Phylogeny and distribution of Y-chromosomal haplotypes in domestic, ancient and wild goats

Isaäc J. Nijman[1,2], Benjamin D. Rosen[3], Zhuqing Zheng[4], Yu Jiang[4], Tristan Cumer[5], Kevin G. Daly[6], Valentin A. Bâlteanu[7], Beate Berger[8], Thor Blichfeldt[9], Geert Boink[10], Sean Carolan[11], Vlatka Cubric-Curik[12], Juha Kantanen[13], Amparo Martínez[14], Raffaele Mazza[15], Negar Khayatzadeh[8], Namshin Kim[16], Nadjet-Amina Ouchene-Khelifi[17], Filipe Pereira[18], Anne da Silva[19], Mojca Simčič[20], Johann Sölkner[8], Alison Sutherland[21], Johannes Tigchelaar[10], Econogene Consortium[22], Paolo Ajmone-Marsan[23], Daniel G. Bradley[6], Licia Colli[23], François Pompanon[5] and Johannes A. Lenstra[1*]

[1] Faculty of Veterinary Medicine, Utrecht University, Netherlands
[2] Center for Molecular Medicine and Oncode Institute, University Medical Center Utrecht, Utrecht University, The Netherlands
[3] Animal Genomics and Improvement Laboratory, Agriculture Research Service, Beltsville, MD, United States
[4] Key Laboratory of Animal Genetics, Breeding and Reproduction of Shaanxi Province, College of Animal Science and Technology, Northwest A&F University, Yangling, China
[5] Université Grenoble Alpes, Université Savoie Mont Blanc, CNRS, LECA, Grenoble, France
[6] Smurfit Institute of Genetics, Trinity College Dublin, Dublin, Ireland
[7] Faculty of Animal Science and Biotechnologies, University of Agricultural Sciences and Veterinary Medicine of Cluj-Napoca, Cluj-Napoca, Romania
[8] University of Natural Resources and Life Sciences Vienna (BOKU)
[9] Norwegian Association of Sheep and Goat Breeders, Aas, Norway
[10] Stichting Zeldzame Huisdierrassen, Wageningen, The Netherlands
[11] Old Irish Goat Society, Mulranny, Ireland
[12] Dep. Animal Science, University of Zagreb, Zagreb, Croatia
[13] Natural Resources Institute Finland (Luke), Helsinki, Finland
[14] Dep. Genética,Universidad de Córdoba, Córdoba, Spain
[15] Laboratorio Genetica e Servizi, Agrotis srl, Cremona, Italy
[16] Korea Research Institute of Bioscience and Biotechnology (KRIBB), Daejeon, South Korea
[17] Laboratory of Biotechnologies related to Animal Reproduction, Science Veterinary Institute, University of Blida, Blida, Algeria
[18] IDENTIFICA, UPTEC, Porto, Portugal
[19] Univ. Limoges, INRA, Pereine EA7500, USC1061 Gamaa, F-87000 Limoges, France
[20] Univ. Ljubljana, Biotechnical Faculty, Dep. Animal Science, Ljubljana, Slovenia
[21] New Zealand Arapawa Goat Association, New Zealand
[22] See the list at the end of this paper
[23] Dip. di Scienze Animali, della Nutrizione e degli Alimenti, Univ. Cattolica del S. Cuore di Piacenza, Piacenza, Italy

[*] **Correspondence:**
J.A. Lenstra
j.a.lenstra@uu.nl

Keywords: goat, genome, Y-chromosome, haplotype, migration, bottleneck, introgression

Abstract

The male-specific part of the Y-chromosome is in mammalian and many other species the longest haplotype that is inherited without recombination. By its paternal transmission it has a small effective population size in species with dominant males. In several species, Y-chromosomal haplotypes are sensitive markers of population history and introgression. Previous studies have identified in domestic goats four major Y-chromosomal haplotypes Y1A, Y1B, Y2A and Y2B with a marked geographic differentiation and several regional variants. In this study we used published whole-genome sequences of 70 male goats from 16 modern breeds, 11 ancient-DNA samples and 29 samples from seven wild goat species. We identified single-copy male-specific SNPs in four scaffolds, containing *SRY*, *ZFY*, *DBY* with *SSX3Y* and *UTY*, and *USP9Y* with *UMN2001*, respectively. Phylogenetic analyses indicated haplogroups corresponding to the haplotypes Y1B, Y2A and Y2B, respectively, but Y1A was split into Y1AA and Y1AB. All haplogroups were detected in ancient DNA samples from southeast Europe and, with the exception of Y1AB, in the bezoar goat, which is the wild ancestor of the domestic goats. Combining these data with those of previous studies and with genotypes obtained by Sanger sequencing or the KASP assay yielded haplogroup distributions for 132 domestic breeds or populations. The phylogeographic differentiation indicated paternal population bottlenecks on all three continents. This possibly occurred during the Neolithic introductions of domestic goats to those continents with a particularly strong influence in Europe along the Danubian route. This study illustrates the power of the Y-chromosomal haplotype for the reconstructing the history of mammalian species with a wide geographic range.

1. Introduction

Because of its absence or recombination, the male part of the mammalian Y-chromosomes is by far the longest haplotype that is stably transmitted across generations (Hughes et al., 2015). Together with its inheritance from father to son, it is a highly informative marker for the paternal origin of species, populations or individuals with a much stronger phylogeographic differentiation than observed for mitochondrial or autosomal DNA. The highly informative Y-chromosomal markers are now widely exploited in population-genetic studies of humans (Jobling and Tyler-Smith, 2017; Kivisild, 2017), cattle (Edwards et al., 2011; Xia et al., 2019), horse (Wallner et al., 2017; Wutke et al., 2018; Felkel et al., 2019a) water buffalo (Zhang et al., 2016), sheep (Meadows and Kijas, 2009; Zhang et al., 2014), camel (Felkel et al., 2019b), pigs (Guirao-Rico et al., 2018) and dogs (Natanaelsson et al., 2006; Oetjens et al., 2018).

A preliminary analysis of the Y-chromosomal diversity in European and Turkish goats defined the three haplotypes Y1A, Y1B and Y2, showing strong geographic differentiation (Lenstra and Econogene Consortium, 2005). The same haplotypes were found in goats from

Portugal and North-Africa (Pereira et al., 2009), Turkey (Cinar Kul et al., 2015), east and south Asia (Waki et al., 2015), Switzerland and Spain (Vidal et al., 2017) with additional haplotypes Y2B in east Asia, Y2C in Turkish Kilis goats, and Y1B2 as well Y1C mainly in Switzerland (Table 1). However, these haplotypes are based on a low number of SNPs in or near *DBY-1, SRY* and *ZFY*. Thus, it is not clear if the haplotypes represent major haplogroups or local variants, if other major haplogroups exist, and which of the Y-chromosomal variants already existed in the earlier domestic goats and in their wild ancestor, the bezoar (Amills et al., 2017).

