goat samples (B). The haplogroup B in the networks is to complete the all set of haplogroups observed. The haplotypes are colored according to populations/regions and scaled according to the number of supporting sequences. The hatch marks in the lines represent the number of mutational steps separating the haplotypes. The abbreviations of Arabian goat populations are provided in Table 1, whereas the abbreviations of regions are as follows: Asia, ASA; Africa, AFR; Europe, EUR; Arab, ARB; and the Canary Islands, CAN. In Supplementary Table S5, the GenBank accession codes are provided for all the shared haplotypes.

0.021, respectively. Compared with haplogroup A, haplogroup G had lower haplotype and nucleotide diversity values (0.955 and 0.0133, respectively).

Median-joining network analysis allow visualization of the relationships between haplotypes and abundance in populations (Bandelt et al., 1999). The use of this analysis also divided all the obtained sequences into three haplogroups, A, B and G, and showed that the haplotype frequencies did not follow any pattern related to population or geographic region (Fig. 2A). To investigate possible past relationships between Arabian goats and goats in other regions, in a separate analysis, we included previously published sequences from Asia, Africa and Europe in our data set (Table S2). The network resulting from this comparison showed that 11 haplotypes belonging to haplogroups A and G were not only shared among Arabian populations but also with populations from neighboring countries in Asia, Africa and Europe (Fig. 2B).

In addition, a calculation of Fu's *Fs* statistic was performed for haplogroups A and G to assess past demographic dynamics. For haplogroup B, the presence of a single representative haplotype precluded this statistical analysis. The presence of population expansions was

Table 1
Genetic diversity indices in native Arabian goat populations and their mtDNA haplogroup distributions.

Population	Code	N[a]	Hd[b] ± SD[c]	Π[d] ± SD	*k*[e] ± SD	H(n)[f]
Iraq	IRQ	17	0.978 ± 0.031	0.035 ± 0.019	14.963 ± 7.044	A(12), G(5)
Kuwait	KWT	10	0.956 ± 0.059	0.019 ± 0.011	7.911 ± 4.022	A(9), G(1)
Oman	OMN	69	0.983 ± 0.006	0.033 ± 0.016	13.836 ± 6.286	A(55), B(4), G(10)
Saudi Arabia	SAU	55	0.996 ± 0.005	0.023 ± 0.012	9.856 ± 4.583	A(50), G(5)
United Arab Emirates	UAE	7	0.952 ± 0.096	0.021 ± 0.013	8.952 ± 4.701	A(7)
Yemen	YEM	9	1.000 ± 0.063	0.017 ± 0.010	7.286 ± 3.819	A(9)
Jordan	JRD	35	0.985 ± 0.012	0.025 ± 0.013	10.724 ± 5.027	A(34), G(1)
Lebanon	LEB	8	1.000 ± 0.063	0.022 ± 0.013	9.321 ± 4.797	A(8)
Palestine	PLT	9	0.889 ± 0.091	0.024 ± 0.013	9.944 ± 5.027	A(9)
Syria	SYR	9	1.000 ± 0.052	0.019 ± 0.011	8.222 ± 4.212	A(9)
Algeria	ALG	14	1.000 ± 0.027	0.028 ± 0.015	11.967 ± 5.763	A(14)
Libya	LBY	7	1.000 ± 0.076	0.015 ± 0.009	6.381 ± 3.442	A(7)
Egypt	EGY	164	0.996 ± 0.002	0.023 ± 0.012	9.735 ± 4.491	A(156), G(8)
Morocco	MRC	156	0.993 ± 0.002	0.022 ± 0.011	9.152 ± 4.232	A(156)
Tunisia	TUN	22	0.991 ± 0.017	0.022 ± 0.012	9.320 ± 4.452	A(22)
Mauritania	MTN	8	1.000 ± 0.063	0.024 ± 0.014	10.000 ± 5.122	A(8)
Sudan	SDN	10	1.000 ± 0.045	0.024 ± 0.014	10.333 ± 5.156	A(9), G(1)
Somalia	SOM	8	1.000 ± 0.096	0.036 ± 0.022	15.400 ± 8.042	A(6), G(2)
Total		617	0.998 ± 0.000	0.025 ± 0.013	10.586 ± 4.830	A(580), B(4), G(33)

[a] Sequence size.
[b] Haplotype diversity.
[c] Standard deviation.
[d] Nucleotide diversity.
[e] Mean number of pairwise differences.
[f] Haplogroup present in each population (number of the haplotype).

