

DOCUMENTING RADIOCARBON EVIDENCES, Y-CHROMOSOME, MITOCHONDRIAL DNA AND AUTOSOMAL MARKERS ON ORIGIN OF DOMESTICATION AND ROUTES OF GOAT GLOBAL DIVERGENCE: A Review

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ABSTRACT: Domestic goat is the first ruminant animal domesticated in the South-west Asia about 10,500 years ago from its *Capra aegagrus* and *Capra falconeri* ancestors. The archaeological evidence links its origin to the region from the Taurus Mountains of Turkey to Pakistan. Molecular data extends the origin upto the Balkans and Carpathian Mountain regions of Romania, and China. Domestic goat followed both the Mediterranean and Danubian routes to disperse into Europe, and the Silk Road and the Khyber Pass to disperse across Asia. From the six haplogroups (A, B, C, D, F and G) of domestic goat globally identified, haplogroup A has a global coverage of 89% in Asia, 98% in Europe, and absolute predominance (100%) in South and Central America; however, the African region is still poorly characterized. The predominance of haplogroups A could be as a result of its earliest domestication. Haplogroup B, C, D, F and G are very rare or even absent (e.g. haplogroups D) in Europe. Haplogroup C is present with very low frequencies in Europe (2%), Asia (1%) and in Mongolia. MtDNA lineage B was detected in few African countries and few countries in Europe, Middle East and Asia. Overall, population expansion events of the wild progenitors of domestic goats were occurred much earlier than the events of domestication.

Keywords: *Capra aegagrus*, *Capra falconeri*, domestic goat, genetic variation, haplogroup.

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INTRODUCTION

Genetic studies of livestock populations focus on questions of domestication, within and among-breed diversity, breed history and adaptive variation (Lenstra et al., 2012). Goats are widely distributed throughout the world (Abdel-Aziz, 2010), and Asia and Africa account for about 81% of the total world goat populations (Garrine, 2007). Recent reports indicated that there are >1,000 goat breeds (Dong et al., 2012; FAO) comprising >868 million goats which are kept around the world (Nomura et al., 2012). The global distribution of goats have been influenced by various factors, which include; commercial trade, wars, or migration of people with their livestock (Clutton-Brock, 2000), exploratory movements of humans throughout the world (Porter, 1996). This was followed by a more rapid global spread as a result of inter continentals trade in livestock across the Mediterranean basin during the Phoenician, Greek and Roman periods (Pariset et al., 2009).

Given the on-going climate change phenomena many developing countries will have to exploit more marginal agricultural areas to goats are better suited (FAO, 2007; Pariset et al., 2009; Castel et al., 2010). To do this, well designed and appropriately implemented goat breeding programs are needed. Such breeding programs and schemes however do not exist in developing countries (Pariset et al., 2009). This might be because that information related to evolution, genetic diversity and utility of goats is very limited or poorly documented.

In order to design good breeding programs, better understanding of the genetic diversity and structures of the existing goat populations need to be understood. Various genetic and radiocarbon dating tools exist and can be used to investigate the origins, domestication and dispersion patterns of goats and other small ruminants (Luikart et al., 2006; Feng-Hua et al., 2015). With this respect, *Capra hircus* is to the growing list of domestic animals that

have been widely surveyed for mtDNA sequence variation (Luikart et al., 2001). Molecular tools provide stronger and increasingly cheaper and quicker means for characterization (Manceau et al., 1999). Hitherto development of molecular tools and procedures phylogenetic relationships and the evolutionary history of *Capra* species were poorly distilled and understood (Pidancier et al., 2006). In addition, available reports so far have some discordance to each other.

This review therefore aims at assessing various reports and past studies on the origin and domestication of indigenous goats globally in order to lay a better understanding of indigenous goat genetic diversity.

ORIGIN AND SOURCE OF GOAT DOMESTICATION

Origin of goat domestication

Goat domestication was an integral part of the rise of agriculture (Fernández et al., 2006) and the adoption of agricultural practices throughout much of the world (Luikart et al., 2006). Goat, the “*poor man’s cow*” (MacHugh et al., 2001), was certainly the first ruminants to be domesticated along with their close relative, sheep (Devendra and McIeroy, 1982; Melinda et al., 2006). It is believed that the goats might have been domesticated in high, rocky mountain regions extending from the Taurus Mountains of Turkey into Pakistan (Epstein, 1971) about 10,500 years ago (Zeder and Hesse, 2000), and then spread quickly following patterns of human migration and trade (Luikart et al., 2001; Fernández et al., 2006). However, the exact location still remains uncertain (Sardina et al., 2006). Payne and Wilson (1999) reported south-west Asia (Iran and Iraq) (the most likely origin of the domestication of goats), south of Levant (Horwitz et al., 1999) (Figure 1) and Mehrgarh (Sultana et al., 2003) to be the ancient centers of goat domestication. The analysis of ancient goat DNA from Inner Mongolia region was closely genetically related to Chinese modern goats suggesting China is also considered the possible center of domestication particularly for sub-haplogroups B1 and B2 (Han et al., 2009). A recent study conducted on mtDNA hypervariable (HVI) region of ancient DNA indicated that Central Zagros has possibly played a key role for domestication of *C. hircus* (Mazdarani et al., 2014).

