Genetic Signatures of a Mediterranean Influence in Iberian Peninsula Sheep Husbandry

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Highly adaptable and versatile populations of domestic sheep, the result of millennia of intense husbandry, are found in almost every corner of the world. Here we describe a genetic survey of sheep from the western fringe of its European distribution. We studied the mitochondrial DNA control region sequences from 161 individuals belonging to 7 Portuguese sheep breeds. Our study revealed a high level of genetic diversity, with an average breed haplotype diversity of 0.983, substantially above that observed in central European breeds, as well as the presence of maternal lineages until now only found in the Middle East and Asia. A broad north–south pattern describes the most important trend in the Portuguese sheep population with a southern population clearly distinct from most other breeds. A recurrent influx of new genetic diversity, probably via the Mediterranean Sea, may explain these patterns and appears to corroborate the importance of this maritime route in the history of both mankind and livestock. Zooarchaeological studies of sheep bones from southern Portugal indicate a marked size increase during the Moslem period that may reflect an improvement of this animal—perhaps part of the well known “Arab agricultural revolution” in Andalusia. This could have been a time when the gene pool of Iberian sheep was substantially enriched and may help to explain the history of modern sheep breeds in this peninsula.

Introduction

The beginning of livestock domestication, some 10 000–11 000 years ago in the “Fertile Crescent,” was a crucial event in human history. The earliest zooarchaeological evidence for domestic sheep comes from sites in present-day Iran, Turkey, and Cyprus (Hahn 1986; Uerpmann 1979; Ryder 1984; Clutton-Brock 1999; Vigne et al. 2003). A pioneering genetic study that examined the karyotypes of the various species of extant wild sheep (Nadler et al. 1973; Bunch et al. 1976) clearly showed that our domestic sheep derive from the Asiatic mouflon (Ovis orientalis) of Anatolia, western Iran, and southwest Iran rather than any of the other species of wild Asiatic sheep like the Urial (Ovis vignei) and the Argali (Ovis ammon). Recent genetic techniques, using mitochondrial DNA (mtDNA) sequence variation, have further refined these early findings by supporting a Southwest Asiatic origin for domestic sheep and excluding any contributions from the Urial and the Argali (Hiendleder, Mainz et al. 1998; Hiendleder et al. 2002).

Phylogenetic analysis of domestic sheep mtDNA has revealed the existence of 2 main haplogroups (HGs), termed A and B. They were first identified in populations of New Zealand sheep (Wood and Phua 1996) and subsequently confirmed in Eurasian breeds. HG B is widespread, whereas HG A appears to be almost entirely confined to Asiatic animals (Hiendleder, Lewalski et al. 1998; Hiendleder, Mainz et al. 1998; Hiendleder et al. 2000). Recently, a third HG (C) was identified in Middle Eastern (Pedrosa et al. 2005; Bruford and Townsend 2006) and Asiatic sheep (Guo et al. 2005) that strongly suggests multiple domestication events similar to the pattern identified in other domestic species such as goat (Luikart et al. 2001), cattle (Troy et al. 2001), and pig (Larson et al. 2005).

Archaeological evidence indicates a probable spread of the Neolithic “package” out of the Near East and across Europe. The routes taken could have been either through the continental heartland up the Danube valley or along the Mediterranean coast (Ryder 1984). The first appearance of the remains of domestic sheep in the western part of Mediterranean Europe dates to approximately 5400 BC and are believed to reflect a rapid spread by sea—part of a process of maritime pioneer colonization (Zilhão 2001). To what extent the Mediterranean route was used in the following millennia for the transport of domesticated animals is however unclear. In fact, the influence of different post-Neolithic cultures in southwest Europe is now becoming increasingly evident (see Table 1, Supplementary Material online, and references cited therein). Many of these colonists who came to the Iberian Peninsula like Phoenicians, Greeks, Romans, and Berbers probably introduced new species of animals and new breeds of livestock, and most of them came by sea. Some colonists may have improved local livestock as well as importing stock from overseas.