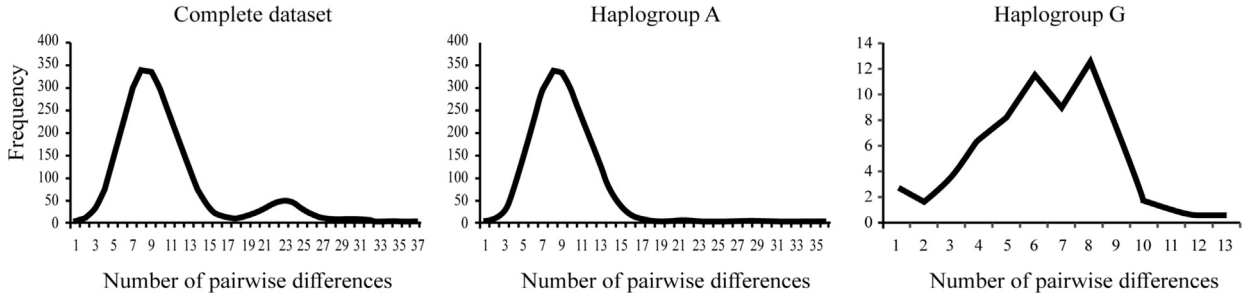

Fig. 3. Mismatch distribution patterns for mtDNA haplogroups of Arabian goats.

supported for both haplogroup A ($Fs = -23.95$) and haplogroup G ($Fs = -9.36$), with high significance ($P < 0.01$). This result appears to match the observed unimodal and smooth bell-shaped mismatch curves that were clearly observed for haplogroup A; for haplogroup G, this match was less clear (Fig. 3). The irregular curve of haplogroup G, which may have resulted from the low sample size (33 samples), would be consistent with recent demographic expansions and is in agreement with previous findings (Naderi et al., 2007). Finally, we used the complete dataset to examine the demographic expansion of Arabian goats; the results also showed population expansion, as detected by highly significant negative *Fs* value ($Fs = -23.75$, $P < 0.005$) and mismatch distributions (Fig. 3).

4. Discussion

Based on the genetic variation parameters, the high degree of polymorphism observed in the analyzed D-loop control region have been explained as the consequence of the high mutation rate in this region; alternatively, this diversity may have resulted from the contributions of wild, highly diverse ancestral stocks (i.e., bezoar) during domestication, as established in the literature (Naderi et al., 2007, 2008; Colli et al., 2015). These findings are consistent with previous studies on goat mitochondrial genomes (Naderi et al., 2007; Colli et al., 2015).

Consistent with the results of previous studies (Naderi et al., 2007; Kibegwa et al., 2016), the 18 Arabian goat populations in our study displayed higher levels of mtDNA diversity (haplotype diversity and nucleotide diversity). The overall haplotype diversity and nucleotide diversity values of the total individuals were 0.998 and 0.025, respectively (Table 1), which indicate higher levels of genetic diversity in Arabian goats compared with that in Iberian, European, West African and Southeast Asian goat populations (Amills et al., 2009; Pereira et al., 2009; Royo et al., 2009). The higher genetic diversity in Arabian goats is likely the result of the proximity of some Arab countries to the goat domestication center or the mixing of populations from different geographical locations (Troy et al., 2001; Beja-Pereira et al., 2004; Agha et al., 2008; Akis et al., 2014).

Our dataset confirms a very weak phylogeography with small genetic differentiation (F_{ST}) between different Arabian goat populations (Table S3). One potential reason for this low genetic differentiation is that there was high historical gene flow between Arabian goat populations, which was likely related to the historical movement of goats across Arab countries under one of the most ancient forms of open herding, known as Bedouin (or nomadic) herding. Trade may also account for the patterns discerned in goat gene pools. Alternatively, the sacrifice of animals (Nahr) during the performance of the Hajj resulted in thousands of animals (including goat, sheep, cattle, and camels) being brought in by traders or people living near the Makah region. This form of import is another key factor that could have contributed to the mixing of animals during transportation to the Arabian Peninsula. Thus, our results suggest that all goat populations of Arab countries share a relatively similar genetic background. This conclusion is consistent with previous results, confirming that the weaker genetic structure observed in small ruminants (e.g., goats and sheep) compared with that of large ruminants (e.g., cattle) is likely a result of the high mobility of small ruminants due to human migration and commercial trade (Luikart et al., 2001; Fernández et al., 2006; Meadows et al., 2007).

