Tracing the History of Goat Pastoralism: New Clues from Mitochondrial and Y Chromosome DNA in North Africa

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Valuable insights into the history of human populations have been obtained by studying the genetic composition of their domesticated species. Here we address some of the long-standing questions about the origin and subsequent movements of goat pastoralism in Northern Africa. We present the first study combining results from mitochondrial DNA (mtDNA) and Y chromosome loci for the genetic characterization of a domestic goat population. Our analyses indicate a remarkably high diversity of maternal and paternal lineages in a sample of indigenous goats from the northwestern fringe of the African continent. Median-joining networks and a multidimensional scaling of ours and almost 2000 published mtDNA sequences revealed a considerable genetic affinity between goat populations from the Maghreb (Northwest Africa) and the Near East. It has been previously shown that goats have a weak phylogeographic structure compatible with high levels of gene flow, as demonstrated by the worldwide dispersal of the predominant mtDNA haplogroup A. In contrast, our results revealed a strong correlation between genetic and geographical distances in 20 populations from different regions of the world. The distribution of Y chromosome haplotypes in Maghrebi goats indicates a common origin for goat patrilines in both Mediterranean coastal regions. Taken together, these results suggest that the colonization and subsequent dispersal of domestic goats in Northern Africa was influenced by the maritime diffusion throughout the Mediterranean Sea and its coastal regions of pastoralist societies whose economy included goat herding. Finally, we also detected traces of gene flow between goat populations from the Maghreb and the Iberian Peninsula corroborating evidence of past cultural and commercial contacts across the Strait of Gibraltar.

Introduction

The domestic goat (*Capra hircus*) is generally considered to have been first domesticated from the wild bezoar goat (*Capra aegagrus*) somewhere in the Fertile Crescent of the Near East some 10,000–11,000 years ago (Zeuner 1963; Mason 1984; Davis 1993; Zeder and Hesse 2000). The rapid spread of domestic goats worldwide was probably the result of different activities, including commercial trade, thieving, warfare, or the migration of people with their livestock (Clutton-Brock 2000).

Archaeological data indicate that domesticated goats were first introduced into the African continent from Southwest Asia (Mason 1984). It is only after 7,000 before present (BP) that clearly identifiable caprine remains begin to show up in the African archaeological record at the eastern Sahara and Red Sea Hills (e.g., at the Sodmein Cave near Quseir, Egypt) (Newman 1995; Hassan 2000). 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). The routes taken could have been either through the present-day Sahara desert by overland diffusion or along the Mediterranean coast (fig. 1). By this time, a new type of culture, known as the Neolithic of Capsian Tradition, characterized by its possession of domesticated animals and the shift from hunting and gathering to self-supporting food production, flourished in the Maghreb (Newman 1995). Archaeological evidence also suggests that trans-Gibraltar human movements were already common since the Terminal Paleolithic period, possibly with an interchange of goods (Straus 2001). Goats and sheep also spread rapidly from the Near East into the central Sahara and the Ethiopian highlands between 6,500 BP and 5,000 BP (Newman 1995; Clutton-Brock 2000). The increasing aridity of North Africa and the southward movement of the tsetse barrier permitted the later migration of herders and their livestock into southern parts of the continent (Smith 1992).

In more recent times, North Africa came under the economic and political influence of different cultures that could have improved the local livestock or even introduced new animals from other regions. Among the most important were the Phoenicians, Ionians, Romans, Arabs (and Berbers) and, more recently, Ottomans and Europeans (Newman 1995).

Despite decades of archaeological research, several questions still remain concerning the origin, timing and trajectory of major human, and livestock migrations throughout the northern African continent. For instance, it is a matter of debate to what extent maritime diffusion across the Mediterranean Sea was important in shaping the gene pool of North African livestock (Zeder 2008). Furthermore, the roles played by different colonists in the development of animal husbandry in Northern Africa remain to be clarified (Newman 1995).

To address these issues, we have analyzed the maternal and paternal lineages in 58 indigenous domestic goats