Table 1. Haplotypes identified previously or in this study by ABI sequencing (Lenstra, 2005; indicated by ddSeq), whole-genome sequencing, KASP genotyping, SRA BLAST searches. Mutations are relative to haplogroup Y1AB, which in previous studies together with Y1AA was represented by haplotype Y1A**.** Haplotype Y1C belongs to the Y1B haplogroup. Most of the diagnostic SNPs used here for KASP or SRA searches are within the segments covered by dideoxy sequencing.

Haplotypes	Diagnostic SNP	Detection	Specificity	Range, breed	Reference
Main types					
Y1AA	NW_017189563.1 g.G280574>T	ddSeq, SRA search	Y1AA	Asia[1]	This study
Y1AB				Europe, Asia[1]	Lenstra, 2005
Y1B	NW_017189563.1 g.T280306>A	ddSeq, SRA search, KASP	Y1B, Y1C	Europe, North Africa	Lenstra, 2005
	NW_017189885.1 g.T104701>C	SRA search	Y1B, Y1C	Europe, North Africa	This study
Y2A	NW_017189563.1 g.G277537>T	ddSeq, SRA search	Y2A, Y2C, Y2C		Lenstra, 2005
	NW_017189563.1 g.A278523>G	ddSeq, SRA search	Y2A, Y2C, Y2C		Lenstra, 2005
	NW_017189563.1 g.T280046>A	ddSeq	Y2A, Y2C, Y2C		Lenstra, 2005
	NW_017189563.1 g.G280433>A	ddSeq	Y2A, Y2C, Y2C		Lenstra, 2005
	NW_017189685.1 g.A43279>C	ddSeq	Y2A, Y2C, Y2C		Lenstra, 2005
	NW_017189685.1 g.C43464>T	ddSeq	Y2A, Y2C, Y2C		Lenstra, 2005
	NW_017189885.1 g.A11686>G	ddSeq, KASP	Y2A, Y2C, Y2C		Lenstra, 2005
Y2B	NW_017189563.1 g.A280113>G	ddSeq, SRA search	Y2B	East, southeast Asia	Waki et al., 2015
Local types					
Y1AB2	NW_017189563.1 g.A277871>G	ddSeq	Y1AB2	Albanian DUK, LIQ; Romanian CAR; German TWZ	This study
Y1B2	NW_017189885.1 g.G12927>A		Y1B2	Switzerland, Italy	Vidal et al., 2017
Y1C	NW_017189563.1 g.A279212>C	ddSeq	Y1C	Swiss PCG, VZC; Italian GAR	Vidal et al., 2017
Y2C	NW_017189885.1 g.A11760>C		Y2C		Cinar-Kul et al., 2015

[1] Y1A is present in Africa and may represent either Y1AA or Y1AB or both

In this study, we use whole-genome sequences (WGSs) to systematically characterize the SNP-level variation in a large part of the single-copy male-specific part of the caprine Y-chromosome. In addition, we determined the Y-chromosomal haplogroups in goats originating from several European, Asian or African countries, in ancient goat DNA samples and in the wild bezoar. We observed a strong phylogeographic structure as the result of paternal bottlenecks during the Neolithic migrations and found evidence for recent introgressions in Asian landraces, which is essential information for breed management and conservation.

2. Methods

2.1 WGS data, filtering and tree construction.

We selected four Y-chromosomal scaffolds carrying single-copy genes without the UMN2303 Y-chromosomal repeat (Table 2). From the Short Read Archive (SRA) a VCF file containing the sequences of these scaffolds in 70 male goats (Table 3), 30 of which were from central and east Asia, and 107 female goats from the same source laboratories. After excluding dense clusters of SNPs, we obtained 5356 SNPs, from which 2350 were hemizygous, were not scored in females, had scores in >95% of the males and had a minor allele frequency of >2% in male domestic goats. Allele-sharing distances were calculated using PLINK, and visualized in a Neighbor-Joining tree by using the programs SPLITSTREE (Huson and Bryant, 2006) and MEGA (Tamura et al., 2011).

2.2 Haplogroups in 132 goat breeds.

We differentiating the major Y-chromosomal haplogroups Y1AA, Y1AB, Y1B, Y2A and Y2B for 1720 domestic goats from 132 breeds by combining data from several sources as detailed per breed in Table 4:

(1) From the goat panel collected for the Econogene project, DNA samples of 353 male goats from 38 European or southwestern Asian breeds were analyzed by PCR amplification and dideoxy-sequencing of segments within the *DBY*, *SRY* and *ZFY* genes (Lenstra and Econogene Consortium, 2005) as described previously for bovine samples (Nijman et al., 2008; Edwards et al., 2011) and using the primers listed in Table 5.

(2) We used published data for 90 goats from 5 Portuguese breeds or from Morocco (Pereira et al., 2009), for 211 goats from 10 Asian breeds (Waki et al., 2015), for 181 goats from 8 Turkish breeds (Cinar Kul et al., 2015) and for 270 goats from 26 Spanish or Swiss breeds (Vidal et al., 2017).

(3) 362 DNA samples (57 breeds) from several sources, including the AdaptMap panel (Colli et al., 2018) were genotyped by the KASP assay (Table 4).

(4) For 90 goats from 15 breeds genotypes were obtained by BLAST searching of the Short-Read Archive (SRA).

Table 2. X- and Y-chromosomal scaffolds for the goat reference genome.

scaffold	length (bp)	genes
NW_017189563.1	528190	*SRY*
NW_017189618.1	458718	*USP9Y, UMN2001*
NW_017189685.1	386696	*DBY, DDX3Y, UTY*
NW_017189885.1	194156	*ZFY*

For samples collected by Cinar-Kul (2015) and Vidal et al. (2017) or analyzed by KASP before genomic data became available, Y1AA and Y1AB have been both scored as Y1A haplotype. Several of these samples did not contain Y1A or belonged to breeds for which additional data were available (Table 3). However, for 31 breeds we only have the Y1A frequency. Likewise, Vidal et al. (2017) and the Kasp assay did not differentiate Y2A and Y2B. Since sequence data indicate that Y2B does not occur in modern domestic goats from Europe, Anatolia and Iran, we assigned all Y2 scores in European and African goats to Y2A.

Genotypes were extracted from WGS data for ancient DNA samples (Daly et al. 2018) and for bezoar samples (Alberto et al., 2018).