The results of our phylogenetic analysis classified Arabian goats into three distinct maternal haplogroups: A, B and G. Haplogroup A is the most represented when considering either the number of individuals or number of haplotypes among the Arabian goat populations and is highly widespread all over Arab countries (Table 1 and Fig. 1), with an average frequency of 94%, which is consistent with the findings of previous studies (Colli et al., 2015) reporting that most domesticated goats carry this haplogroup. Among the other two haplogroups (B and G), B was rare and only observed in a few individuals from Oman in the Arabian Peninsula. Because haplogroup B is mostly found throughout Central and South Asia, this haplogroup likely originated in this area (Chen et al., 2005; Ruo-Yu et al., 2006; Naderi et al., 2007; Colli et al., 2015) and was distributed to other locations through human migration or commercial trade. Therefore, two explanations are possible for the presence of haplogroup B in this part of the Arabian Peninsula.

First, the long history of Arabian Peninsula as a trading platform between the continents of Asia and Africa and as the bridge for communication between Asian and African peoples. In particular, the sultanate of Oman is located in the southeast corner of the Arabian Peninsula and is well known for its role as a trading center between the Indian subcontinent and the east coast of Africa due to the passage of vessels traveling between the two continents (Nicolini, 2002; Al-Saadi, 2012). This fact is interesting because haplogroup B found in Omani goats, was also found among Pakistani goat populations (Naderi et al., 2007; Naqvi et al., 2017); therefore, it is very possible that people emigrating from this region (e.g., Baluchistan) to Oman likely brought with them goats carrying this haplogroup. Similar introgression has been supported by the domestication process of other species, such as cattle and chickens, based on microsatellite and mtDNA analyses, respectively (Mahgoub et al., 2013; Al-Qamashoui, 2014).

A second explanation, albeit less probable, suggests that haplogroup B might have reached the Arabian Peninsula (Oman) from other geographic regions that are far from the Indian Ocean, such as China. Previous studies have indicated that at least one subgroup of haplogroup B likely originated from China, in Eastern Asia (Chen et al., 2005; Ruo-Yu et al., 2006). Indeed, the presence of haplogroup B in Chinese goats gives rise to an interesting hypothesis that the arrival of haplogroup B in the Arabian Peninsula (Oman) was a result of Chinese merchant ships in approximately the 5th century AD (Al-Saadi, 2012) or after the early 15th century AD as a result of Chinese maritime expeditions to South Asia, the Arabian Peninsula and East Africa (Duyvendak, 1939; Beaujard, 2005; Al-Saadi, 2012).

The high frequency of haplogroup G (22/33) in the Arabian Peninsula and, in particular, the large difference between sequences of this haplogroup, may indicate that haplogroup G may have been present in Arabian goats for longer and that is also supported by the close

geographic proximity of this region to center of origin - Iran and Turkey (Naderi et al., 2007; Colli et al., 2015). In a recent study, haplogroup G was found among Egyptian goat breeds, and it was postulated that this haplogroup might have arrived from East (Iran) and Northeast (Turkey) Asia via trade routes (Ahmed et al., 2017). Indeed, the presence of haplogroup G among the goats from Egypt, Sudan, Somalia and Kenya from North and East Africa (Colli et al., 2015; Githui et al., 2016; Kibegwa et al., 2016; Othman and Mahfouz, 2016; Ahmed et al., 2017) supports that the long-lasting trade between the Arabian Peninsula and Africa via terrestrial and marine routes was primarily responsible for the spread of this haplogroup out of its center of origin. Finally, when considering either the number of individuals or frequency distribution among the eight Arabian goat populations, this evidence indicates that the mtDNA haplogroup G is the second most predominant type in the Arab region.