In contrast to this, the Balkans or Carpathian Mountain regions of Romania and Southern France were also suggested to be the origin of goats following a divergent lineage C and distinct lineage 3 found in Switzerland and Slovenia (Fernandez et al., 2006; Luikart et al., 2006; Pereira et al., 2009). However, the limited sample size casts doubts on these suggested regions to be the other centre of domestications of *C. hircus*. In addition, this is contrary to the hypothesis of domestication stated by Luikart et al. (2001) for lineage C, which is far from putative domestication, centers (Naderi et al., 2008) and questions the previous premises of domestication in general. Moreover, the presence of lineage A and C in South-east and Central Europe could be accompanied by the first Neolithic migration waves (Colli et al., 2015).

Sources of wild gene pool of goat domestication

Historical as well as archeological evidences indicate that the domestic goats might have been domesticated from two wild *Capris* (*C. aegagrus* and *C. falconeri*) species (Epstein, 1971), and from markhor (*C. falconeri*) in West Asia and the ibex in East Asia (Harris, 1962). However, it was earlier proposed that bezoar (*C. aegagrus*) is the most likely ancestor of domestic goats (Harris, 1962; and Zeuner, 1963). The MtDNA analysis strengthened this idea, hence a least four different strains of wild *Capra* might have been the source of the modern domestic goats (Sultana et al., 2003). The three species of the wild goat, bezoars (*C. aegagrus*), markhors (*C. falconeri*) and ibex (*C. ibex*), are closely related to the modern domestic goat (*C. hircus*). According to the studies of Mannen et al. (2001) and Sultana et al. (2003), the bezoar goat is the closest and likely be matriarchal ancestor of domestic goats. A recent extensive whole mitochondrial genome analysis confirmed the bezoar (*C. aegagrus*) is the most contributor for formation of the identified haplogroups of *C. hircus* (Colli et al., 2015). Sindh Ibex (*C. aegagrus blythi*) was also indicated as a possible contributor to the genetics of domestic goats (Sultana et al., 2003). Luikart et al. (2001) also concluded the presence of multiple maternal origins of goats, however, the monophyletic and paraphyletic trees (Naderi et al., 2008) obtained do not support multiple origins.

Luikart et al. (2001) indicated that three goat lineages arose from genetically discrete populations rather than from a single wild population and the possible multiple maternal lineages could have been originated via introgression rather than separate domestication events. This idea strengthens the paraphyletic tree nature rather than monophyletic tree. The three distinct lineages could be related to either (i) three separate maternal origins from genetically distinct populations, or (ii) one origin from an extremely large population containing three highly divergent lineages. However, all the domestic goat lineages (A, B, C and D) examined in Indian goat populations fall into a single monophyletic group that is distinct from all available wild goat sequences (Joshi et al., 2004), and the authors hypothesized that the contributing lineages found in India goats were derived from an unknown population that might have become rare or extinct.

There are still discordances between mtDNA and Y-chromosome phylogenies at which the intimations can be explained. According to Pidancier et al. (2006) the following remain unresolved: i) Amplification of nuclear-mtDNA copies; that is, laboratory artifacts and in most cases authors use many bone samples, for which nuclear amplification is less probable than mitochondrial amplification because of DNA quantity and quality ii) selection, iii) lineage sorting of ancestral polymorphisms or iv) horizontal transfer of genes which may result from hybridization and introgression in mammals. In relation with the latter hypothesis, the mtDNA control region and Y-chromosome analyses indicated the possible case of recent introgressive hybridization in *Capra* between *C. cylindricornis* individuals from Daghestan groups and Daghestan *C. aegagrus* rather than with its conspecifics (Pidancier et al., 2006).

However, in spite of some contradiction, the closest possible wild source of the present domestic goat is the bezoars (*C. aegagrus*). This is also supported by the following evidences: the branch length between the *cyt b* and mtDNA control region is shortest from domestic goats to the wild goat *C. aegagrus* (Manceau et al., 1999; Luikart et al., 2006). The mtDNA analysis revealed that the domestic goat originated from Bezoar goat (*C. aegagrus*) (Takada et al., 1997; Manceau et al., 1999; MacHugh and Bradley, 2001; Colli et al., 2015). These are consistent with the Y-chromosome and autosomal (microsatellite) marker based findings of Luikart et al. (2006) and Pidancier et al. (2006), as with those of morphological studies, archaeological data, and inferred geographical distribution of wild *Capra spp* (Smith, 1998). In addition to the above maternal and paternal origin evidences, the paleontological evidence also supports the *C. aegagrus* to be the closest ancestor of domestic goats (Porter, 1996). The second-closest taxon to domestic goats, based on the Y chromosome, is *C. falconeri*, which is a species separated from both domestic goats and *C. aegagrus* by two to three mutations (Luikart et al., 2006).