3. Results and Discussion

The four selected scaffolds (Table 1) cover together 1,567,760 bp of the male-specific part of the caprine Y-chromosome and contain the SNPs that in previous work defined the major haplotypes Y1A, Y1B, Y2A and Y2B (Table 1). A phylogenetic tree of the Y-chromosomes of 70 goats (Fig. 1) shows five major haplogroups. Three haplogroups contains the previously identified haplotypes Y1B, Y2A and Y2B, whereas the Y1A haplotypes belong to either haplogroups Y1AA and Y1AB. In this panel we did not find goats with the local Y1C and Y2C sequences (Table 1).

Remarkably, with the exception of Y1B the haplogroups have all been found in Iranian bezoar samples (Fig. 3, Table 4), whereas all haplogroups, including Y1B, were detected in ancient goat samples.

Geographic plots of haplogroup frequencies show a considerable spatial differentiation, which resonates the strong phylogeography displayed by autosomal SNPs (Colli et al., 2018), but is in clear contrast with the phylogenetic structure displayed by mtDNA haplogroups (Luikart et al., 2001; Naderi et al., 2007, 2008; Zhao et al., 2014b, 2014a). Most likely, by a series of bottlenecks in the male lineage subcontinents have different major haplogroups, while none has a global-wide coverage:

- Haplogroup Y2B is absent in Europe, Africa and west Asia, but became a major haplotype in east Asia and southeast Asian, where Y2A is not represented. In contrast, it is observed in ancient goat from Medieval Georgia and Neolithic Iran (ca. 6,000 BCE), supporting an origin of east Asian goat from regions east of Zagros Mountains.
- Y2A is in northern and central Europe only found in the crossbred AngloNubian (see below), but is the predominant haplogroup in central, eastern and southern Africa.
- Haplogroup Y1B is predominant in northern Europe, but outside Europe and North African has only been found in one Karamonja animal, in the Korean native breed and in exported

Saanen populations. The different Y2A and Y1B frequencies in north-central vs southern Europe may reflect the Neolithic migrations following the Danube and the Mediterranean routes, respectively (Cymbron et al., 2005; Tresset and Vigne, 2007; Rivollat et al., 2015) with the strongest bottlenecks along the northernmost migrations.
- Y1AA is sporadic in Europea and has been observed also in Neolithic Serbia (ca. 6,000 BCE), but is present in Asia (Fig. 3).

Deviations from the general pattern may very well reflect major introgressions. A well-known example is the Anglo-Nubian, which originated in England by crossing Indian or African imported goats with local breeds and is in our panel the only northern-European breed carrying Y2A.

There were two out-of-range findings of Y1B, in the Uganda Karamonja and in the Korean native breeds. Because of the popularity of Swiss dairy goats in both Uganda (NAADS, 2005) and Korea (Kim et al., 2019), crossbreeding again is the most likely explanation.

We conclude that the Y-chromosomal haplotype distribution reveals expansion and crossbreeding events, as observed also for the human paternal lineages (Poznik et al., 2016; Batini and Jobling, 2017), and illustrates the power of Y-chromosomal markers for inferring the genetic origin of mammalian populations.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Authors' contributions

IJN, PAM and JAL designed the study; IJN carried out and analyzed the ABI sequencing; TF, BD, BR, ZZ and YJ analyzed the WGS data; TC and FPo supplied the bezoar genotypes; KGD and DGB supplied the aDNA data; BR supplied most of the African samples for KASP genotyping; BB, VAB, TB, SC, VC-C, AdS, JK, NK, AM, RM, FPe MS, AS, JS and JT collected material or data for other breeds; JAL performed the downstream analysis and wrote the first draft; and KGD, AM, FPe, MS and PAM contributed to the text**.**

Funding

This study was supported by the Croatian Science Foundation (Project ANAGRAMS-IP-2018-01-8708 "Application of NGS in assessment of genomic variability in ruminants" and by the European Union (projects ECONOGENE QLK5–CT2001–02461. We are grateful to Dr E. Cuppen (Utrecht Medical Centre) for access to the dideoxy sequencing facilities.

Acknowldegements.

This study has benefited from an interaction with Vargoats consortium (http://www.goatgenome.org/vargoats.html).

Availability of data

The SRA data are in the public domain.

Members of the Econogene Consortium:

Albania: Hoda Anila, Dobi Petrit, Dep. Animal Production, Fac. Agriculture, Tirana; **Austria:** Baumung Roswitha, Univ. Natural Resources Applied Life Sciences, Vienna; **Belgium:** Baret Philippe, Fadlaoui Aziz, Dep. Animal Genetics, Univ. Cath. Louvain, Louvain-la-Neuve; **Cyprus:** Papachristoforou Christos, Agricult. Research Instit., Nicosia; **Egypt:** El-Barody M.A.A., Animal Production Dep., Fac. Agriculture, Minia Univ. **France:** Taberlet Pierre, England Phillip, Luikart Gordon, Beja-Pereira Albano, Zundel Stéphanie, Laboratoire d'Ecologie Alpine (LECA), Univ. Joseph Fourier, Grenoble; Trommetter Michel, Inst. Recherche Agronomique, Unité d'Économie Sociologie Rurales, Grenoble ; **Germany:** Erhardt Georg, Brandt Horst, Ibeagha-Awemu Eveline, Lühken, Gesine, Daniela Krugmann, Prinzenberg Eva-Maria, Lipsky Shirin, Gutscher Katja, Peter Christina, Inst. Tierzucht Haustiergenetik, Justus-Liebig Univ. Giessen; Roosen Jutta, Bertaglia Marco, Dep. Food Economics Consumption Studies, Univ. Kiel; **Greece:** Georgoudis Andreas, Al Tarrayrah, Jamil, Kliambas Georgios, Kutita Olga, Karetsou Katerina, Aristotle Univ. Thessaloniki, Fac. Agriculture, Thessaloniki; Ligda Christina, National Agric. Research Foundation, Thessaloniki; **Hungary:** Istvan Anton, Fesus Lazlo, Research Inst. Animal Breeding Nutrition, Dep. Genetics, Herceghalom; **Italy:** Ajmone-Marsan Paolo, Canali Gabriele, Milanesi Elisabetta, Pellecchia Marco, Università Cattolica S. Cuore, Piacenza; Carta Antonello, Sechi Tiziana, Ist. Zootecnico Caseario Sardegna, Sassari; Cicogna Mario, Fornarelli Francesca, Giovenzana Stefano, Marilli Marta, Ist. Zootecnia Generale, Univ. Studi di Milano; Marletta Donata, Bordonaro S., D'Urso Giuseppe, Dip. Scienze Agronomiche Produzioni Animali, Univ. Studi Catania; Pilla Fabio, D'Andrea Mariasilvia, Dip. Scienze Animali Vegetali Ambiente, Univ. Molise, Campobasso; Valentini Alessio, Cappuccio Irene, Pariset Lorraine, Dip. Produzioni Animali, Univ. Tuscia, Viterbo; **Jordan:** Abo-Shehada Mahamoud, Fac. Veterinary Medicine, Jordan Univ. Science Technology; **Netherlands:** Lenstra Johannes A., Nijman, Isaäc J., Van Cann, Lisette M., Fac. Veterinary Medicine, Utrecht Univ.; **Poland:** Niznikowski Roman, Dominik Popielarczyk, Strzelec Ewa, Dep. Sheep Goat Breeding, Warsaw Agricultural Univ.; **Romania:** Vlaic Augustin, Dep. Animal Genetics, Faculty Zootechnics, Univ. Cluj-Napoca; **Spain:** Dunner Susana, Canon Javier, Cortes Oscar, Garcia David, Univ. Complutense Madrid; **Switzerland:** Caloz Régis, EPFL, Lausanne; Obexer-Ruff Gabriela, Marie-Louise Glowatzki, Institut für Genetik Ernährung und Haltung von Haustieren, Universität Bern; **Turkey:** Ertugrul Okan, Veterinary Fac., Ankara Univ.; Togan Inci, Koban Evren, Dep. Biology, Middle East Technical Univ., Ankara; **UK:** Bruford Mike, Perez Trinidad, Juma Gabriela, School Biosciences, Cardiff Univ.; Hewitt Godfrey, Dalamitra Stella, Wiskin Louise, Taylor Martin, Biological Sciences, Univ. East Anglia, Norwich; Jones Sam, The Sheep Trust, Scarpa Riccardo, Environment Dep., Univ. York