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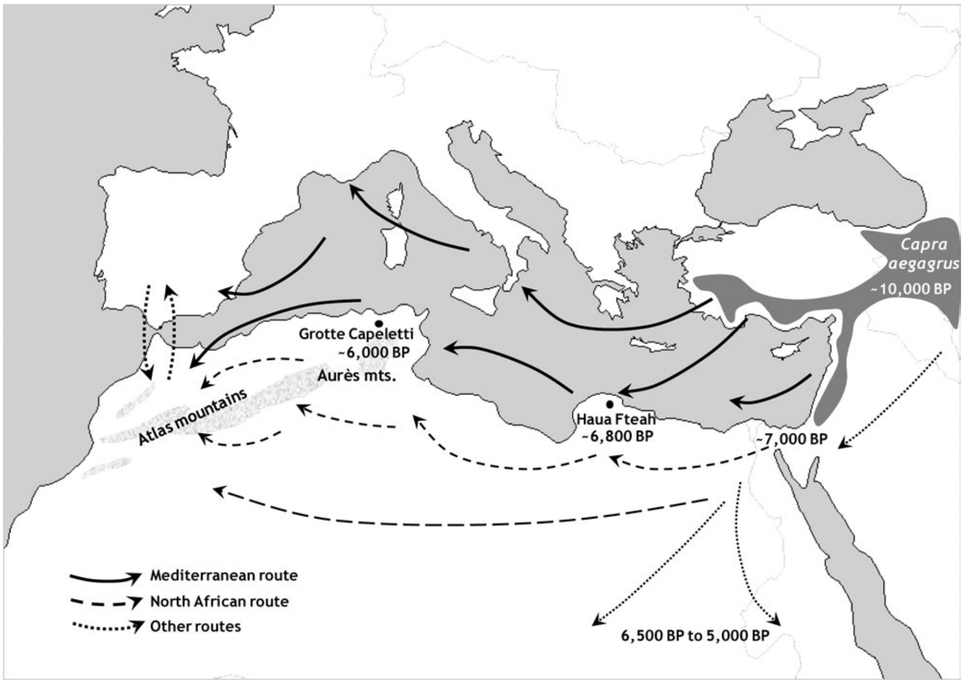

FIG. 1.—The spread of goat pastoralism in Northern Africa. Arrows mark the two hypothesized routes for the dispersal of domestic goats from their domestication areas (dark-gray zone) into the North African continent. The locations of some archaeological sites where ovicaprine remains were identified are also indicated. Adapted from Newman (1995), Zeder (2008), and Fernandez et al. (2006).

sampled along the northwestern fringe of the African continent. A set of mitochondrial DNA (mtDNA) and Y-chromosomal data was assembled and analyzed together with published information from goat populations worldwide. Our analyses indicate extensive genetic diversity in both maternal and paternal lineages of Maghrebi goats with substantial genetic affinities with Near-Eastern populations. Moreover, a phylogeographic interpretation of our data reveals several traces of African–Iberian contacts.

Materials and Methods

Sample Collection and DNA Extraction

A total of 58 blood samples were collected on FTA cards (Whatman, Clifton, NJ) from local populations of the black Moroccan goat type (*C. hircus*) in valleys south of the Atlas Mountains (Souss valley). Only one sample per breeder was collected to ensure that individuals were not closely related. A set of 44 male goat samples from five Portuguese breeds (Bravia, Serrana, Charnequeira, Serpentina, and Algarvia) were used for Y chromosome genotyping (Pereira et al. 2008). The mtDNA analysis of these 44 samples has been previously described (Pereira et al. 2005). DNA was extracted according to a standard phenol–chloroform extraction protocol (Sambrook et al. 1989).

mtDNA Control-Region Sequencing

The first hypervariable segment of the mtDNA control region, covering nucleotide positions from 15707 to 16187 according to the goat mtDNA reference sequence (Parma et al. 2003), was amplified using the primers CPRF 5′-CGCTCGCCTACACACAAATA-3′ and CPRR 5′-GAAGAGTGGGCGATTTTAGG-3′ (Pereira et al. 2005). Polymerase chain reactions (PCRs) were performed by combining 2 μl of extracted DNA, 1.25 μl of each primer (2 μM), and 6.25 μl of 2× PCR Master Mix (Fermentas International Inc, Ontario, Canada) carried out in a 12.5-μl final volume. PCRs were performed as follows: initial denaturing step of 95 °C for 2 min; 35 cycles at 95 °C for 30 s, 62 °C for 30 s, 72 °C for 1 min; and a final extension step of 72 °C for 10 min. The sequencing reaction was performed by combining 2.5 μl of amplified DNA, 0.5 μl of primer CPRF (2.5 μM), and 2 μl of Big Dye Sequencing Kit (Applied Biosystems, Foster City, CA). The sequencing amplification protocol consisted of one cycle of 2 min at 96 °C, followed by 35 cycles of 15 s at 96 °C, 9 s at 50 °C, and 2 min at 60 °C, with a final extension step of 10 min at 60 °C. Sequencing reaction products were purified using Sephadex G-50 Fine (GE Healthcare, UK) and were sequenced on an ABI 3130XL Automated Sequencer (Applied Biosystems).

Typing of Goat Y Chromosome Single-Nucleotide Polymorphisms

Four biallelic Y chromosome polymorphisms in the *SRY* gene (Lenstra 2005) were genotyped by single-base–sequencing reaction (PCR and extension primers are given in supplementary table S1, Supplementary Material online) as described in Pereira et al. (2008). Differentiation of the single-nucleotide polymorphisms (SNPs) alleles was performed by capillary electrophoresis and multicolor fluorescence detection on an ABI Prism 310 Genetic Analyzer (Applied Biosystems).