IDENTIFICATION OF LINEAGE, DISPERSION ROUTES AND GLOBAL COVERAGE OF DOMESTIC GOATS

Identification of lineages

There is no clear definition between lineage and haplogroup. While Luikart et al. (2001) and Sultana et al. (2003) put both alternatively. Nomura et al. (2013) indicated lineage is source of wild ancestor whereas haplogroup is common ancestor. For this paper, both terminologies have been used interchangeably. Bearing this in mind, various scholars have identified six lineages of domestic goat which dispersed throughout the world following various routes of dispersion at different times. Luikart et al. (2001) identified three lineages (A, B, C) by sequencing HVI. Sultana et al. (2003) revealed four lineages (A, B, C and D) by sequencing both *d*-loop and *cyt b* regions in Pakistan's goats. Joshi et al. (2004) revealed five lineages (A, B, C, D and E) in Indian goats. Naderi et al. (2007) identified six lineages (A, B, C, D, F, G) from sequencing of HVI and disproved existence of haplogroup E rather those haplotypes which were named by this haplogroup created sub-haplogroup B1 and B2 which were moved to North, East and South East Asia. Studies have also reported the presence of sub-haplogroups (Han et al., 2010, Nomural et al., 2013; Akis et al., 2014; Colli et al., 2015). The ancient DNA analysis indicated that goats from haplogroup B were detected in the Swiss Alps which were later replaced by haplogroup A and C (Schlumbaum et al., 2010). Chen et al. (2005) had also found four mitochondrial lineages (A, B, C and D) in Chinese goat breeds. Similarly, by amplifying HVI, Nomura et al. (2013) confirmed the presence of all previously identified lineages/haplogroups except lineage G. This could be because of the divergence regions of the later lineage only towards to South-west Asia and Europe, and it could be also because of their limited focus to South, East and South-east Asia. A recent and extensive study conducted on whole mitochondrial genome revealed various clades of haplogroups (A1-A7, B1, C1a, D1 and G) (Colli et al., 2015).

However, based on the microsatellite markers, the three lineages identified by Nomura et al. (2012) differ slightly from those reported by Luikart et al. (2001) particularly for the Asian goat populations. Nomura et al. (2012) investigated two different lineages, which dispersed to South and South-East Asian countries. However, these haplogroups were considered earlier as a lineage (Luikart et al., 2001). On the other hand, the two different lineages identified by Luikart et al. (2001) which spread to North (Mongolia) and East Asia regions were merged and reported as a lineage (Nomura et al., 2012). Besides, an additional lineage which was moved to South-East Asia (including Taiwan, Japan and Korea) was also identified. In general, wider wild origins/lines are found in Asia than other parts of the world, as a result the regional genetic diversity is also comparatively higher.

Dispersion routes and global coverage of domestic goat

Domestic goats had been diverged following various routes of divergence globally from its initial domestication areas. It had followed Mediterranean and Danubian routes to arrive in Europe and was aligned with the routes of Neolithic culture diffusion in the region (Fernández et al., 2006). Civilizations like Phoenicians, Greeks, Romans and Berbers probably introduced new species of animals and new breeds of livestock in South-west Europe

following the sea route (Pariset et al., 2009). The archaeological data and radio carbon dates on bones indicated, in Western Europe, goats had arrived earlier through Mediterranean route compared with the Danubian route (Zilhão, 2001; Voruz, 1999; Guilaine, 2003). In Asia, dispersion of the three types of lineages from the domestication centre followed two main routes (the Silk Road and the Khyber Pass) (Devendra and Nozawa, 1976). The latter route was one of the known Silk Roads in the world found between Afghanistan and Pakistan and served for the migration of the Nubian goat type, which had descended from the Savannah type, to Indian subcontinent. Similarly, the former route to Asia served for expansion of both Bezoar-type and Savannah-type goat (Devendra and Nozawa, 1976).

Based on the microsatellite evidence, the East Asian cluster corresponded morphologically to the Bezoar type and the Mongolian cluster corresponded to the Savannah type (Nomura et al., 2012). Taiwan goats are direct descendants of Chinese indigenous goats during the seventeenth century by immigrants, and the Savannah type reached back to Mongolia from the Indian subcontinent and China (Nomura et al., 2012). The genetic subdivisions of East Asian goats were consistent with the migration history of goats and also with morphological and geographical classifications (Nomura et al., 2012). Amills et al. (2008) tried to fairly address wide geographical distribution of the populations and reported the existence of genetic variation at continental level despite smaller sample sizes used in many of the study populations. The haplogroups of the wild bezoar did not decline in population size since the Early Holocene suggesting the bezoar populations were not modified so much by humans (Naderi et al., 2008).