References

Alberto, F. J., Boyer, F., Orozco-Terwengel, P., Streeter, I., Servin, B., De Villemereuil, P., et al. (2018). Convergent genomic signatures of domestication in sheep and goats. *Nat. Commun.* 9. doi:10.1038/s41467-018-03206-y.

Amills, M., Capote, J., and Tosser-Klopp, G. (2017). Goat domestication and breeding: a jigsaw of historical, biological and molecular data with missing pieces. *Anim. Genet.* 48, 631–644. doi:10.1111/age.12598.

Batini, C., and Jobling, M. A. (2017). Detecting past male-mediated expansions using the Y chromosome. *Hum. Genet.* 136, 547–557. doi:10.1007/s00439-017-1781-z.

Cinar Kul, B., Bilgen, N., Lenstra, J. A., Korkmaz Agaoglu, O., Akyuz, B., and Ertugrul, O. (2015). Y-chromosomal variation of local goat breeds of Turkey close to the domestication centre. *J. Anim. Breed. Genet.* 132, 449–453. doi:10.1111/jbg.12154.

Colli, L., Milanesi, M., Talenti, A., Bertolini, F., Chen, M., Crisà, A., et al. (2018). Genome-wide SNP profiling of worldwide goat populations reveals strong partitioning of diversity and highlights post-domestication migration routes. *Genet. Sel. Evol.* 50, 1–20. doi:10.1186/s12711-018-0422-x.

Cymbron, T., Freeman, A. R., Malheiro, M. I., Vigne, J. D., and Bradley, D. G. (2005). Microsatellite diversity suggests different histories for Mediterranean and Northern European cattle populations. *Proc. R. Soc. B Biol. Sci.* 272, 1837–1843. doi:10.1098/rspb.2005.3138.

Edwards, C. J., Ginja, C., Kantanen, J., Pérez-Pardal, L., Tresset, A., Stock, F., et al. (2011).

286 Dual origins of dairy cattle farming - Evidence from a comprehensive survey of
287 european Y-chromosomal variation. *PLoS One* 6. doi:10.1371/journal.pone.0015922.
288 Felkel, S., Vogl, C., Rigler, D., Dobretsberger, V., Chowdhary, B. P., Distl, O., et al. (2019a).
289 The horse Y chromosome as an informative marker for tracing sire lines. *Sci. Rep.* 9, 1–
290 12. doi:10.1038/s41598-019-42640-w.
291 Felkel, S., Wallner, B., Chuluunbat, B., Yadamsuren, A., Faye, B., Brem, G., et al. (2019b). A
292 first Y-chromosomal haplotype network to investigate Male-driven population dynamics
293 in domestic and wild bactrian camels. *Front. Genet.* 10, 1–7.
294 doi:10.3389/fgene.2019.00423.
295 Guirao-Rico, S., Ramirez, O., Ojeda, A., Amills, M., and Ramos-Onsins, S. E. (2018).
296 Porcine Y-chromosome variation is consistent with the occurrence of paternal gene flow
297 from non-Asian to Asian populations. *Heredity (Edinb).* 120, 63–76.
298 doi:10.1038/s41437-017-0002-9.
299 Hughes, J. F., Skaletsky, H., Koutseva, N., Pyntikova, T., and Page, D. C. (2015). Sex
300 chromosome-to-autosome transposition events counter Y-chromosome gene loss in
301 mammals. *Genome Biol.* 16, 1–9. doi:10.1186/s13059-015-0667-4.
302 Huson, D. H., and Bryant, D. (2006). Application of phylogenetic networks in evolutionary
303 studies. *Mol. Biol. Evol.* 23, 254–267. doi:10.1093/molbev/msj030.
304 Jobling, M. A., and Tyler-Smith, C. (2017). Human Y-chromosome variation in the genome-
305 sequencing era. *Nat. Rev. Genet.* 18, 485–497. doi:10.1038/nrg.2017.36.
306 Kim, J. Y., Jeong, S., Kim, K. H., Lim, W. J., Lee, H. Y., and Kim, N. (2019). Discovery of
307 genomic characteristics and selection signatures in Korean indigenous goats through
308 comparison of 10 goat breeds. *Front. Genet.* 10, 1–17. doi:10.3389/fgene.2019.00699.
309 Kivisild, T. (2017). The study of human Y chromosome variation through ancient DNA.
310 *Hum. Genet.* 136, 529–546. doi:10.1007/s00439-017-1773-z.
311 Lenstra, J. A., and Econogene Consortium (2005). Evolutionary and demographic history of
312 sheep and goats suggested by nuclear, mtDNA and Y-chromosomal markers. in *The role
313 of biotechnology for the characterization of crop, forestry, animal and fishery genetic
314 resources* (Turin).
315 Luikart, G., Gielly, L., Excoffier, L., Vigne, J., Bouvet, J., and Taberlet, P. (2001). Multiple
316 maternal origins and weak phylogeographic structure in domestic goats. *Proc. Natl.
317 Acad. Sci. U. S. A.* 98, 5927–5932. doi:10.1073ypnas.091591198.
318 Meadows, J. R. S., and Kijas, J. W. (2009). Re-sequencing regions of the ovine Y
319 chromosome in domestic and wild sheep reveals novel paternal haplotypes. *Anim. Genet.*
320 40, 119–123. doi:10.1111/j.1365-2052.2008.01799.x.
321 NAADS (2005). Goat Production Manual.
322 Naderi, S., Rezaei, H. R., Pompanon, F., Blum, M. G. B., Negrini, R., Naghash, H. R., et al.
323 (2008). The goat domestication process inferred from large-scale mitochondrial DNA
324 analysis of wild and domestic individuals. *Proc. Natl. Acad. Sci. U. S. A.* 105, 17659–
325 17664. doi:10.1073/pnas.0804782105.
326 Naderi, S., Rezaei, H. R., Taberlet, P., Zundel, S., Rafat, S. A., Naghash, H. R., et al. (2007).
327 Large-scale mitochondrial DNA analysis of the domestic goat reveals six haplogroups
328 with high diversity. *PLoS One* 2. doi:10.1371/journal.pone.0001012.
329 Natanaelsson, C., Oskarsson, M. C. R., Angleby, H., Lundeberg, J., Kirkness, E., and
330 Savolainen, P. (2006). Dog Y chromosomal DNA sequence: Identification, sequencing
331 and SNP discovery. *BMC Genet.* 7. doi:10.1186/1471-2156-7-45.
332 Nijman, I. J., Van Boxtel, D. C. J., Van Cann, L. M., Marnoch, Y., Cuppen, E., and Lenstra, J.
333 A. (2008). Phylogeny of Y chromosomes from bovine species. *Cladistics* 24, 723–726.
334 doi:10.1111/j.1096-0031.2008.00201.x.
335 Oetjens, M. T., Martin, A., Veeramah, K. R., and Kidd, J. M. (2018). Analysis of the canid Y-