Data Analysis

Sequences were aligned with the reference goat control-region sequence (Parma et al. 2003) using the ClustalW software implemented by the BioEdit program (http://www.mbio.ncsu.edu/BioEdit/bioedit.html). All sequences have been deposited in GenBank with the accession numbers GQ168962–GQ169019. These sequences were aligned to 1912 goat mtDNA sequences (fragment 15707–16187) available in GenBank (supplementary table S2, Supplementary Material online). Median-joining networks were calculated using Network 4.2.0.1 (Bandelt et al. 1999) with positions weighted in inverse proportion to the number of mutations observed for each position in a first run. Diversity measures, F_{ST} genetic distances, mismatch distributions (Slatkin and Hudson 1991), and tests of selective neutrality (Tajima 1989; Fu 1997) were all obtained using Arlequin 2.0 software (Schneider et al. 2000). The F_{ST} genetic distance matrix was summarized in two dimensions using multidimensional scaling (MDS) analysis as implemented by the STATISTICA program (StatSoft, Inc., Tulsa, OK).

Results

Mitochondrial Lineages of Moroccan Domestic Goats

Analysis of the 58 goat control-region sequences, from nucleotide positions 15707 to 16187, resulted in 55 sequences of 481 bp, 2 of 558 bp, and 1 of 635 bp. The sequence alignment shows that this length variation results from the duplication of a 77-bp motif in the control region near the proline tRNA gene. According to previous studies, the most frequent state corresponds to the 481-bp variant, which contains two copies of the 77-bp motif arranged in tandem. The occurrence of a tandem array with three repeated units (the 558-bp variant) has been observed so far only in five animals worldwide (Luikart et al. 2001; Sultana et al. 2003; Pereira et al. 2005). The proportion of sequences with three and four repeat units is significantly higher (P value <0.05) in Morocco than in a larger sample (Luikart et al. 2001) of individuals from different world regions (5.2% and 0.49% frequency, respectively). A control-region sequence with four copies of the repeated motif (the 635-bp variant) was identified for the first time. The three sequences with more than two of the 77-bp repeat units were not included in the following analyses in order to avoid incorrect alignments between sequences with different lengths.

All haplotypes belong to haplogroup A, which is predominant in most goat populations worldwide (Takada et al. 1997; Luikart et al. 2001; Mannen et al. 2001; Sultana et al. 2003; Amills et al. 2004; Azor et al. 2005; Chen et al. 2005; Pereira et al. 2005; Liu et al. 2006; Naderi et al. 2007). A high diversity of female mtDNA lineages was observed in the Moroccan population with 54 different haplotypes observed in 55 individuals defined by 81 polymorphic sites. The level of genetic diversity observed in the Maghrebi goat population is similar to the one observed in the Near-Eastern population (table 1).

A bell-shaped mismatch distribution with a mean value of 9.566 was observed in the Moroccan sample (supplementary fig. S1, Supplementary Material online). Statistically significant negative values were obtained in two tests of selective neutrality: Fu's F_S statistic (-24.664; P value < 0.001) and Tajima's D (-1.603; P value $= 0.0288$).

Phylogeography of Goat mtDNA Lineages in the Mediterranean Basin

The phylogenetic relationship between Moroccan goat haplotypes was inferred using the median-joining network analysis (supplementary fig. S2, Supplementary Material online). The network topology revealed a substantial divergence among haplotypes, with a large number of independent branches giving rise to multiple subbranches separated by several mutations.

Figure 2 shows the median-joining network constructed with all available haplogroup A sequences from North African goats: 60 from Morocco (Luikart et al. 2001 and this study); 6 from Algeria (Luikart et al. 2001; Amills et al. 2004); 6 from Tunisia; and 11 from Egypt (Luikart et al. 2001). These sequences cover nucleotide positions 15725–16187 to allow maximum comparability between published data. No identical lineages were observed, and most Tunisian haplotypes are located on peripheral branches of the network. The pattern of diversity indicates that most Moroccan haplotypes are not derived from Egyptian lineages (fig. 2).

To provide further resolution on the Mediterranean domestic goat phylogeography, a median-joining network was constructed with 598 mtDNA haplogroup A sequences from goat populations across the Mediterranean basin (fig. 3 and supplementary table S3, Supplementary Material online). The majority of sequences from the Maghreb, the Near East, and Egypt were found scattered along a group of related branches (upper left part of the network of fig. 3). A close relationship between the Maghrebi and Iberian samples is clear in several branches of the network, with three haplotypes shared between animals from both regions. As expected, haplotypes from Egypt are often close to sequences from the Near East, but Maghrebi lineages are not derived from Egyptian haplotypes. Although the network has no clearly defined root sequences, two interior high-frequent haplotypes are distinguished by having several mutational connections. The haplotype identified as "a" in figure 3 was found to be shared between Sicily and Iberia (three individuals from Sicily, seven from Portugal, and one from Spain), whereas haplotype "b" was only found in seven Portuguese goats. A third haplotype "c" identified in a Turkish goat is the root of 12 branches, including one leading to a North African haplotype (fig. 3). The high frequency of haplotypes "a" and "b" suggests that they have probably been present in the population for a long time.