The oldest established sheep breed in the world, the Merino, was developed in Iberia. Klein (1920, p 3–6) suggested that this breed was introduced into the Iberian Peninsula by, and named after, the Beni Merin Berbers, one of the North African tribes that settled in large numbers in the southern part of Iberia while under Almohad rule (from the mid 12th century). Moslems introduced new techniques—especially those concerning irrigation—that enabled the growth of exotic varieties like sugarcane, rice, cotton, and citrus trees. This is referred to as the “Arab agricultural revolution” (Watson 1974; Glick 1979; El Faı́z 2000). But although the literature speaks much of oranges and lemons, apart from the famous Arab horses, we know little about the rest of the livestock sector.

Patterns of genetic diversity found in modern sheep breeds from Iberia that could shed some light on the history of circum-Mediterranean migrations are largely unknown. Therefore, we attempted to characterize the female side of...
sheep history by studying the mtDNA of 7 Portuguese breeds, belonging to the 3 main Iberian branches: Merino, Churra, and Bordaleiro.

Our results show an extremely high level of genetic diversity and the presence of lineages until now only found in the Near East and Asia. The same pattern was found in domestic goats (Pereira et al. 2005), providing molecular evidence for an intense gene flow between the Near East and Iberia via a Mediterranean—perhaps maritime—route.

The combination of our genetic data with archaeological evidence for the improvement of sheep during the Moslem period in Portugal (Davis 2006) strongly suggest that the Iberian Peninsula has been an important center for development and improvement of this domesticate.

Materials and Methods
Sample Collection and DNA Extraction

We collected bloodstains on FTA cards (Whatman, UK) from 161 unrelated sheep belonging to 7 Portuguese breeds: Churra Badana (n = 26), Churra da Terra Quente (n = 24), Mondegueria (n = 14), and Churra Algarvia (n = 35) from the Churra type; Campaniça (n = 20) and Saloia (n = 32) from the Bordaleiro type; and Merino Preto (n = 10) from the Merino type. All animals sampled belonged to pure indigenous breeds and were registered with their respective breeders association to ensure that they were not closely related. We performed DNA extraction according to the Chelex 100 method.

DNA Amplification and Sequencing

The complete mtDNA control region between positions 15437 and 16616, according to the ovine reference sequence (Hiendleder, Mainz et al. 1998), was amplified in 2 overlapping fragments using 2 pairs of primers (for fragment 1, S1F: 5’-CCCCCATATCAACACCACAAA-3’ and S1R: 5’-CATGGTGAAACAGGCTCTGA-3’, and for fragment 2, S2F: 5’-TGTTGACGCATAGCATATC-3’ and S2R: 5’-CATCTAGGCATTTCGATGCC-3’). Polymerase chain reaction products were sequenced on both forward and reverse directions on an ABI 3100 Automated Sequencer using the Big Dye Sequencing Kit (AB Applied Biosystems, Foster City, CA).

Data Analysis

The sequences obtained were compared by alignment to the ovine reference sequence (AF010406; Hiendleder, Mainz et al. 1998) and have been deposited in GenBank with the accession numbers DQ491576–DQ491736. A large database was constructed using all complete mtDNA control region sequences available in GenBank: L29055 (Zardoya et al. 1995); Z35228–Z35268, Z35293 (Wood and Phua 1996); AF039577–AF039578 (Hiendleder, Mainz et al. 1998); AF010406 and AF010407 (Hiendleder, Lewalski et al. 1998); AY091495–AY091500 (Hiendleder et al. 2002); AY829376–AY829430 (Guo et al. 2005); AY582800–AY582820 (De Ascencio et al. 2004); as well as all available partial sequences—DQ97431–DQ97468 (Pedrosa et al. 2005) and AY879343–AY879463 (Meadows et al. 2005).

Diversity measures, analysis of molecular variance (AMOVA), $F_{ST}$ genetic distances, exact test of population differentiation, mismatch distributions, and the Fu’s $F_{S}$ statistic were all obtained using Arlequin 2.0 (Schneider et al. 2000). The $F_{ST}$ genetic distance matrix was summarized in 2 major trends or dimensions using multidimensional scaling (MDS) analysis as implemented by the STATISTICA program (StatSoft, Inc. [Tulsa, OK] 1999). The value for each breed in each dimension can then be used to interpolate a synthetic surface map, which illustrates geographically the major genetic trends across the Portuguese sheep population. A geographic coordinate for each breed’s place of origin was taken as a central point in the relevant sampling area. Maps were constructed using the Spatial Analyst v2.0 extension of ArcView GIS 3.2. Median-joining networks (Bandelt et al. 1999) were calculated using Network 4.1.1.0 (http://www.fluxus-engineering.com) with positions weighted in inverse proportion to the maximum number of mutations obtained for each position in a first run.