Despite the inherent and unavoidable bias of sampling, haplogroup A is the earliest (~10,000 YA) expanded lineage and is known to occur throughout the world including Africa and parts of Asia, haplogroup F is linked to Europe (particularly in Sicily) and haplogroup D limited to Asia (Luikart et al., 2001; Naderi et al., 2007, 2008; Pereira et al., 2005, 2009; Han et al., 2010; Hughes et al., 2012). The global coverage of haplogroup A is 89% in Asia, and 98% in Europe (Pereira et al., 2005). However, though Pereira (*ibid*) reported 100% pre-dominance of haplogroup A in Middle East and Africa, Naderi et al. (2007) detected Haplogroup G (in Egypt, Saudi Arabia Turkey and Iran), haplogroup B in Namibia and South Africa together with haplogroup A. This haplogroup was also detected in Canary Islands and southern and eastern Asian countries: Pakistan, India, Malaysia, China and Mongolia (Amills et al., 2004; Pereira et al., 2005; Luikart et al., 2006; Han et al., 2010; Nomura et al., 2013). The ancient DNA showed that goats from sub-haplogroup B1 were present in alpine areas of Switzerland in 4500 YA (Schlumbaum et al., 2010); and this haplogroup is the result of a second domestication event (Luikart et al., 2001) and represents a relatively recent expansion (Pereira et al., 2005). Haplogroups A and C show conspicuous rapid expansion and haplogroups B and G show slow expansions; population size of haplogroup F has been slowly declined (Nomura et al., 2013).

Recent studies have also indicated the presence of haplogroup A and G in Kenya (Kibegwa et al., 2015) and Ethiopia in which 89% of the haplotypes from the total 231 haplotypes detected belongs to haplogroup A (Getinet, 2016). Akis et al. (2014, 2016) also reported the presence of haplogroups A, B1, C, D and G in Anatolia region. There is an absolute predominance of lineage A in the Atlantic archipelagos and SCA (Amills et al., 2008). Lineages B, C, D, F and G are absent in SCA goats (Amills et al., 2008), and are also very rare or even absent in Europe (haplogroup D) (Luikart et al., 2001; Joshi et al., 2004; Amills et al., 2004; Azor et al., 2005; Pereira et al. 2005; Naderi et al. 2007). The ancient DNA showed existence of Haplogroup B in Swiss Alps in former times (Schlumbaum et al., 2010). In general, the contribution of haplogroup B, D, F and G in domestic goats is very low (7.69%) (Naderi et al., 2008).

Though the origin and evolution of haplogroup C still remains controversial, it is present with very low frequencies in Europe (<5%) (for example, Iberian Peninsula, Slovenia and Switzerland), Asia (1%) and in Mongolia which represent recent secondary expansion (Luikart et al., 2001; Pereira et al., 2005). It is also found in Near Eastern populations except in Pakistan (Luikart et al., 2001; Sultana et al., 2003), and recently in Corsica (Hughes et al., 2012) and Anatolia (Akis et al., 2014). This dispersion may suggest older origin (Pereira et al., 2005); however, the sampling employed was less comprehensive. Fernández et al. (2006) also explained both lineages A and C coexist in Europe, and were represented among the first populations of domestic goats that entered into Western Europe. This coexistence of lineages A and C in southwestern Europe, since as early as the beginning of the Neolithic, may have resulted from either the succession of different waves of goats bearing different haplotypes between the first Impressa (7,700–7,500 B.P.) and Cardial (7,500–7,000 B.P.) time periods, or from one wave bearing all of the diversity as early as the first Impressa steps (Fernández et al., 2006), which is the first arrival of goats to this region. This finding is consistent with the first waves of arrival of Neolithic farmers (7,500YA) through the Mediterranean route.

Unlike the absence of a strong phylogeographic structure in the Spanish peninsula, European, African and Asian populations, the ancestral Canarias goat mitochondrial haplotypes are still highly ubiquitous in some of the breeds providing a recognizable population structure (Amills et al., 2004). On the other hand, from the historical perspective Iberian livestock were extensively transported from South of Spain and Portugal to America, and

similarly from Portugal, Africa and Canary Islands to Cape Verde by Portuguese sailors during the 15th century (Rodero et al., 1992). The similar haplotypes obtained in Cape Verde with Canary Islands (Amills et al., 2008) can be a very good witness despite the limited contribution of the Atlantic archipelagos to the large-scale population process (Rodero et al., 1992).