A median-joining network was also constructed with all available sequences from Morocco and the nearby

Table 1
Sample Size (*n*), Diversity Measures, Fu's F_S, and Tajima's *D* Values for 20 Domestic Goat Populations Obtained with mtDNA Haplogroup A Sequences (Positions 15707–16187)

Population	*n*	No. of Haplotypes	Haplotype Diversity	Mean No. of Pairwise Differences	Nucleotide Diversity	Fu's F_S	Tajima's *D* (*P* Value)	Origin of Samples and References
Northwest Africa	72	71	0.9996 ± 0.0024	9.776 ± 4.529	0.022 ± 0.011	−24.592	−1.526 (0.044)	Morocco (Luikart et al. 2001; this study), Algeria (Luikart et al. 2001), and Tunisia (Luikart et al. 2001)
Egypt	11	11	1.000	8.145 ± 4.096	0.018 ± 0.010	−4.921	−0.683 (0.265)	Luikart et al. (2001)
Turkey	18	18	1.000	8.823 ± 4.269	0.020 ± 0.011	−11.262	−1.204 (0.110)	Luikart et al. (2001)
Near East	22	21	0.9957 ± 0.0153	7.870 ± 3.807	0.018 ± 0.010	−13.753	−1.772 (0.027)	Saudi Arabia, Jordan, Iraq, and Syria (Luikart et al. 2001)
Portugal	371	173	0.9935 ± 0.0010	9.725 ± 4.467	0.022 ± 0.011	−24.045	−1.157 (0.107)	Luikart et al. (2001) and Pereira et al. (2005)
Spain	80	73	0.9975 ± 0.0025	9.872 ± 4.565	0.022 ± 0.011	−24.552	−1.461 (0.047)	Luikart et al. (2001), Amills et al. (2004), and Azor et al. (2005)
Canary Islands	21	12	0.9000 ± 0.0459	7.200 ± 3.515	0.016 ± 0.009	−1.010	−0.413 (0.379)	Luikart et al. (2001) and Amills et al. (2004)
Sicily	63	27	0.9611 ± 0.0084	6.862 ± 3.273	0.016 ± 0.008	−6.908	−0.886 (0.192)	Sardina et al. (2006)
North Europe	17	17	1.000	8.838 ± 4.289	0.020 ± 0.011	−10.176	−0.837 (0.227)	Iceland, Norway, Sweden, Ireland, United Kingdom, Denmark, Germany, and Poland (Luikart et al. 2001)
France	13	13	1.000	9.679 ± 4.746	0.022 ± 0.012	−5.877	−0.270 (0.432)	Luikart et al. (2001)
Switzerland	49	49	1.000	9.178 ± 4.294	0.021 ± 0.011	−24.725	−1.190 (0.107)	Luikart et al. (2001)
Greece	12	12	1.000	9.212 ± 4.559	0.021 ± 0.012	−5.265	−0.590 (0.288)	Luikart et al. (2001)
East Europe	19	19	1.000	9.871 ± 4.727	0.022 ± 0.012	−11.443	−1.474 (0.054)	Slovenia, Romania, and Ukraine (Luikart et al. 2001)
Mozambique	56	24	0.9325 ± 0.0169	3.349 ± 1.742	0.008 ± 0.004	−13.513	−1.814 (0.005)	Pereira F, Queirós S, Maciel S, Amorim A, unpublished data
South Africa	10	10	1.000	2.267 ± 1.357	0.005 ± 0.003	−9.839	−1.590 (0.048)	Luikart et al. (2001)
China	484	212	0.9900 ± 0.0012	8.970 ± 4.139	0.020 ± 0.010	−23.965	−1.265 (0.078)	Luikart et al. (2001), Chen et al. (2005), Zhang et al. (2004), and Liu et al. (2005) (GenBank direct submission)
Mongolia	13	13	1.000	10.256 ± 5.010	0.023 ± 0.013	−5.622	−0.720 (0.238)	Luikart et al. (2001)
Pakistan	51	46	0.9961 ± 0.0048	8.041 ± 3.796	0.018 ± 0.010	−24.879	−1.607 (0.033)	Takada et al. (1997), Luikart et al. (2001), and Sultana et al. (2003)
India	357	178	0.9924 ± 0.0010	8.042 ± 3.744	0.018 ± 0.009	−24.215	−1.535 (0.027)	Luikart et al. (2001) and Joshi et al. (2004)
Southeast Asia	8	7	0.9643 ± 0.0772	7.679 ± 4.007	0.017 ± 0.010	−0.973	0.249 (0.638)	Malaysia, Vietnam, and Laos (Luikart et al. 2001; Mannen et al. 2001)