Results

mtDNA Variation in Portuguese Sheep Breeds

The complete mtDNA control region (~1180 bp) sequences from 161 unrelated animals revealed 134 different haplotypes with 195 polymorphic sites. Four copies of a tandem repeated motif in the tRNAPro proximal part of the control region were found in all individuals with the exception of 2 sheep, from the Saloia and Badana breeds, each of which had 3 copies.

Most individuals (93.8%) belong to HG B, 7 to HG A (4.3%; from Saloia, Churra Badana, Churra da Terra Quente, and Churra Algarvia breeds), and 3 to HG C (1.9%; from Churra Badana and Churra Algarvia breeds). Only 2 haplotypes were found to be shared between breeds (Saloia and Churra Algarvia). A high diversity was observed in all breeds with average haplotype diversity of 0.985, and mean number of pairwise differences ranged between 10.621 and 12.359 (Table 2, Supplementary Material online). In order to discern the affinities between different Portuguese breeds, pairwise $F_{ST}$ genetic distances were calculated, and an exact test of population differentiation was performed. They show that the southern breed (Churra Algarvia) presents the largest genetic distances when compared with other breeds (table 1). AMOVA (Excoffier et al. 1992) revealed that most of this variation (98.5%) occurs within breeds, whereas just 1.5% is due to the variation between breeds.

MDS analysis of the matrix of interbreed $F_{ST}$ values was performed, and the geographical variation in each dimension was visualized by interpolating observed values to produce a synthetic surface map of Portugal. A broad north–south trend was observed for the first dimension, with the extreme southern breed (Churra Algarvia) standing out as the most differentiated (fig. 1). The correlation between dimension 1 values and the latitude of the sample populations is positive ($R^2 = 0.48, P = 0.084$). No discernible trend was observed for the second dimension (data not shown).
Ovine mtDNA Lineages Phylogeography

All publicly available mtDNA control region sequences (n = 449) were assembled into a single database. Alignment of these sequences covering nucleotide positions 16093–16616 only, to allow maximum comparability between published data, defined 193 different haplotypes. The phylogenetic relationship between these was reconstructed in a median-joining network (Figure 1, Supplementary Material online). The Portuguese sequences fall into the 3 previously identified HGs (A, B, and C), which are readily apparent in the network.

HG B is the most widespread, reaching a frequency of 75% followed by HG A (19%) and HG C (6%). A median-joining network calculated for HG B haplotypes revealed a complex distribution of lineages, with Portuguese sequences scattered along different branches (most

### Table 1

<table>
<thead>
<tr>
<th>Breed 1</th>
<th>Breed 2</th>
<th>FST</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Churra Badana</td>
<td>Churra Terra Quente</td>
<td>0.005 ± 0.012</td>
<td>0.323</td>
</tr>
<tr>
<td>Churra Badana</td>
<td>Mondegueira</td>
<td>0.029 ± 0.066*</td>
<td>0.002</td>
</tr>
<tr>
<td>Churra Badana</td>
<td>Campaniça</td>
<td>0.019 ± 0.006</td>
<td>0.001</td>
</tr>
<tr>
<td>Churra Badana</td>
<td>Merino Preto</td>
<td>0.019 ± 0.006</td>
<td>0.001</td>
</tr>
<tr>
<td>Churra Badana</td>
<td>Saloia</td>
<td>0.010 (0.004)</td>
<td>0.004</td>
</tr>
<tr>
<td>Churra Badana</td>
<td>Merino Preto</td>
<td>0.019 (0.049)</td>
<td>0.002</td>
</tr>
<tr>
<td>Churra Badana</td>
<td>Saloia</td>
<td>0.010 (0.04)</td>
<td>0.003</td>
</tr>
<tr>
<td>Churra Badana</td>
<td>Merino Preto</td>
<td>0.019 (0.098)</td>
<td>0.003</td>
</tr>
</tbody>
</table>

NGLE.—Significant values of exact tests of population differentiation are shown above the diagonal. * Significant values (P < 0.05).