The network analysis results indicate strong effects of human intervention in promoting gene flow between populations via the commercial trade and transportation of goats among regions of the Old World. Clear evidence supporting this hypothesis was obtained within the 11 shared haplotypes in the two haplogroups A and G, with some of the Arabian goats showing the same haplotypes as those from neighboring regions of Asia, Africa and Europe, including the nearby Canary Islands, as presented in Table S5 and Fig. 2B. Despite the haplogroup A be very cosmopolitan, three haplotypes from group A are shared between animals from Tunisia and Algeria in North Africa with Iberian Peninsula and Italy in Southern Europe, respectively (Table S5). In fact there was a previous observation of gene flow between North African and European goat populations (Pereira et al., 2009) using mtDNA and Y-chromosome markers. The same thin evidence was also found between extant Arabian and Canarian goats. Also in this case, only two shared haplotypes were found, both from world-wide dispersed haplogroup A (Table S5 and Fig. 2B), therefore the origin of the extant Canarian goats although previously proposed to be from the African continent (Fresno et al., 1992; Amills et al., 2004; Fregel et al., 2009), receives little support from our data.

A close relationship among the Arabian, Asian and African goat populations was clear from the seven shared haplotypes of haplogroups A and G among the animals in these three regions (Fig. 2B). Evidence of directional overland diffusion from the Near East to Northwest Africa and Southeast Africa was also provided by the phylogeographic analysis of goat haplotypes (A and G) in the Arabian region. Based on the networks in Fig. 2A and B and Table S5, there are indications of the movement of domestic goats from the Arabian Peninsula via Egypt to North Africa towards Morocco across Tunisia and Algeria; the other route extended from Egypt directly to Sudan following the Nile Valley to Kenya and Somalia. This corroborates the occurrence of past cultural and commercial contact between the Arab region and both Asia and Africa or might be also attributed to the distinct geography of the Arab region, which is located between three Old World continents.

However, we cannot discard the effects of recent (within the past two decades) crossbreeding programs for livestock species in many Arab countries, which have involved the importation of exotic breeds to improve the productivity of various local breeds (FAO, 2014). It is possible that these crossbreeding activities have recently introduced these haplogroups to Arab countries from commercial breeds of goats from Asia (Angora, Cashmere, Jamnapari, Beetal and Barbari), Africa (Boer) and Europe (Saanen, Alpin, Anglo-Nubian and Toggenburg) (FAO, 2007; Shrestha and Fahmy, 2007). These haplotypes therefore could represent signatures of the recent introgression of commercial breed mtDNA haplotypes into native Arabian goat breeds.

Mismatch distributions and Fu's *Fs* statistic calculations, the two main methods used to assess population expansion events, were used in this study. Mismatch distributions (pairwise comparisons) of mtDNA have been widely used to explore such demographic events (Rogers and Harpending, 1992). Fu's *Fs* statistic, which is based on the probability of having a number of alleles greater or equal to the observed number in a sample drawn from a stationary population (Fu, 1997), is considered a very useful statistic detecting population expansion (Liao et al., 2010). The significantly negative Fu's *Fs* estimates obtained in the current study, which are comparable with estimates from other populations (Zhao et al., 2014; Awotunde et al., 2015), are consistent with demographic population expansion, such as that expected for populations expanding after the domestication of a relatively few number of founder-individuals (Luikart et al., 2001).

In conclusion, the information regarding maternal genetic diversity collected in this study essentially represents the first assessment of the genetic diversity and origin of Arabian goat populations. The results of the present study indicated that Arabian goat populations harbor abundant genetic diversity and belong to three mtDNA haplogroups (A, B and G) as a result of their distinct geographical distribution. Haplogroup G is the second most predominant haplogroup in Arab countries, and we speculate that Arab traders and settlers were responsible for the spread of this haplogroup from its center of origin.

Acknowledgments

We are extremely thankful to Muhammad Khlouf and Mohammad Al-Sanosi for providing the samples from Palestine and Egypt, respectively. In addition, we would like to thank the following people who provided valuable assistance during the sampling process: Mohammad Al-Shaikh and Mohammad Khalf from Iraq; Mustafa Al-Hashmi and Ahmed Ali from Somalia; Mahmood Al-Qadhi and Salem Al-Huraizi from Yemen; Ibrahim Al-Shahi and Saeid Al-Shaali from the UAE; Sameer Murad from Lebanon; Ahmed Saidan and Ayoob Al-Shahi from Oman; Abdulrahman Nedjima and Kahina Zenadi from Algeria; Yacoub Seif from Mauritania; and finally, Latifa Joulami from Morocco.**Funding**

This work was supported by the Ministry of Higher Education (MOHE) of the Sultanate of Oman (PGE047856/2013); the Portuguese Foundation for Science and Technology (FCT) through an IF-FCT, Portugal (COMPETE FUNDS and SFRH/BPD/79913/2011); Secretary of Higher Education for Science and Technology of Ecuador (SENESCYT) (AR7L1030/2012); and the European Social Fund and the Human Potential Operational Program (POPH/FSE).