chromosome phylogeny using short-read sequencing data reveals the presence of distinct haplogroups among Neolithic European dogs. *BMC Genomics* 19, 1–9. doi:10.1186/s12864-018-4749-z.

Pereira, F., Queirós, S., Gusmão, L., Nijman, I. J., Cuppen, E., Lenstra, J. A., et al. (2009). Tracing the history of goat pastoralism: New clues from mitochondrial and y chromosome DNA in North Africa. *Mol. Biol. Evol.* 26, 2765–2773. doi:10.1093/molbev/msp200.

Poznik, G. D., Xue, Y., Mendez, F. L., Willems, T. F., Massaia, A., Wilson Sayres, M. A., et al. (2016). Punctuated bursts in human male demography inferred from 1,244 worldwide Y-chromosome sequences. *Nat. Genet.* 48, 593–599. doi:10.1038/ng.3559.

Rivollat, M., Mendisco, F., Pemonge, M. H., Safi, A., Saint-Marc, D., Brémond, A., et al. (2015). When the waves of European neolithization met: First paleogenetic evidence from early farmers in the Southern Paris Basin. *PLoS One* 10, 1–16. doi:10.1371/journal.pone.0125521.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., and Kumar, S. (2011). MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.* 28, 2731–2739. doi:10.1093/molbev/msr121.

Tresset, A., and Vigne, J.-D. (2007). "Substitution of species, techniques and symbols at the Mesolithic-Neolithic transition in Western Europe," in *Going Over: The Mesolithic-Neolithic Transition in North-West Europe* (British Academy). doi:10.5871/bacad/9780197264140.003.0010.

Vidal, O., Drögemüller, C., Obexer-Ruff, G., Reber, I., Jordana, J., Martínez, A., et al. (2017). Differential distribution of Y-chromosome haplotypes in Swiss and Southern European goat breeds. *Sci. Rep.* 7, 1–6. doi:10.1038/s41598-017-15593-1.

Waki, A., Sasazaki, S., Kobayashi, E., and Mannen, H. (2015). Paternal phylogeography and genetic diversity of East Asian goats. *Anim. Genet.* 46, 337–339. doi:10.1111/age.12293.

Wallner, B., Palmieri, N., Vogl, C., Rigler, D., Bozlak, E., Druml, T., et al. (2017). Y Chromosome Uncovers the Recent Oriental Origin of Modern Stallions. *Curr. Biol.* 27, 2029-2035.e5. doi:10.1016/j.cub.2017.05.086.

Wutke, S., Sandoval-Castellanos, E., Benecke, N., Döhle, H. J., Friederich, S., Gonzalez, J., et al. (2018). Decline of genetic diversity in ancient domestic stallions in Europe. *Sci. Adv.* 4. doi:10.1126/sciadv.aap9691.

Xia, X., Yao, Y., Li, C., Zhang, F., Qu, K., Chen, H., et al. (2019). Genetic diversity of Chinese cattle revealed by Y-SNP and Y-STR markers. *Anim. Genet.* 50, 64–69. doi:10.1111/age.12742.

Zhang, M., Peng, W. F., Yang, G. L., Lv, F. H., Liu, M. J., Li, W. R., et al. (2014). Y chromosome haplotype diversity of domestic sheep (Ovis aries) in northern Eurasia. *Anim. Genet.* 45, 903–907. doi:10.1111/age.12214.

Zhang, Y., Lu, Y., Yindee, M., Li, K. Y., Kuo, H. Y., Ju, Y. Ten, et al. (2016). Strong and stable geographic differentiation of swamp buffalo maternal and paternal lineages indicates domestication in the China/Indochina border region. *Mol. Ecol.* 25, 1530–1550. doi:10.1111/mec.13518.

Zhao, W., Zhong, T., Wang, L. J., Li, L., and Zhang, H. P. (2014a). Extensive female-mediated gene flow and low phylogeography among seventeen goat breeds in southwest China. *Biochem. Genet.* 52, 355–364. doi:10.1007/s10528-014-9652-y.

Zhao, Y., Zhao, R., Zhao, Z., Xu, H., Zhao, E., and Zhang, J. (2014b). Genetic diversity and molecular phylogeography of Chinese domestic goats by large-scale mitochondrial DNA analysis. *Mol. Biol. Rep.* 41, 3695–3704. doi:10.1007/s11033-014-3234-2.