Fig. 1.—Synthetic map of Portugal illustrating the geographic variation in the first dimension of genetic diversity obtained from MDS analysis of interbreed FST values. Crosses indicate sample locations as follows: Churra Badana (CB), Churra da Terra Quente (CT), Mondegueira (MO), Saloia (SA), Campaniça (CA), Merino Preto (MO), and Churra Algarvia (AL).
European haplotypes identified in the network B of fig. 2). The most frequent haplotype is central to the network and was found worldwide, including several Iberian sheep. Three haplotypes shared by Portuguese and Middle Eastern breeds and one by Portuguese and Asiatic animals were found just one mutational step away from this central haplotype.

The distribution of HG B lineages, calculated for breeds with at least 10 sampled individuals, revealed that all Portuguese breeds present a substantially higher haplotype diversity than the central European ones. Even when compared with a mixed sample composed of individuals from 5 different Turkish breeds, the Portuguese populations presented a higher diversity of maternal lineages (table 2).

The median-joining network calculated for HG A haplotypes revealed a simpler pattern in which most sequences are just one mutation derived from the most frequent haplotype—the probable ancestor of this HG (network A of fig. 2). Although extremely rare in Europe, we found considerably different lineages in the Portuguese sample: 2 from the central haplotype, 2 one step derived, and 3 in distant branches of the network.

We also identified, for the first time, European haplotypes belonging to HG C. Remarkably, 2 sequences previously assigned to HG C (Guo et al. 2005) were connected, although distantly, to HG A in the network constructed with all sequences (Figure 1, Supplementary Material online). A careful inspection of these sequences revealed that they present several unique polymorphic positions. The 3 Portuguese sequences belong to 2 different lineages on distinct branches of the median-joining network of HG C (network C of fig. 2). The central haplotype is shared by Asiatic and Near Eastern breeds, but the scarce number of sequences available so far prevents us from drawing more definite phylogeographic conclusions.

Table 2

<table>
<thead>
<tr>
<th>Breed</th>
<th>Number of Haplotypes</th>
<th>Haplotype Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Portuguese</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Churra Badana</td>
<td>23</td>
<td>0.980 ± 0.020</td>
</tr>
<tr>
<td>Churra Terra Quente</td>
<td>23</td>
<td>0.997 ± 0.014</td>
</tr>
<tr>
<td>Mondegueira</td>
<td>13</td>
<td>0.974 ± 0.039</td>
</tr>
<tr>
<td>Churra Algarvia</td>
<td>32</td>
<td>0.966 ± 0.014</td>
</tr>
<tr>
<td>Campanaia</td>
<td>20</td>
<td>0.990 ± 0.019</td>
</tr>
<tr>
<td>Soria</td>
<td>29</td>
<td>0.998 ± 0.010</td>
</tr>
<tr>
<td>Merino Preto</td>
<td>10</td>
<td>0.978 ± 0.054</td>
</tr>
<tr>
<td>Central European&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carynthian sheep</td>
<td>18</td>
<td>0.680 ± 0.109</td>
</tr>
<tr>
<td>Forest sheep</td>
<td>10</td>
<td>0.778 ± 0.138</td>
</tr>
<tr>
<td>Tyrolean stone sheep</td>
<td>12</td>
<td>0.909 ± 0.056</td>
</tr>
<tr>
<td>Tyrolean mountain sheep</td>
<td>12</td>
<td>0.924 ± 0.058</td>
</tr>
<tr>
<td>Turkish&lt;sup&gt;b&lt;/sup&gt;</td>
<td>19</td>
<td>0.953 ± 0.028</td>
</tr>
</tbody>
</table>

<sup>a</sup> Meadows et al. (2005).

<sup>b</sup> For a mixed sample of individuals from 5 different Turkish breeds, Pedrosa et al. (2005).