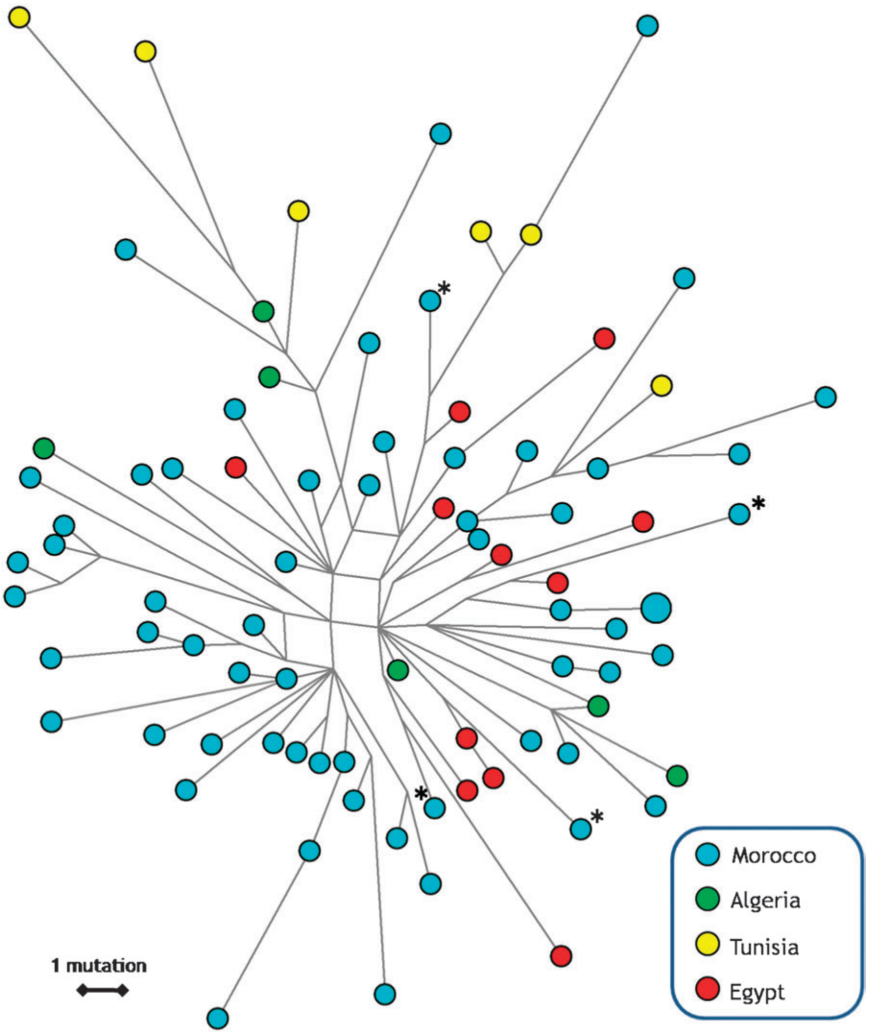

FIG. 2.—Median-joining network depicting the relationships between mtDNA haplogroup A lineages in goat populations from North Africa. Shared ancestry between Moroccan and other northern African lineages is denoted by an asterisk (*). A control region segment from positions 15725 to 16187 was used. The area of the circles is proportional to the frequency of individuals in the sample.

Canary Islands (Luikart et al. 2001; Amills et al. 2004; this study). No signs of recent gene flow between these regions were observed, with most sequences from the Canary Islands clustered into a single branch of the network (supplementary fig. S3, Supplementary Material online).

Y Chromosome Lineages of Moroccan Domestic Goats

Distribution of Y chromosome haplotypes Y1A, Y1B, and Y2 in goats from Europe and the Near East showed a strong geographical partitioning (Lenstra 2005; supplementary table S4, Supplementary Material online). A fourth haplotype Y1C was found in Switzerland (supplementary table S4, Supplementary Material online). The analysis of 46 Moroccan male goats revealed the presence of the three main lineages, with the most frequent haplotype Y2 reaching 76.09% frequency. Haplotypes Y1A and Y1B occur at 19.57% and 4.35% frequency, respectively. No Y1C individuals were identified in our study. A sample of 44 male goats from five Portuguese goat breeds was also screened for the Y-chromosomal SNPs. Only haplotypes Y2 (75%) and Y1B (25%) were observed in the Portuguese breeds. The haplotype frequencies in Morocco, Portugal, and five Spanish breeds (Lenstra 2005; Joost 2006) are shown graphically in figure 4.