However, the mtDNA analysis indicated that the initial goats (that is, variant B) arrived in the Canary Islands by the first settlers 3000YA (Amills et al., 2004). Capote et al. (2004) had also reported the first inhabitants of the Canary Islands settled at the archipelago carrying a small number of domestic animals in 2200YA. Despite the time variation seen in these reports, the first settlers of the Islands are believed to be the Berber people of Morocco though there is no clear evidence till now. Especially the *caprine* breeds of Canary Islands are likely to have North African origin, and were isolated for 1700 years until Spanish colonization but had an important influence in the constitution of the American mosaic of breeds and breed types (Capote et al., 2004). It is also reported that the majority of the Canarian domestic animals prior to the colonization are of virtually unknown origin but assumed to most probably be from the African continent, for instance, the three types of Canarian Caprines (Fresno et al., 1992) look like the African relatives. However, mtDNA analysis of Pereira et al. (2009) could not substantiate this assumption of gene flow into the Canary Islands from the Maghreb (North West African countries except Egypt) rather the Y-chromosome analysis. The latter analysis revealed presence of three main haplotypes (Pereira et al., 2009) with the most frequent haplotype Y2 reaching 76.09% frequency in Morocco. Haplotypes Y1A and Y1B occur at 19.57% and 4.35%, respectively, which is consistent with findings of Amills et al. (2004) though it contradicts the mtDNA analysis of Pereira et al. (2009). In support of the mtDNA analysis, the plot of pair wise F_{ST} genetic distances indicates that the Canary goats are closer to Middle East goat than North Africa goat (Pereira et al., 2009) suggesting the Canary goats diverged from the centre of origin via Mediterranean Sea instead of terrestrial routes. This idea can be strengthened by the presence of strong phylogeographic relationships among Canary island populations compared with other regions (Amills et al., 2004).

In general, despite this discordance of inference between the mtDNA and Y-chromosome, male flocks from Asia might have moved via Morocco to Canary Islands. But, still it does not necessary mean the origin of Canarian goat population is only from Africa. The maternal origin has also strong implication about the other origin of Canarian goats to be directly from the center of origin via Mediterranean Sea.

The presence of variant A found in some of the breeds in the Canary Islands (Amills et al., 2004) might be because of the introgression between the native goats (variant B) with other European and African breeds around 500-600YA following the Spanish colonization (Capote et al., 1999). Y-chromosome analysis also supported the presence of bidirectional gene flow between Africa and southern Iberia (Pereira et al., 2009). However, there is no genetic footprint of Iberian goats rather that of Canarias's in South and Central American (SCA). It is argued that the Iberian populations had a poor phylogeographic structure at the time of the American colonization, and the Canarian goats contributed to the foundation of the current genetic pool of SCA goat breeds (two Andean populations of Chile and Argentina have descended from Canarian goats) (Amills et al., 2008). Morphological similarity between Canarian and American goats is the other supporting evidence about the contribution of the Canarian goats to their American counterparts (Capote et al., 2004). In connection with this, there is a high diversity of mtDNA lineages in Moroccan populations with 54 different (all belong to haplogroup A) haplotypes (Pereira et al., 2009) which are similar in number and type of South and Central American goat haplotypes (Amills et al., 2008). Besides, Pereira et al. (2009) did not report the existence of this variant B in Morocco. However, there is no concrete evidence about either the transportation of goats from the Canary Islands to SCA at a considerable scale or rapidly disseminated in SCA with one or few introduction events (Amills et al., 2008).

Still the point which needs to be clear is that if variant B is found in Canary Islands and Morocco, and all haplotypes found in SCA that belong to lineage A are descendants of the Canary Islands, why variant B is not found in SCA? This could possibly be due to the limited coverage of the study populations in SCA and small sample size used and/or might be because of the absence of examining the divergence from paternal perspective that could probably indicate the connection it would have had with Africa. The other possible reasons might be variant B could have been extinct in SCA or it could have been only lineages A which was transported to SCA. On the other hand, the regional analysis of genetic diversity suggests nucleotide and haplotype diversities are particularly reduced into two Andean populations located in Chile and Argentina compared to Cape Verdean goats implying these two populations descended from Canarian goats (Amills et al., 2008).