Conflict of interest

None. We declare that we have no financial or personal relationships with other people or organizations in Arab countries who could inappropriately influence our work. Additionally, our work is focused only on population genetics; therefore, the collected samples were not used for any commercial purposes or analyses related to diseases or sanitary states of the sampled animals.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.livsci.2017.09.017.

References

Agha, S., Pilla, F., Galal, S., Shaat, I., D'andrea, M., Reale, S., Abdelsalam, A., Li, M., 2008. Genetic diversity in Egyptian and Italian goat breeds measured with microsatellite polymorphism. J. Anim. Breed. Genet. 125, 194–200.

Ahmed, S., Grobler, P., Madisha, T., Kotze, A., 2017. Mitochondrial D-loop sequences reveal a mixture of endemism and immigration in Egyptian goat populations. Mitochondrial DNA A DNA Mapp. Seq. Anal. 28, 711–716.

Akis, I., Oztabak, K., Mengi, A., Un, C., 2014. Mitochondrial DNA diversity of Anatolian indigenous domestic goats. J. Anim. Breed. Genet. 131, 487–495.

Al-Qamashoui, B., 2014. Towards Conservation of Omani Local Chicken: Management, Performance and Genetic Diversity. Faculty of Agricultural Sciences, Georg-August-Universität Göttingen, Göttingen, Germany, pp. 82.

Al-Saadi, A.S., 2012. The origins of Omani-China friendship: a historical review. J. Middle