Genetic Distances between Domestic Goat Populations

A more complete picture of the relationship between domestic goat populations was obtained from an MDS plot of pairwise F_{ST} genetic distances. All available mtDNA sequences from haplogroup A were divided into 20 groups formed by sequences from individuals sharing a common geographical location in order to obtain adequate sample sizes for comparative analysis (table 1). The MDS plot obtained from the matrix of interpopulation F_{ST} values reveals a strong correspondence between genetic and geographic distances (fig. 5). The population from the Maghreb that includes all sequences from Morocco is closer to the Near-Eastern population (F_{ST} = 0.014; P value = 0.046 ± 0.008) than to any other population.

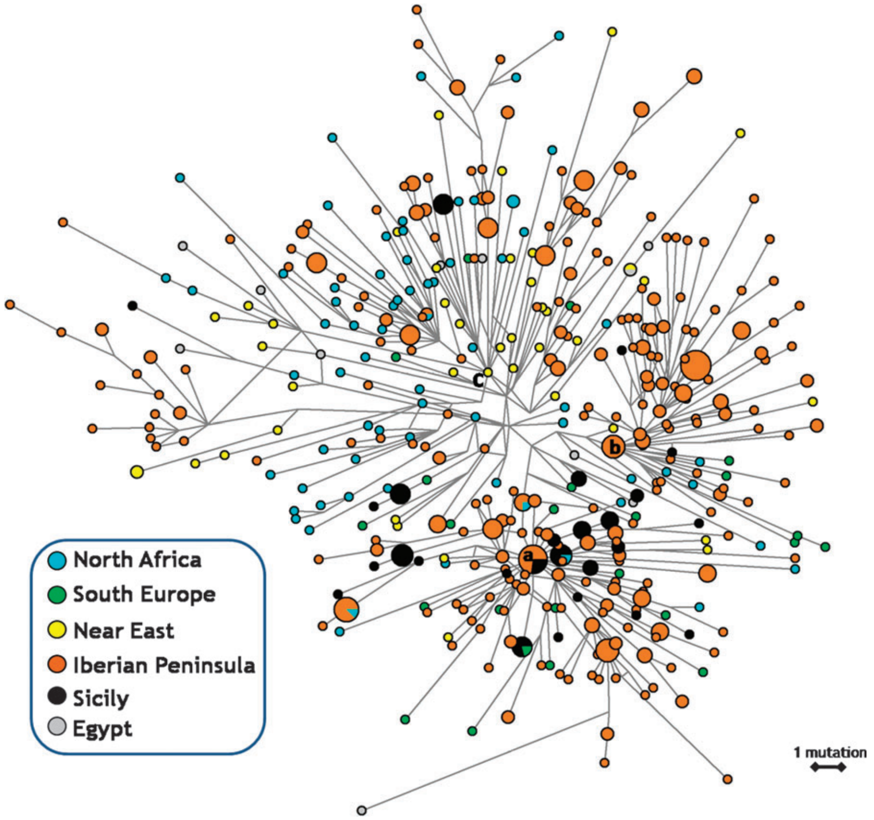

FIG. 3.—Median-joining network depicting the relationships between mitochondrial haplotypes in goat populations from the Mediterranean basin. The mtDNA control-region segment from positions 15746 to 16187 was used. The area of the circles is proportional to the frequency of specimens in the sample; "a," "b," and "c" denote three internal haplotypes with several mutational connections.

Discussion

Goats are vital to the subsistence and economy of many people in the African continent, especially in ecologically marginal areas such as mountains or arid zones where other domestic animals cannot be easily kept (FAO 2007). Studying the genetic history of indigenous domestic populations can provide crucial clues about past human migrations, including the main pathways used for the commercial transport of livestock in historical times. In order to elucidate the origin and major movements of goat pastoralists in Northern Africa, we performed a genetic survey of an indigenous goat population of the Maghreb using the high resolution offered by uniparentally transmitted genetic markers (mtDNA and Y chromosome).

One important outstanding question concerns the path of arrival of domestic goats into North Africa. Their transport from the place where they were originally domesticated could have occurred along two routes (fig. 1): a North African land one, along which herders and their domesticated livestock expanded through the continental heartland (overland diffusion), or a Mediterranean maritime one, with short- or long-distance colonization occurring along the shores of the Mediterranean Sea (maritime diffusion). Our analysis provides evidence for the use of the Mediterranean route in the east-to-west movement of domestic goats, in addition to the terrestrial transport along the North African continent. The high level of diversity found in the Maghrebi goat population (table 1 and supplementary fig. S2, Supplementary Material online) is not compatible with a simple scenario of unidirectional overland diffusion of goats, in which farmers transporting these livestock westwards only took small samples of the more diverse eastern stocks. This would create a gradual decrease in the number and diversity of lineages as the distance increases from areas of domestication. For instance, cattle showed a broad decline in diversity from the Near East to West Europe (Troy et al. 2001). However, the same was not observed for goats and sheep in Southern Europe (Pereira et al. 2005, 2006; Chessa et al. 2009). A recurrent influx of new genetic diversity via the Mediterranean Sea may explain the observed pattern in Southern Europe and Northern Africa (fig. 1). Ancient DNA evidence from goat bones collected in Southern Europe has already confirmed the existence of extensive gene flow via the Mediterranean route dating back to the early neolithization of Europe (Fernandez et al. 2006). A more extensive sampling would be required in order to reconstruct more completely the pattern of gene flow in North Africa.