Despite the limited molecular data report, the archaeological data indicate that domestic goats were first introduced into the African continent through the i) Mediterranean coast ii) Red Sea Hills iii) overland via the Sinai Peninsula and Nile Delta in 7,000YA (Hassan, 2000; Gifford-Gonzalez and Hanotte, 2011) (Figure1). Similarly, the archaeological data suggested that goats and sheep spread rapidly from the Near East into the Central Sahara and Ethiopian highlands between 6,500 BP and 5,000 BP (Clutton-Brock, 2000) and later expanded to south because of, besides the tsetse barrier, the increasing aridity of North Africa (Smith, 1992). Radiocarbon dates of goat and

sheep bones from various archaeological sites along the North African coast (dated 6,000 BP at Grotte Capeletti in Algeria or 6,800 BP at Haua Fteah in Cyrenaica, Libya) are similar to those excavated in the eastern Sahara, suggesting a very rapid dispersal of small ruminants from Southwest Asia into North Africa between 7,000 BP and 6,000 BP (Hassan, 2000). In contrast to this, mtDNA diversity (lineage A) suggested recent time of expansion (<3,000YA) in the African continent via south of Saharan desert (Luikart et al., 2006). The route of introduction into the African region is believed either through the present-day Sahara desert by overland diffusion or along the Mediterranean coast (Hassan, 2000) (Figure 2). The mtDNA and Y-chromosome analyses strengthened the use of both Mediterranean route in the east-to-west movement of domestic goats and the terrestrial transport along the North African continent (Pereira et al., 2009).

However, there is no indication of Median joining network on the movement of domestic goat from Egypt to North Africa towards Morocco, rather this route might be extended from Egypt directly to Ethiopia following the Nile Valley. The absence of Egypt route to North-west Africa seems contradictory with the archeological findings. In general, Figure 2 summarizes the global dispersion routes of *C.hircus* from center of domestication areas.

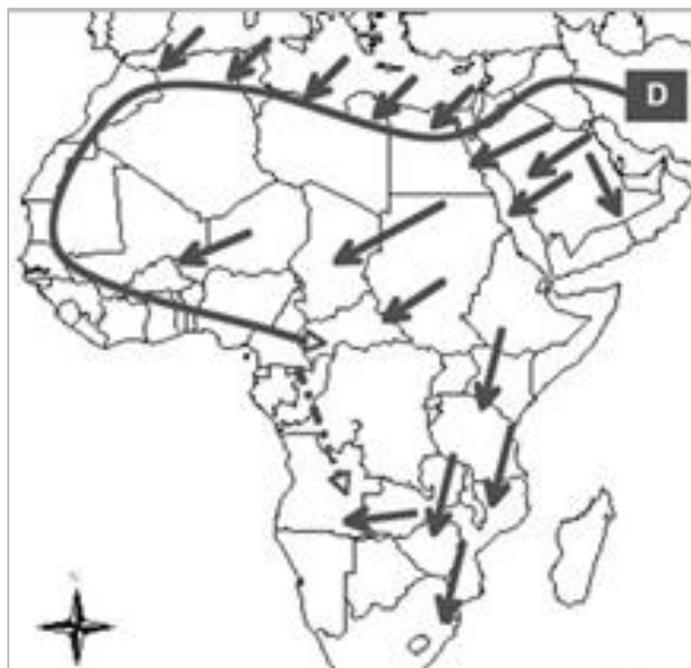


Figure 1 - Origin and divergence of goat into Africa:based on archaeological information (Gifford-Gonzalez and Hanotte, 2011).



Figure 2 - Summary of global dispersion routes of domestic goat: inferred from various reported discussed in the text. Divergence of *Capra hircus* haplogroups: the time and expansion

More fossils being exposed in regions of geological activity (Pagani et al., 2012) and as a consequence, do not always point to the real divergence time. It is because of the fact that the first stratigraphic appearance of taxa in the fossil record may be subject to sporadic sedimentary disruptions due to erosion or lack of sedimentation during regression and/or irregular sedimentary processes (Nomura et al., 2013). In addition, only very few paleontological data are available for species of the genus *Capra* because their preferred mountainous habitats are not favorable for fossil preservation (Simpson, 1945). Instead, scholars have employed various molecular techniques to be able to know time of divergence of organisms since last decade.

Molecular techniques have been used to date divergence of the wild progenitors (Nomura et al., 2013). Sequence divergence (SD), the estimated divergence times between the mtDNA lineages A and D for goats have been estimated to be from 260,483-371,052YA (Sultana et al., 2003). Given the time variation, the estimated times for most recent common ancestors (MRCAs) of each haplogroup (32,300 to 90,950 YA) and the times of nodes with star-like branching pattern (17,210 and 90,950YA) can be indicative for prior expansion of goats before domestication (10,000YA) (Zeder and Hesse, 2000; Nomura et al., 2013). Lineage A is believed to have been expanded initially about 10,000YA, and then the less abundant lineages may have expanded about 6,000 to 6,110YA (lineage C), and 2,130 -2,600YA (Asian lineage B) (Luikart et al., 2001 and 2006). However, Fernández et al. (2006) indicated the third event of domestication (haplogroup C) dated 7,500YA in Southern France. The latter is however inconsistent with the previous premises in both place of origin and time of domestication.