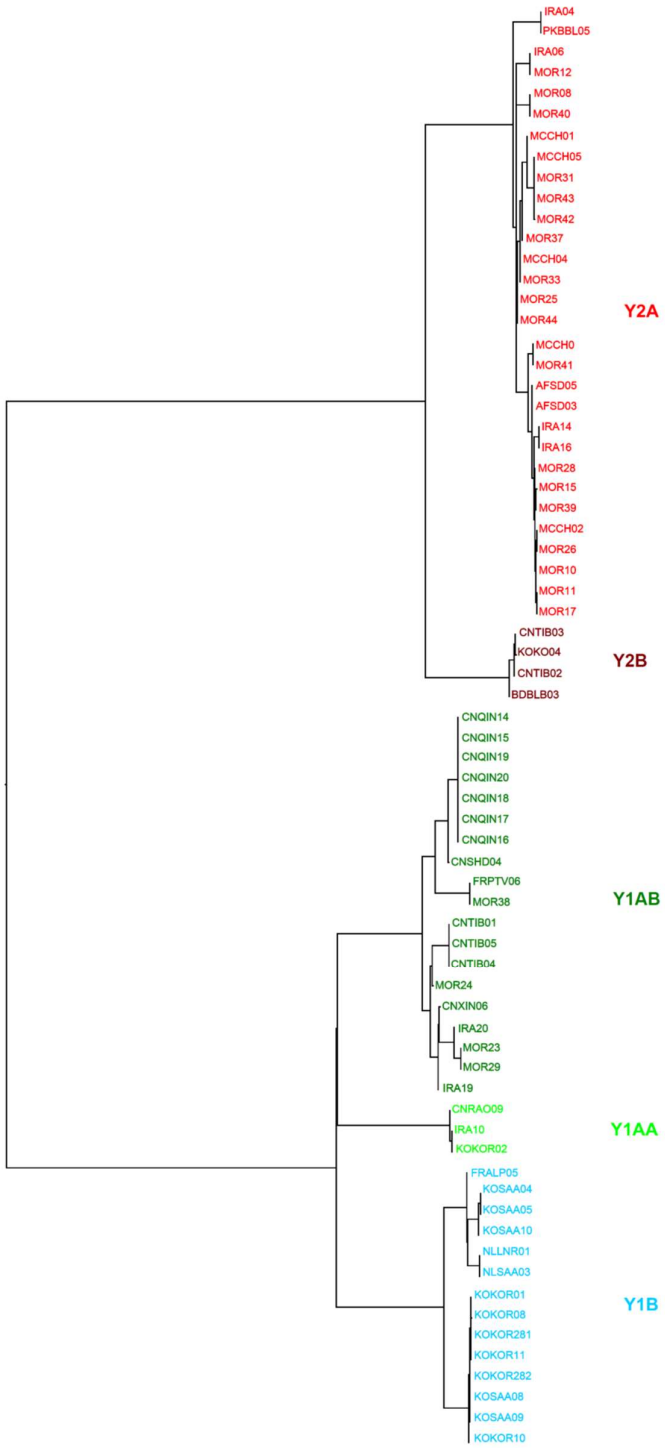
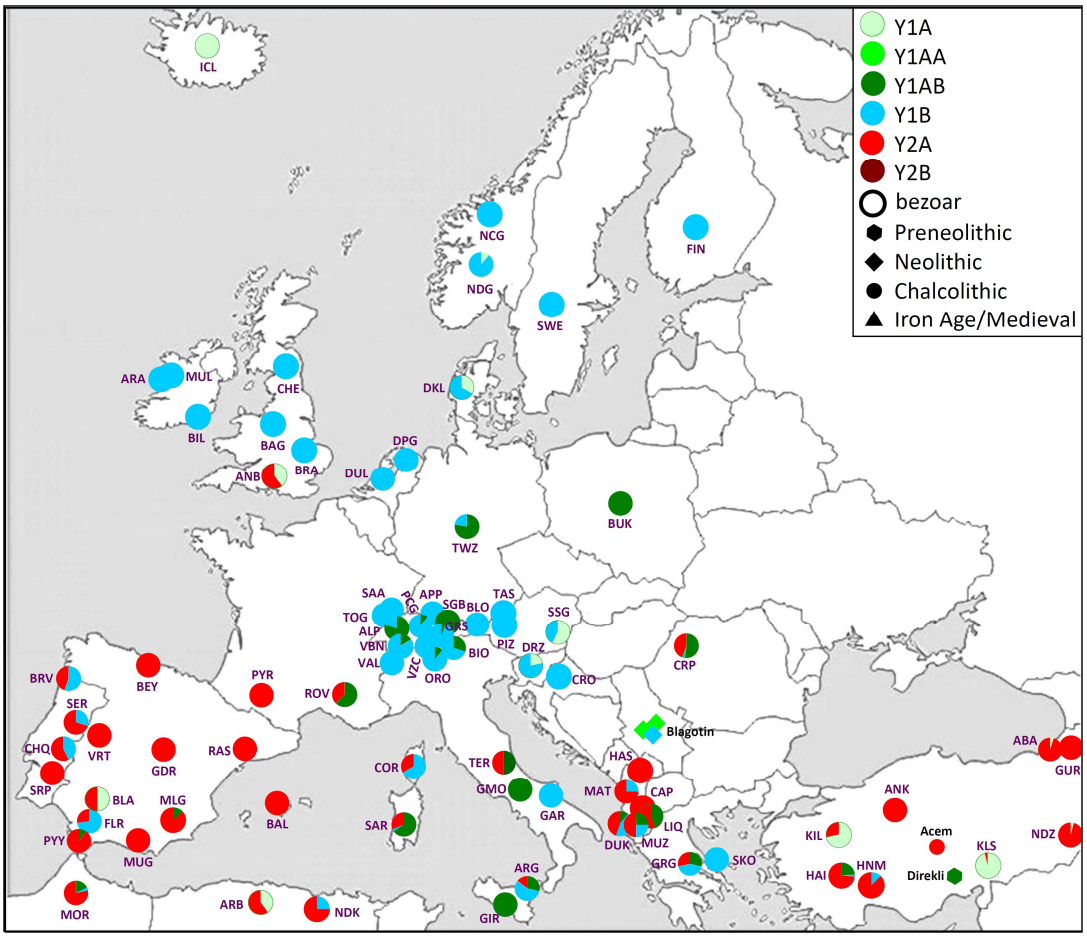
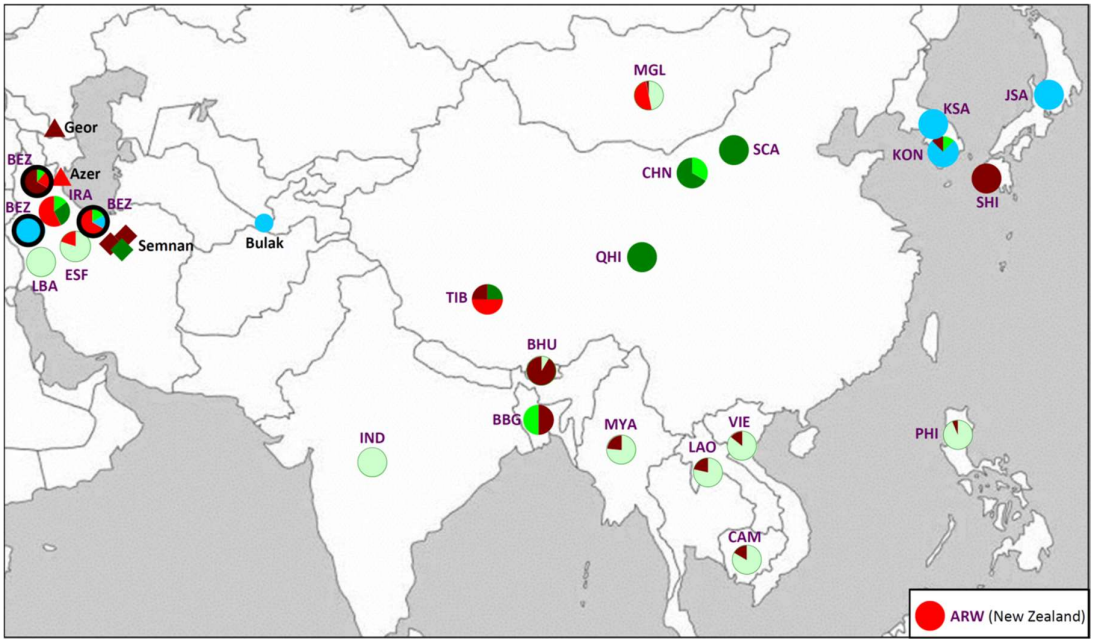