Traces of demographic expansions were detected in the Moroccan goat population, with a bell-shaped mismatch distribution (supplementary fig. S1, Supplementary Material online) and a large negative Fu's F_S value (-24.664; P value < 0.001) for the mtDNA control region. These results are in agreement with previous data from goat populations worldwide (Luikart et al. 2001; Naderi et al. 2007). It should be noticed that factors other than population

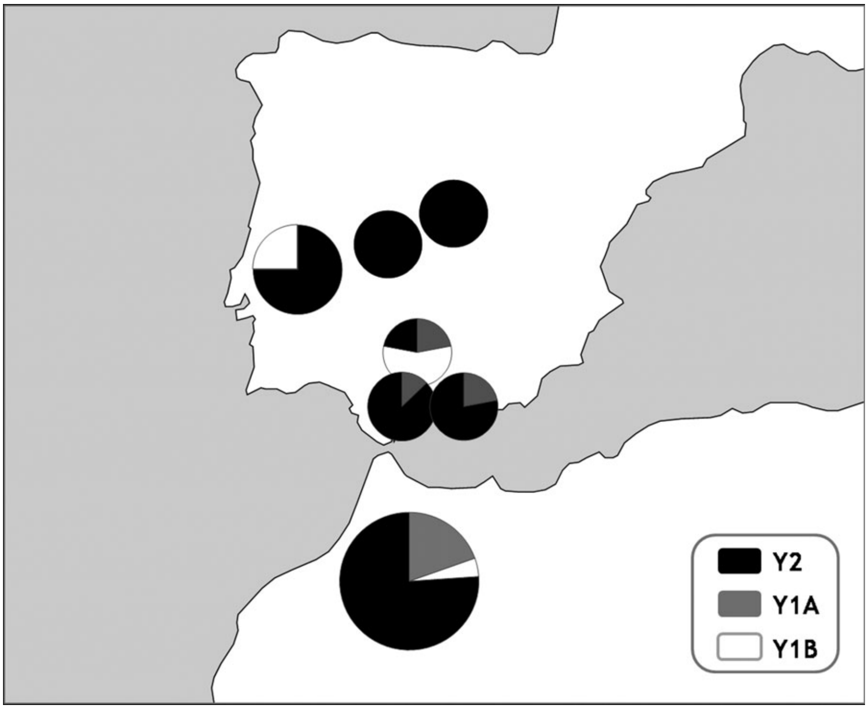

Fig. 4.—Goat patrilines in the Maghreb and the Iberian Peninsula. The pie charts depict the frequency of Y-chromosomal haplotypes Y2, Y1A, and Y1B in different populations. The frequencies for the five Spanish breeds are from Joost (2006).

growth (such as selection, population bottlenecks, or heterogeneity of mutation rates among sites) are also consistent with these results and with the significant negative Tajima's *D* value (−1.603; *P* value = 0.0288).

Evidence against the scenario of unidirectional overland diffusion from the Near East to Northwest Africa is also provided by the phylogeographical analysis of goat lineages in the Mediterranean basin. It is clear from the networks of figures 2 and 3 that the Moroccan lineages are not derived from the Egyptian ones, as should be expected assuming a terrestrial route for the dispersal of these animals throughout Northern Africa (fig. 1). Shared ancestry between Moroccan and other northern African lineages was only detected in a few lineages (fig. 2). In fact, several branches of the haplogroup A network support a close phylogenetic relationship of Maghrebi and Near-Eastern lineages (fig. 3). No evidence for extensive gene flow between populations from the Canary Islands and the