For Indian goat populations, the MRCA calibrated against the fossil record was 103,000-143,000 or 201,000-280,000YA (Joshi et al., 2004) which agrees with the study of Luikart et al. (2001) particularly for lineage A. For the goat populations in Pakistan, the new lineage D revealed high sequence diversity (SD) from lineage A and may be the oldest branch under domestication, while lineages B and C showed lower SD and might have been domesticated during an advanced stage of the domestication process (Sultana et al., 2003). Apart from this, the four lineages (A, B, C, and D) of *Cyt b* indicated that the estimated MRCA of the domestic goat lineages was 427,006 to 597,806YA (Sultana et al., 2003); however, lineage D diverged from lineage A more recently (265,038-371,052YA). This finding is strengthened by the *d*-loop average SD value estimation (4.59%) of the four lineages (A, B, C and D) and 2.8% of lineages A and D, which is the most recent divergence (Sultana et al., 2003). However, this seems too early compared to the mtDNA HVI analysis of Joshi et al. (2004) that showed the three lineages (A, B and C) had diverged over 200,000YA. The mt-lineages exhibiting lower (higher) SD could have been captured and adopted at later (earlier) periods of domestication (Sultana et al., 2003). The ancient divergence time and the different geographical localizations of the lineages suggest the likelihood of either multiple domestication events or introgression of additional lineages after the original domestication (Joshi et al., 2004).

GOAT POPULATION DIFFERENTIATION AND GENE FLOW

Despite the huge global goat population size, the genetic diversity of goats as revealed by maternal mitochondrial and nuclear (microsatellite) DNA marker studies contemporary domestic goats (*C. hircus*) show far weaker intercontinental population structuring than other livestock species (Luikart et al., 2001). The highest proportion (90%) of the current domestic goat mtDNA haplotypes belongs to haplogroup A which could not have been changed dramatically in the expanding goat population since domestication (Naderi et al., 2008). This suggests that haplogroup A goats, may have been dispersed more often, more successfully and more extensively than other livestock (Luikart et al., 2001; Fernández et al., 2006; Nomura et al., 2012). The genetic distance between the Portuguese goat breeds is not positively correlated with the geographical distribution of these breeds (Pereira et al., 2005). This therefore is a very good example for the above argument from a micro-geography perspective. Geographically most distant breeds (Algarvia and Bravia) show the lowest genetic distance ($F_{ST}=0.020$), while the most divergent breeds are Serpentina and Charnequeira ($F_{ST}=0.083$) with a closer geographical distribution. In addition, the genetic variation estimated by MNA and AR (allelic richness) within-country populations of Asian goats was lower than that of European breeds (Nomura et al., 2012). The average F_{ST} (0.13, 0.07) estimates of Asia (Nomura et al., 2012) and European goat breeds (Cañón et al., 2006) strengthened this notion. This lack of relationship between genetic distances and microgeography can be interpreted to mean and to have resulted from complex and diverse female stocks in the origins of Portuguese breeds and/or extensive successive introduction of extraneous female individuals (Pereira et al., 2005).

From the macrogeography perspective, like horse (*Equus caballus*) (Kim et al., 1999), there is low mtDNA population structure in domestic goats compared to cattle (Luikart et al., 2001; MacHugh and Bradley, 2001). Only about 10% of the total mtDNA variation in domestic goats (*C. hircus*) was due to differences among continents (Luikart et al., 2006). It is far lower than estimates of 54–80% intercontinental variation in cattle for the same mtDNA region (HVI). Investigation of negative values, the converse is also true for the positive values, in all bezoars

made in Tajima's D (Tajima, 1989) estimates indicate the presence of population expansion events of bezoars that are closer to domestic goat since recently (Nomura et al., 2013). These all finding imply that geographical location has little relevance to the mtDNA type that a particular animal possesses or the absence of clear tie between the genetic make-up of goats and geography rather at within-population level (MacHugh and Bradley, 2001; Amills et al., 2008). This might also be due to the extensive intercontinental dispersion and high gene flow of goats compared with cattle (Luikart et al., 2006). A relative lack of breed standardization, herdbook breeding, parentage control and rigorous management might have facilitated gene flow between geographically nearby breeds (Cañón et al., 2006).

Moreover, the founder effect has also contributed to the decreased genetic diversity. For instance, upon the conquest and colonization of the New World by the Spanish and Portuguese, goats and other livestock species were massively transported through the Atlantic Ocean for food in exploratory and military expeditions (Rodero et al., 1992). In Brazil, goats were first introduced by Portuguese settlers during the beginning of 16th century (Machado et al., 2000). This depicts the current gene pool of South and Central America goats was founded in the last five centuries (Amills et al., 2008). Similarly, Mongolian goat populations have the lowest genetic distance in contrary to the geographical distances (Takahashi et al., 2008; Nomura et al., 2012). However, Pariset et al. (2009) revealed significant and positively correlated genetic and geographic distances.