Discussion

Both archaeological and genetic evidence indicate that the domestication of wild sheep occurred within a somewhat restricted area of southwestern Asia some 10 000 or 11 000 years ago. In the following millennia, domesticated sheep were spread rapidly into different regions—a spread that is generally associated with the expansion of Neolithic communities (Ryder 1984). Subsequent selective breeding for desirable traits such as wool, milk, and meat production as well as environmental tolerance was responsible for the development of highly productive and well-adapted sheep populations. The original location of the first appearance of the most important improvements in animal breeding is still a matter of debate.

Here, we present genetic data consistent with a continental Mediterranean influence on Iberian sheep populations. Although on the periphery of the distribution of Eurasian sheep, the 7 Portuguese breeds studied by us reveal a remarkably high level of genetic diversity in their mitochondrial gene pool when compared with other European breeds (table 2). In the absence of a continuous gene flow, we might expect a decrease in diversity as the distance increases from the heart of domestication. This pattern is observed in cattle (Troy et al. 2001) and, according to some, also in sheep (Bruford and Townsend 2006). Interestingly, our data do not support these claims and reveal instead a high degree of haplotype and HG diversity in Iberia, similar to the one previously detected in goats (Pereira et al. 2005). Considerable genetic variation has also been revealed by autosomal microsatellite markers in several Iberian breeds, particularly in the Merino type (Arranz et al. 1998; Diez-Tascón et al. 2000; Rendo et al. 2004).

Although the differentiated geographical distribution of the 3 ovine HGs suggests that HG B had witnessed a much older population expansion than HG A or HG C, both the occurrence of HG C in our sample and the pattern of diversity observed within each of them do not support this
scenario. Sheep domestication may have occurred within a relative short time, when compared with what has been implied in goats (Luikart et al. 2001). Indirect evidence supporting this hypothesis can be seen in the mismatch distribution graphs and also from the mean number of pairwise differences that are not significantly different among the 3 HGs (Figure 3, Supplementary Material online).

Phylogenetic examination reveals that the Portuguese lineages fit within the 3 main sheep HGs previously described. The unique observation of HG C in our study is the first evidence for the presence of this infrequent HG outside the putative domestication areas. Moreover, HG A, previously referred to as an “Asiatic lineage” (Hiendleder, Mainz et al. 1998) due to its high frequency in breeds of Asiatic origin, was also identified in 4 Portuguese breeds with considerably divergent lineages (network A of fig. 2). It is most interesting that when compared with a previous study, in which almost 700 individuals were analyzed (Bruford and Townsend 2006), there is a significant difference (P < 0.001) between the proportion of sequences from HGs A and C in the Portuguese sample (9 out of 161) when compared with the proportion in the remainder of Europe, where less than 10 HG A lineages were identified.

The presence of these rare lineages and the high diversity found in Iberia can be explained either as the legacy of ancient introductions or the product of more recent intrusions from imported oriental breeds over the past 150 years of intense modern breeding. Our results tend to support the former hypothesis because 1) we sampled only pure indigenous breeds from small villages avoiding recently improved animals from intensive, industrial breeders; 2) there is no historical reference to recent crossing of Portuguese breeds with animals from the Near East or Asia; 3) there are considerable morphological differences between Iberian breeds (thin-tailed sheep) and Near Eastern and most Asiatic breeds (fat-tailed and fat-rumped breeds); and 4) the Portuguese representatives of the “Asiatic” HG show a profound sequence heterogeneity and are scattered in the corresponding network.

In this respect, another related and important question is the route or routes used for the introduction of domestic sheep into Iberia. The most plausible explanation for our results is the extensive use of a Mediterranean route with the transport of animals made by sea and/or along Mediterranean coastal regions. Indeed, if a central European continental pathway had been the main route, it would have left its imprint along the way, with a higher frequency of these HGs in Europe. Because we still know very little about the nature of the genetic pattern of North African sheep, the importance of a terrestrial route along the African Mediterranean coast and its influence on Iberia, either during or before the Moslem period, remains to be clarified. However, evidence from the Cairo Genizah indicates quite clearly that in the 11th and 12th centuries the Mediterranean world was a kind of medieval common market forming a free trade area (Goitein 1967). This communications network, shared by Christians, Jews, and Moslems expressed the notion that there was blessing in movement “fi’l-haraka baraka” (Glick 1979, p 27). So too the Atlantic maritime trade between Spain, Portugal, and the Maghreb at this time is well documented by Picard (1997).

