

EVOLUTIONARY AND DEMOGRAPHIC HISTORY OF SHEEP AND GOATS SUGGESTED BY NUCLEAR, mtDNA AND Y-CHROMOSOME MARKERS

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Summary

The genetic diversity of European and Middle-Eastern sheep and goat breeds has been investigated with 5 types of markers: microsatellites, AFLPs, SNPs, mitochondrial DNA and Y-chromosomal DNA in sheep and goat. This allows a direct comparison of these marker systems and reveals similarities and differences in the genetic constitution and history of sheep and goat.

Keywords

Sheep, goat, diversity, microsatellites, Y-chromosome

Contribution

Population-genetic studies of livestock species are not only relevant for the purpose of conservation [1], but also contribute to insight in the process of domestication [2]. However, most reports on the molecular diversity of livestock species are restricted to a geographically narrow range of breeds and use only one type of marker. The concerted efforts of the Econogene project in sheep and goat diversity allow for the first time the comparison of 5

types of genetic markers: microsatellites, AFLP patterns, SNPs, mitochondrial DNA and Y-chromosomal DNA. The last two types of markers indicate maternal and paternal lineages, respectively. In addition, this study permits the comparison of the genetic constitution of sheep and goat, two closely related species which are similar in size and have been subject to the same or comparable breeding objectives. Here we present a preliminary analysis of datasets that have resulted from the Econogene project. Although we mention names linked to specific contribution, this work has only been possible by the collective effort of the Econogene Consortium.

Level of diversity. Y-chromosomal DNA (I.J. Nijman, Utrecht) as well AFLP patterns (R. Negrini, P. Ajmone Marsan, Piacenza) indicate that goats are genetically more diverse than sheep. This may reflect the degree of diversity of the ancestor species, the domestic base population and/or the level of later introgression from feral animals. However, sheep has a higher within-breed variation, indicating also a different partitioning of diversity.

Phylogeographical trends.

Mitochondrial DNA sequences from sheep (T. Perez, M. Bruford, Cardiff) fall in three groups, with, interestingly, a single outlier sequence from an one Turkish animal. All sequences clearly differ from those of the wild ancestor species. This has been interpreted as reflecting three different domestication events [2]. The frequencies of the sequences from two groups in Europe decrease from South-East to North-West. Similar observations have been reported for goats [3]. This cline very likely reflects the prehistoric introduction of livestock species in Europe and is also evident from a separation of Southern and Eastern breeds from the North-Western European breeds by AFLP as well as microsatellite markers.

Model-based clustering [4] of goat microsatellite genotypes (S. Dunner, J. Cañon, P. García-Atance, Madrid; G. Obexer-Ruff, Bern; results not shown) reveals at least four discrete clusters: East-Mediterranean, Central Mediterranean, West-Mediterranean, and Central with Northern Europe, respectively. In breeds from the last cluster, the average number of microsatellite alleles is clearly less than in the Mediterranean breeds. In order to visualize genetic distances of goat breeds, we used NeighborNet graphs [5]. These graphs combine the Neighbor-Joining principle with a network algorithm and are superior to Neighbor-Joining trees, especially if the phylogeny is not hierarchical (tree-like). As shown in Fig. 1, the clusters deduced from model-based clustering correspond to regions in the graph.

Fig. 1 also shows the relative frequencies of three goat Y-chromosomal haplotypes A3, A4 and B as markers of the paternal lineages. Most Asian breeds have haplotype B, but one Turkish breed has also A3. This suggests that both the A and the B haplotypes were introduced in Europe, but have now variable frequencies in different breeds. In the goat breeds from the Central and Northern Europe cluster, A3 and A4 are predominant (Fig. 1), confirming a common origin as suggested by the genetic distances. Haplotypes A3 and A4 are more common in Italy than in other Mediterranean breeds. This may indicate an exchange of paternal lineages across the Italian peninsula.

Also for sheep breeds (C. Peter, G. Erhardt, Giessen; S. Dellamitra, G. Hewitt, Norwich; T. Perez, M. Bruford, Cardiff; results not shown), the number of microsatellites alleles correlates with geographical location, but follows a gradual South-East to North-West gradient. There is a clear clustering of Merino breeds from various locations with other breeds of Spanish origin. However, for the Central and Western-European breeds the genetic distances did not correlate well with geographical distances. Interestingly, a group of breeds from different origin but relatively short mutual genetic distances share a Y-chromosomal SNP allele (I.J. Nijman, Utrecht, [6]).