On the other side, the within population variation estimated values are the other indications of the weak structuring of goat breeds that support the utilization of domestic goats as a portable food resource accompanying human migratory movements (Amills et al., 2008). Hence, around 69% of the genetic variation corresponds to the within-population component for South and Central American goats and almost similar to Iberian and European breeds, but haplotype diversities were somewhat lower (Amills et al., 2008). Apparently, almost similar estimates (78.7% and 77%) of within breed genetic variations were reported in European, African and Asian goat mitochondrial sequences (Luikart et al., 2001; and Naderi et al., 2007). Still this estimation is higher (83%) for Indian goats (Joshi et al., 2004). From the AMOVA analysis 96.65% of variation occurs within breeds, the remaining 3.35% from among breed variation, for Portuguese goat populations (Pereira et al., 2005). However, for the latter report, comparatively high within breed diversity found in all breeds and the sharing of some haplotypes with other foreign breeds is consistent with the repeated introduction of exotic animals into the Portuguese gene pool in last centuries (Pereira et al., 2005). All the above estimates are very high compared with the within breed (45%) and amongst-group components of the total variation of cattle (Luikart et al., 2001).

Despite the above reports which revealed the weak phylogeographic structure in goat compared to other domestic animals, there is significant mtDNA variation among Indian goat breeds (Joshi et al., 2004). However, this study was limited only to mtDNA and did not include autosomal and/or Y-chromosomal markers, and hence was unable to show the overall gene flow from paternal perspective.

CONCLUSION

With respect to the global coverage of the study of origin of goat, Africa has been poorly addressed compared to other parts of the world. Maternal origins of domestic goats have been checked in African countries that include Algeria, Egypt, Libya, Morocco, Nigeria, Senegal, Tunisia, Mozambique, Namibia, South Africa, Zimbabwe, Kenya and Ethiopia (Luikart et al., 2001; Naderi et al., 2007; Awotunde et al., 2015; Kibegwa et al., 2015; Getinet, 2016). With the exception of Ethiopia, the number of animals included the studies ranges from one to 60 in those countries listed. Recently, large number of animals (N=309) from 13 goat populations were employed to check maternal origin and populations dynamics of Ethiopian indigenous goat populations by the first author of this paper (Getinet, 2016). This calls for more detailed investigation in Africa with the view to elaborate genetic lineages and patterns of dispersions. Population size, sample size and sampling in general highly determine the strength of evidence generated about source of origin of domestication and divergence of species. The report by Nomura et al. (2013) can be a very good indication of how sampling matters in this regard. Sampling of haplogroups focused on haplogroups A and B1 while apparently overlooking others. As a consequence, contribution of haplogroups other than haplogroup A might have been underestimated (MacHugh and Bradley, 2001). Haplogroup A takes the lion share of the present global goat genetic divergence studies. Similarly, some works conducted earlier, like Luikart et al. (2001, 2006), had limitation of small sample size and the wild samples were from zoo where hybridization is likely and attribution can be dubious. With respect to sample size, Luikart et al. (2006) confirmed that samples from additional wild populations of *C. falconeri*, the second closest specie next to *C. aegagrus* to domestic goat, are needed to clarify the possibility that *C. falconeri* gave rise to Cashmere breeds or to other domestic goats from eastern Asia. Despite the wide area coverage, Amills et al. (2008) had also used small sample size.

On the other hand, inferences about the location of origin from a single type of molecular data (diversity levels) can be made with caution because they can either be unsatisfactory or even potentially misleading. It is therefore imperative to triangulate information against other analyses, such as the geographic distribution of lineages and historical or temporal distributions (for example, using ancient DNA) (Luikart et al., 2006). There are good starts, but they are few in number, on the inclusion of ancient DNA for the study of maternal origins of domestic goats (Luikart et al., 2006; Han et al., 2010; Schlumbaum et al., 2010; Hughes et al., 2012; Mazdarani et al., 2014; Akis et al., 2016). In addition, despite the highly informative nature of mtDNA data for the study of origin and divergence of species, it is essential to complement it with inferences made from Y-chromosome since the latter is free of recombination (MacHugh and Bradley, 2001). The effort made in combining mtDNA with Y-chromosome in the study of origin and divergence of goat populations is very much limited.

Luikart et al. (2006) had also suggested that ancient DNA sequencing in combination with extensive sampling of contemporary local breeds provides exciting potential as a method of inferring the origins and diffusion of domestic taxa, especially to combine archaeozoological and ancient DNA studies to assess the pattern of diffusion of DNA lineages through time and space. Because of the variation in fruitfulness of vitality of the two DNA types it is highly recommended to combine the nuclear DNA with mtDNA for the study of population structure.

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Competing Interest

The authors declared that there is no competing interest.

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