East. Islam. Stud. 6, 84–105.
Amills, M., Capote, J., Tomàs, A., Kelly, L., Obexer-Ruff, G., Angiolillo, A., Sanchez, A., 2004. Strong phylogeographic relationships among three goat breeds from the Canary Islands. J. Dairy Res. 71, 257–262.
Amills, M., Ramírez, O., Tomàs, A., Badaoui, B., Marmi, J., Acosta, J., Sànchez, A., Capote, J., 2009. Mitochondrial DNA diversity and origins of South and Central American goats. Anim. Genet. 40, 315–322.
Awotunde, E.O., Bemji, M.N., Olowofeso, O., James, I.J., Ajayi, O., Adebambo, A.O., 2015. Mitochondrial DNA sequence analyses and phylogenetic relationships among two Nigerian goat breeds and the South African Kalahari Red. Anim. Biotechnol. 26, 180–187.
Bandelt, H.-J., Forster, P., Röhl, A., 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. 16, 37–48.
Beaujard, P., 2005. The Indian Ocean in Eurasian and African world-systems before the sixteenth century. J. World Hist. 16, 411–465.
Beja-Pereira, A., England, P.R., Ferrand, N., Jordan, S., Bakhiet, A.O., Abdalla, M.A., Mashkour, M., Jordana, J., Taberlet, P., Luikart, G., 2004. African origins of the domestic donkey. Science 304, 1781.
Benjelloun, B., Pompanon, F., Bati, M.B., Chentouf, M., Ibnelbachyr, M., El Amiri, B., Rioux, D., Boulanouar, B., Taberlet, P., 2011. Mitochondrial DNA polymorphism in Moroccan goats. Small Rumin. Res. 98, 201–205.
Brunner, U., 2000. The Great Dam and the Sabean oasis of Ma'rib. Irrig. Drain. Syst. 14, 167–182.
Chen, S.-Y., Su, Y.-H., Wu, S.-F., Sha, T., Zhang, Y.-P., 2005. Mitochondrial diversity and phylogeographic structure of Chinese domestic goats. Mol. Phylogenet. Evol. 37, 804–814.
Colli, L., Lancioni, H., Cardinali, I., Olivieri, A., Capodiferro, M.R., Pellecchia, M., Rzepus, M., Zamani, W., Naderi, S., Gandini, F., 2015. Whole mitochondrial genomes unveil the impact of domestication on goat matrilineal variability. BMC Genom. 16, 1115.
Duyvendak, J.J.L., 1939. The true dates of the Chinese maritime expeditions in the early fifteenth century. T'oung Pao 34, 341–413.
Excoffier, L., Lischer, H.E., 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10, 564–567.
FAO, 2007. The State of the World's Animal Genetic Resources for Food and Agriculture. Commission on Genetic Resources for Food and Agriculture, Rome.
FAO, 2014. Characterization and value addition to local breeds and their products in the Near East and North Africa – Regional Workshop, Rabat, Morocco, 19-21 November 2012. Animal Production and Health Report No. 3, Rome.
Fernández, H., Hughes, S., Vigne, J.-D., Helmer, D., Hodgins, G., Miquel, C., Hänni, C., Luikart, G., Taberlet, P., 2006. Divergent mtDNA lineages of goats in an Early Neolithic site, far from the initial domestication areas. Proc. Natl. Acad. Sci. USA 103, 15375–15379.
Fregel, R., Pestano, J., Arnay, M., Cabrera, V.M., Larruga, J.M., Gonzalez, A.M., 2009. The maternal aborigine colonization of La Palma (Canary Islands). Eur. J. Hum. Genet. 17, 1314–1324.
Fresno, M., Capote, J.F., Camacho, M.E., Darmanin, N., Delgado, J.V., 1992. The canary islands breeds: past, present and future. Arch. Zootec. 41, 513–518.
Fu, Y.-X., 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147, 915–925.
Githui, E., Kibegwa, F., Kamau, J., Mutura, S., Okwany, Z., Ngigi, D., Mwangi, E., 2016. Genetic relationships of indigenous goats reared by pastoralists in Kenya based on mitochondria D-loop sequence. Anim. Genet. Resour. 59, 73–80.
Jawād, A., 1968. Detailed History of Arabs Before Islam. University of Baghdad, Baghdad.
Kibegwa, F., Githui, K., Jung'a, J., Badamana, M., Nyamu, M., 2016. Mitochondrial DNA variation of indigenous goats in Narok and Isiolo counties of Kenya. J. Anim. Breed. Genet. 133, 238–247.
Liao, P.-C., Kuo, D.-C., Lin, C.-C., Ho, K.-C., Lin, T.-P., Hwang, S.-Y., 2010. Historical spatial range expansion and a very recent bottleneck of Cinnamomum kanehirae Hay. (Lauraceae) in Taiwan inferred from nuclear genes. BMC Evol. Biol. 10, 124.
Lin, B., Odahara, S., Ishida, M., Kato, T., Sasazaki, S., Nozawa, K., Mannen, H., 2013. Molecular phylogeography and genetic diversity of East Asian goats. Anim. Genet. 44, 79–85.
Luikart, G., Gielly, L., Excoffier, L., Vigne, J.-D., Bouvet, J., Taberlet, P., 2001. Multiple maternal origins and weak phylogeographic structure in domestic goats. Proc. Natl. Acad. Sci. USA 98, 5927–5932.