Fig. 1. Neighbor-joining tree of allele-sharing distances calculated on the basis of 2350 hemizygous male-specific SNPs extracted from WGS of 70 male goats (Table 3) and the markhor sequence as an outgroup. AFSD, Sudan; BDBLB, Black Bengal; CNQIN, Qinghai; CNRAO, Henan Raoshan White; CNSHD, Shandong Yimeng Black; CNTIB, Tibetan; CNXIN, Xinjiang; FRALP, French Alpine; FRPTV, Poitou; IRA, Iran; KOKOR, Korea native; KOSAA, Korean Saanen; MOR, Morocco; NLLNR, Dutch Landrace; NLDSA, Dutch Saanen; PKBBL, Pakistan Beetal Black.

(A)

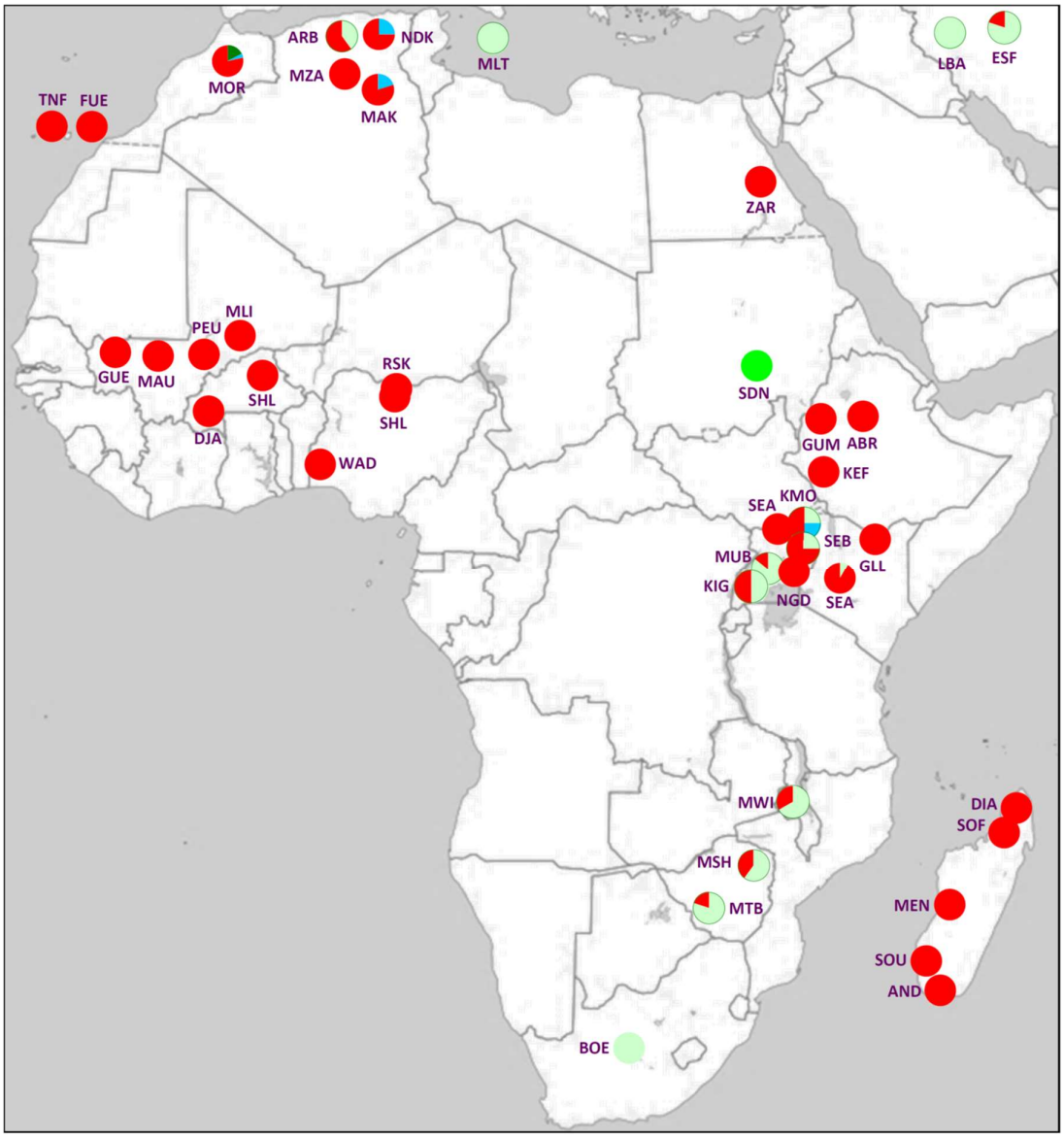


(B)