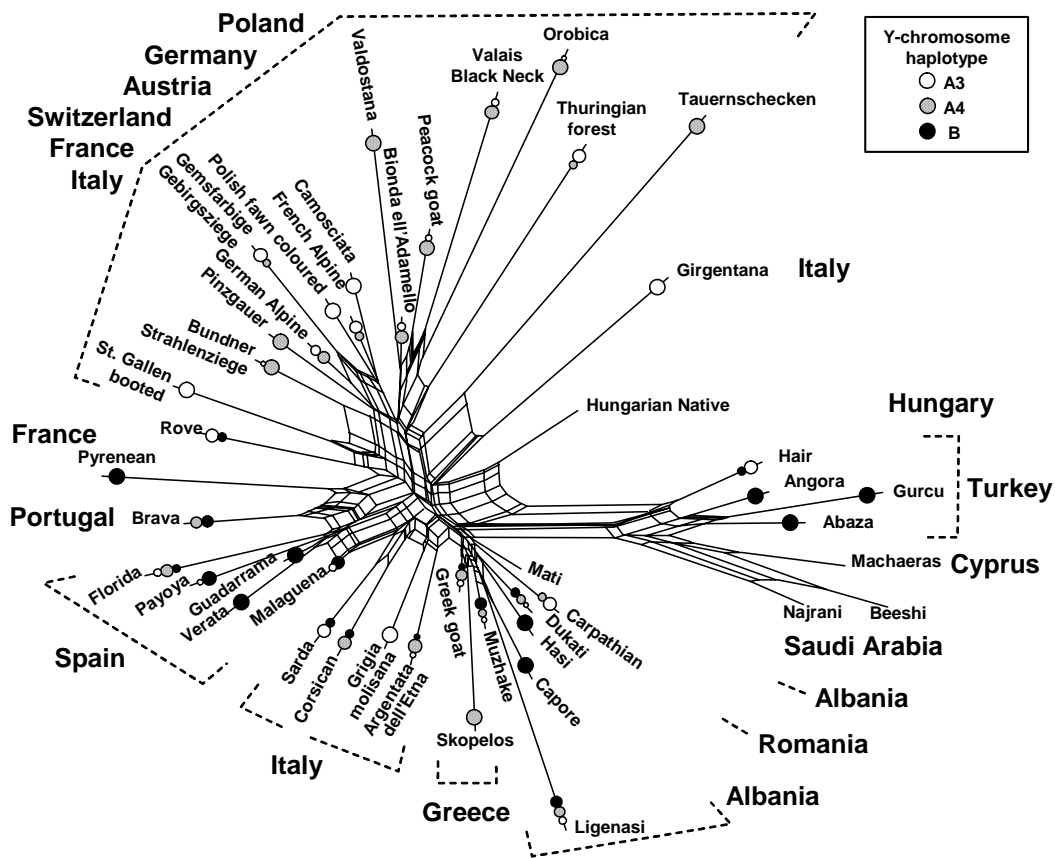


Fig. 1. NeighborNet graph of Nei standard genetic distances. The sizes of the open, hatched and filled circles indicate frequencies of Y-chromosomal haplotypes A3, A4 and B, respectively.

It is also noteworthy that most breeds in which both Y-chromosomal alleles were found (Welsh Mountain, Swaledale, Thones & Marthod, Pomerian, Kamieniec, Tsigiaia, Churra Braganzana, Shkodrane) also had relatively more different microsatellite alleles than neighboring breeds. It may be hypothesized that the breeding of sheep, more often than with goats, involved the import of sires from other regions.

The gradual transition from Asia via Balkan breeds to Central, Northern and Western in Europe is apparent from the networks of genetic distances of both goat and sheep breeds. A similar observation has been made for cattle (European Cattle Genetic Diversity Consortium, unpublished results, [7]). In addition, the networks suggest that all three livestock species underwent in Central, Northern and Western Europe a ‘genetic explosion, resulting in a high level of genetic and phenotypic differentiation in spite of a decrease in the number of microsatellite alleles.

Breed formation. A typical feature of the genetic constitution of livestock breeds is the existence of distinct breeds, genetically isolated to various degrees and subject to a systematic selection of animals conforming to the breeding objectives. This is reflected in differences in allele frequencies rather than in breed-specific alleles, with the highest degree of breed specificity observed for the Y-chromosomal haplotypes. The lengths of terminal branches in phylogenetic trees or NeighborNet networks (Fig. 1) correspond to the effect of genetic drift,

which depends on both genetic isolation and population size. Microsatellites and AFLP identify a number of breeds with relatively large genetic distances from most other breeds, like the Italian Orobica and the Austrian Tauernschecken goats and the German graue gehörnte Heideschnucke sheep. Unique genetic properties may have contributed to genetic isolation, like the characteristic coat color pattern of the Tauernschecken. However, the identification of gene variants that encode the breed-specific phenotypes, such as coat color, morphology, production traits and adaptation to local conditions, remains a challenge of the future.

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