Another signature of a direct Mediterranean influence in Iberia is the north–south trend observed for the interbreed genetic distances (fig. 1). The influx of new stock through the south of the Iberian Peninsula is compatible with this trend, as well as with the fact that the southernmost breed (Churra Algarvia) is the one that displays the highest degree of differentiation and the greatest interbreed genetic distances. This interpretation does not result from the presence of “exotic” A or C HGs, which are relatively rare and shared with other breeds, but mainly from the peculiar patterns of sequences observed inside HG B as they are located at the tips of long branches of the Portuguese HG B network (Figure 2, Supplementary Material online). Previous studies, revealing an unexpectedly high diversity in breeds of Iberian domestic goats (Pereira et al. 2005) and a differential cattle migration along the Mediterranean coast (Cymbron et al. 2005), further substantiate the importance of the Mediterranean Sea in the history of the movement of people and their livestock.

Both archaeological and historical evidence indicate that after the Neolithic the Iberian Peninsula experienced extensive contact with the outside world, leading to the introduction of new crops and animals (Table 1, Supplementary Material online). Besides prehistoric contacts, a possible influx of domestic sheep could have occurred when the Phoenicians and Greeks established their important trading colonies in the southern part of Iberia. These lasted several centuries. Important developments in farming methods also occurred during Roman times with probable consequences for sheep husbandry. However, the clearest evidence for an improvement of Iberian sheep is to be seen in the Moslem period. A substantial osteometric change in this period is identified in sheep bones from southern Portugal collected from a succession of archaeological sites dating from the third millennium BC to the present day (Davis 2006). This observation suggests a significant improvement of local stocks during the Moslem period, which, as is well known, had a major and long-lasting influence on the economy and culture of Iberia between the early 8th and the late 15th century.

Both genetic and zoological observations on modern and ancient Portuguese sheep highlight the important role that Iberia played in livestock developments. Despite its position on the western edge of continental Europe, the Mediterranean Sea acted as a natural corridor connecting the peninsula to the Near East, North Africa, and southeastern Europe either through long-distance migratory movements or shorter ones like the crossing of the Straits of Gibraltar. This, together with climatic similarities to the Near East, may have allowed the influx of genetic diversity essential for selective breeding of desirable traits. This is particularly plausible for domestic sheep and goat given their environmental adaptability and the ease with which they can be transported (see Luikart et al. 2001). Particularly relevant in Iberia must have been the continued arrival of new civilizations that brought with them new agricultural techniques. These may well have included selective breeding of smaller ruminants such as sheep. One other factor that is worth bearing in mind is the enormous topographic and climatic diversity found within Iberia. This peninsula encompasses extremely arid regions,
a subtropical Mediterranean climate, and mountainous areas with extremely cold winters, a climatic and environmental diversity that may well have stimulated the development of different specialized breeds.

The importance of Iberian sheep husbandry is evident in the successful types of sheep that are found in the region today. The most remarkable of these is the fine-wool Merino that was probably developed during the first Greek incursions into Iberia, more intensely during the later Islamic period, and subsequently with the establishment by “Alfonso the Learned” in 1273 of the Mesta—the sheep holders association in Castile (Klein 2000). From the 18th century onward, Merinos were spread all over the world and are now the most numerous sheep breed and the major source of the world’s wool supply. Crosses between Merino and other sheep breeds have given rise to several of the world’s most productive breeds, such as the Ile-de-France and Merino-Landschaf. Another Iberian sheep breed, the carpet-wool Churra, was very important in the colonization of the New World and was the first to be introduced into the Americas (Ryder 1983, 1984).

Finally, the amount of genetic diversity found in Iberian breeds of sheep also shows that management and conservation strategies must involve regions located further away from the putative centers of domestication.

Supplementary Material

Supplementary Tables 1 and 2 and Figures 1–3 are available at Molecular Biology and Evolution online (http://www.mbe.oxfordjournals.org/).

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