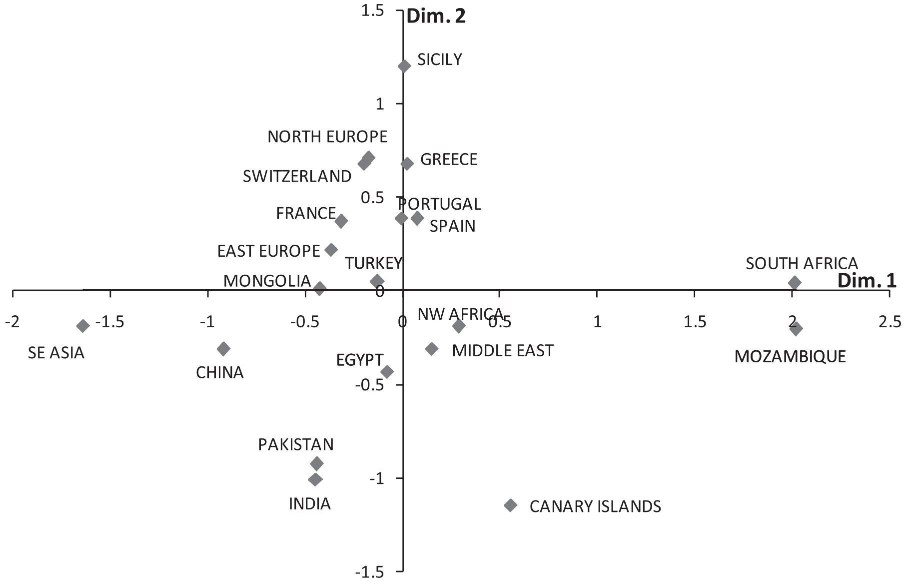

Fig. 5.—MDS plot of pairwise F_{ST} genetic distances between 20 domestic goat populations worldwide, calculated using mtDNA control-region sequences.

Maghreb was observed (supplementary fig. S3, Supplementary Material online). Genetic similarity between populations from Northwest Africa and the Middle East is also evident in the MDS plot of pairwise F_{ST} genetic distances (fig. 5).

It has been proposed that goats have a weak phylogeographic structure because of their high mobility and versatility in feeding habitats (Luikart et al. 2001). This was mainly based on the wide dispersal of the dominant haplogroup A. However, frequencies of other mtDNA haplogroups (Naderi et al. 2007), microsatellite alleles (Canon et al. 2006), Y chromosomal haplotypes (Lenstra 2005; supplementary table S4, Supplementary Material online), as well as haplogroup A sequences (fig 5) show a considerable correlation with geography. The first dimension of the MDS correlates with the longitude, which is particularly evident when excluding South African populations (supplementary fig. S4, Supplementary Material online). These results suggest that after the expansion of domestic goats, differentiation among regions has been established and maintained.

The distribution of Y chromosome haplotypes in Maghrebi goats also suggests the use of multiple routes for the transportation of this livestock species throughout Northern Africa. First, the three main Y-chromosomal goat lineages (haplotypes Y1A, Y1B, and Y2) were all observed in the Moroccan population, suggesting multiple introgressions or the initial colonization of Northwest Africa by a large stock of domestic goats. Second, the most frequent haplotype observed in Morocco and Iberia was Y2, which was previously reported to have a high frequency in breeds from South-Eastern Europe and Near-Eastern breeds (Lenstra 2005; Joost 2006; supplementary table S4, Supplementary Material online).

The question of whether domestic goats were transported between the Maghreb and the Iberian Peninsula or were independently introduced and improved in both regions is relevant to our understanding of African–Iberian cultural and commercial contacts in the past. We have identified a number of mtDNA haplotypes shared between different West Mediterranean populations, namely from Portugal, Spain, Northwest Africa, and Sicily (supplementary table S5, Supplementary Material online). Moreover, several haplotypes from Iberia and the Maghreb were found to be separated by just a few mutations in the median-joining network analysis (fig. 3). In four cases, the same haplotype was identified in animals from both regions (fig. 3 and supplementary table S5, Supplementary Material online). Similar Y chromosome haplotype frequencies were also observed in Morocco and in three southern Iberian goat breeds (fig. 4). Haplotype Y1A has about the same frequency in breeds near either side of the Strait of Gibraltar, but is, together with haplotype Y1B, most common in Central-Northern European as well as in Italy (Lenstra 2005; Joost 2006; supplementary table S4, Supplementary Material online). This observation is most consistent with bidirectional gene flow between Africa and southern Iberia, causing admixture in both the mtDNA and Y-chromosomal gene pools. Similar observations have been made in cattle mitochondrial DNA (Cymbron et al. 1999; Anderung et al. 2005).

Our findings are consistent with a high level of goat transportation across the Mediterranean basin and the North African continent. The colonization of the Mediterranean shores by people whose economy included goat herding might have been facilitated by the high adaptability of this species to harsh conditions and the ease with which they can be transported (Zeuner 1963; Mason 1984). The observed enrichment of the North African goat gene pool emphasizes the importance of the Mediterranean Sea as a route for the movement of livestock and humans in a continual network of trade and commercial exchange. Finally, the observation of admixture across the Strait of Gibraltar reinforces the importance of past contacts between the Maghreb and the Iberian Peninsula.

Supplementary Material

Supplementary figures S1–S4 and tables S1–S5 are available at *Molecular Biology and Evolution* online (http://www.mbe.oxfordjournals.org/).

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