Mahgoub, O., Babiker, H.A., Kadim, It, Al-Kindi, M., Hassan, S., Al-Marzoooqi, W., Eltahir, Y.E., Al-Abri, M.A., Al-Khayat, A., Al-Sinani, K.R., Hilal Al-Khanjari, H., Costa, V., Chen, S., Beja-Pereira, A., 2013. Disclosing the origin and diversity of Omani cattle. Anim. Genet. 44, 336–339.
Martin, B.G., 1974. Arab migrations to East Africa in medieval times. Int. J. Afr. Hist. Stud. 7, 367–390.
Meadows, J.R.S., Cemal, I., Karaca, O., Gootwine, E., Kijas, J.W., 2007. Five ovine mitochondrial lineages identified from sheep breeds of the near East. Genetics 175, 1371–1379.
Naderi, S., Rezaei, H.-R., Pompanon, F., Blum, M.G., Negrini, R., Naghash, H.-R., Balkız, Ö., Mashkour, M., Gaggiotti, O.E., Ajmone-Marsan, P., 2008. The goat domestication process inferred from large-scale mitochondrial DNA analysis of wild and domestic individuals. Proc. Natl. Acad. Sci. USA 105, 17659–17664.
Naderi, S., Rezaei, H.-R., Taberlet, P., Zundel, S., Rafat, S.-A., Naghash, H.-R., El-Barody, M.A.A., Ertugrul, O., Pompanon, F., for the Econogene, C., 2007. Large-scale mitochondrial DNA analysis of the domestic goat reveals six haplogroups with high diversity. PLoS One 2, e1012.
Naqvi, A.N., Bukhari, J.F., Vahidi, S.M.F., Utsunomiya, Y.T., Garcia, J.F., Babar, M.E., Han, J.-L., Pichler, R., Periasamy, K., 2017. Microsatellite based genetic diversity and mitochondrial DNA D-Loop variation in economically important goat breeds of Pakistan. Small Rumin. Res. 148, 62–71.
Nicolini, B., 2002. Historical and political links between Gwādar and Muscat from 19th-century testimonies. Proc. Semin. Arab. Stud. 32, 281–286.
Othman, O.E., Mahfouz, E.R., 2016. Genetic biodiversity, affinities and phylogeny of four goat breeds in Egypt. J. Biol. Sci. 16, 86.
Parma, P., Feligini, M., Greeppi, G., Enne, G., 2003. The complete nucleotide sequence of goat (*Capra hircus*) mitochondrial genome. Goat mitochondrial genome. DNA Seq. 14, 199–203.
Pereira, F., Queirós, S., Gusmão, L., Nijman, I.J., Cuppen, E., Lenstra, J.A., Consortium, E., Davis, S.J., Nejmeddine, F., Amorim, A., 2009. Tracing the history of goat pastoralism: new clues from mitochondrial and Y chromosome DNA in North Africa. Mol. Biol. Evol. 26, 2765–2773.
Piras, D., Doro, M.G., Casu, G., Melis, P.M., Vaccargiu, S., Piras, I., Parracciani, D., Stradoni, R., Frongia, B., Lai, G., 2012. Haplotype affinities resolve a major component of goat (*Capra hircus*) MtDNA D-loop diversity and reveal specific features of the Sardinian stock. PloS One 7, e30785.
Rogers, A.R., Harpending, H., 1992. Population growth makes waves in the distribution of pairwise genetic differences. Mol. Biol. Evol. 9, 552–569.
Royo, L., Traoré, A., Tamboura, H., Álvarez, I., Kaboré, A., Fernández, I., Ouédraogo-Sanou, G., Toguyeni, A., Sawadogo, L., Goyache, F., 2009. Analysis of mitochondrial DNA diversity in Burkina Faso populations confirms the maternal genetic homogeneity of the West African goat. Anim. Genet 40, 344–347.
Ruo-Yu, L., Gong-She, Y., Chu-Zhao, L., 2006. The genetic diversity of mtDNA D-loop and the origin of Chinese goats. Anim. Genet. Sin. 33, 420–428.
Sardina, M.T., Ballester, M., Marmi, J., Finocchiaro, R., Van Kaam, J.B.C.H.M., Portolano, B., Folch, J.M., 2006. Phylogenetic analysis of Sicilian goats reveals a new mtDNA lineage. Anim. Genet. 37, 376–378.
Shrestha, J.N.B., Fahmy, M.H., 2007. Breeding goats for meat production: 2. cross-breeding and formation of composite population. Small Rumin. Res. 67, 93–112.
Tamura, K., Stecher, G., Peterson, D., Filipski, A., Kumar, S., 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. Mol. Biol. Evol. 30, 2725–2729.
Troy, C.S., MacHugh, D.E., Bailey, J.F., Magee, D.A., Loftus, R.T., Cunningham, P., Chamberlain, A.T., Sykes, B.C., Bradley, D.G., 2001. Genetic evidence for Near-Eastern origins of European cattle. Nature 410, 1088–1091.
Vigne, J.-D., 2011. The origins of animal domestication and husbandry: a major change in the history of humanity and the biosphere. C. R. Biol. 334, 171–181.
Zeder, M.A., Hesse, B., 2000. The initial domestication of goats (*Capra hircus*) in the Zagros Mountains 10,000 years ago. Science 287, 2254–2257.
Zhao, Y., Zhao, R., Zhao, Z., Xu, H., Zhao, E., Zhang, J., 2014. Genetic diversity and molecular phylogeography of Chinese domestic goats by large-scale mitochondrial DNA analysis. Mol. Biol. Rep. 41, 3695–3704.