446 **(C)**

447



448 **Fig. 2.** Haplogroup distributions of **(A)** European breeds; **(B)** Asian breeds; **(C)** African
449 breeds; **(A, B)**, European and Asian ancient DNA samples; and **(B)** Iranian bezoars. Breeds
450 represented by a single goat are not plotted or are combined with other breeds from the same
451 country as indicated in Table 4. Breed codes: ABA, Abaza; ALP, Alpine; ANB,
452 AngloNubian; AND, Androy; ANK, Angora;Ankara; APP, Appenzell; ARA, Arabia; ARG,
453 Argentata dell'Etna; ARR, Arran; ARW, Arapawa; BAG, Bagot; BAL, Balearic; BBG, Black
454 Bengal; BEY, Bermeya; BHU, Bhutan; BIO, Bionda dell'Amadello; BLA, Blanca Andaluzza;
455 BLB, Bilbery; BLO, Blobe; BOE, Boer; BRA, British Alpine; BRV, Bravia; BUK, Polish
456 Fawn Colored; CAM, Cambodja; CAP, Capore; CHN, North China (Xinjiang, Henan
457 Raoshan White, Shandong); CHQ, Charnequeira; CHV, Cheviot; COR, Corsican; CRO,
458 Croatian Spotted; CRP, Carpathian; DIA, Diana; DJA, Djallonke; DKL, Danish Landrace;
459 DPG, Dutch Pied Goat; DRZ, Dreznica; DUK, Dukati; DUL, Dutch Nordic Goat; ESF,
460 Esfahan; ETH, Ethiopian (Abergelle, Gumez, Keffa); FIN, Finnish; FLR, Florida; FUE,
461 Fuenteventura (Ajuy, Majorera); GAL, Galla; GAR, Garganica; GDR, Guadarrama; GGT,
462 Girgentata; GMO, Grigia Molisana; GRG, Greek; GRS, Grisons Striped; GUE, Guéra; GUR,
463 Gurcu; HAI, Hair; HAS, Hasi; HNM, Honamli; IND, Indian; IRA, Iranian; JPA, Shjiba; JSA,
464 Japanese Saanen; KIG, Kigezi; KIL, Kil; KLS, Kilis; KMO, Karamonja; KON, Korean
465 Native; KSA, Korean Saanen; LAO, Laos; LBA, Lori-Bakhtiari; lCL, Icelandic; LIQ,
466 Liqenasi; MAK, Makatia; MAT, Mati; MAU, Maure; MEN, Menabe; MGL, Mongolian;
467 MLG, Malagueña; MLI, Naine, Soudanaise Targui; MLT, Maltese; MLW, Malawi (Balaka-
468 Ulonge, Dedza;Lilongwe; MOR, Moroccan; MSH, Mashona; MTB, Matebele; MUB,
469 Mubende; MUG, Murciano Granadina; MUL, Mulranny; MUZ, Muzhake; MYA, Myanmar;
470 MZA, M'Zabite; NCG, Norwegian Coastal; NDG, Norwegian Dairy; NDZ, Norduz; NGD,
471 Nganda; NKA, Naine de Kabylie; ORO, Orobica; PCG, Peacock; PEU, Peulh; PHI,
472 Philippines; PIZ, Pinzgauer; PYR, Pyrenean; PYY, Payoya; QHI, Qinhai; RAS, Rasquera;
473 ROV, Rove; RSK, Nigerian Maradi (Red Sokoto); SAA, Saanen; SAR, Sarda; SCA, Shaanbe
474 Cashmere; SDN, Sudan; SEA, Small East African (Kenya, Uganda); SEB, Sebei; SRP,
475 Serpentina; SER, Serrana; SGB, St Gallen Booted; SHL, Shahel; SHL, Nigerian Sahel; SKO,
476 Skopelos; SOF, Sofia; SOU, Southwest; SSG, Steirische Schecken; TAS, Tauernschecken;
477 TER, Teramo; TIB, Tibetan; TNF, Tinerfena (Norte, Sud); TOG, Toggenburg; TWZ,
478 Thuringian Forest; VAL, Valdostana; VBN, Valais Blackneck; VIE, Vietnam; VRT, Verata;
479 VZC, Verzasca; WAD, West African Dwarf; ZAR, Zaraiba.

480

Table 3. Codes and SRA accession numbers of WGS data used for Fig. 1.

code [1]	our code	SRA accession	breed	haplogroup	reference
BDCH03	BDBLB03	SRX2982563	Black Bengal	Y2B	[1]
CNNCH04	CNSHD04	SRX2982510	Shandong Yimeng black	Y1AB	[1]
CNNCH06	CNXIN06	SRX2982522	Xinjiang	Y1AB	[1]
CNNCH14	CNQIN14	SRX2982537	Qinghai	Y1AB	[1]
CNNCH15	CNQIN15	SRX2982502	Qinghai	Y1AB	[1]
CNNCH16	CNQIN16	SRX2982503	Qinghai	Y1AB	[1]
CNNCH17	CNQIN17	SRX2982504	Qinghai	Y1AB	[1]
CNNCH18	CNQIN18	SRX2982511	Qinghai	Y1AB	[1]
CNNCH19	CNQIN19	SRX2982507	Qinghai	Y1AB	[1]
CNNCH20	CNQIN20	SRX2982487	Qinghai	Y1AB	[1]
CNSCH09	CNRAO09	SRX2982486	Raoshan Henan	Y1AA	[1]
CNTCH01	CNTIB01	SRX2982520	Tibetan	Y1AB	[1]
CNTCH02	CNTIB02	SRX2982521	Tibetan	Y2B	[1]
CNTCH03	CNTIB03	SRX2982513	Tibetan	Y2B	[1]
CNTCH04	CNTIB04	SRX2982514	Tibetan	Y1AB	[1]
CNTCH05	CNTIB05	SRX2982515	Tibetan	Y1AB	[1]
FRCH06	FRPTV06	SRX2982542	Poitou	Y1AB	[1]
NLCH01	NLLNR01	SRX2982482	Dutch Landrace	Y1B	[1]
NLCH03	NLDSA03	SRX2982490:	Dutch Saanen	Y1B	[1]
PKCH05	PKBBL05	SRX2982568	Beetal Black	Y2A	[1]
SDCH03	AFSD03	SRX5417024	Sudan	Y2A	[1]
SDCH05	AFSD05	SRX5417026	Sudan	Y2A	[1]
FRCH05	FRALP05	SRX2982481	Alpine	Y1B	[1]
	KOSAA04	ERX2360419	Korean Saanen	Y1B2	[2]
	KOSAA05	ERX2360420	Korean Saanen	Y1B2	[2]
	KOSAA08	ERX2360423	Korean Saanen	Y1B	[2]
	KOSAA09	ERX2360424	Korean Saanen	Y1B	[2]
	KOSAA10	ERX2360425	Korean Saanen	Y1B2	[2]
	KOKOR01	ERX2360430	Korean Saanen	Y1B	[2]
	KOKOR02	ERX2360431	Korean Saanen	Y1AA	[2]
	KOKOR08	ERX2360437	Korean Saanen	Y1B	[2]
	KOKOR10	ERX2360439	Korean Saanen	Y1B	[2]
	KOKOR11	ERX2360440	Korean Saanen	Y1B	[2]
	KOKOR281	ERX2360442	Korean Saanen	Y1B	[2]
	KOKOR282	ERX2360443	Korean Saanen	Y1B	[2]
	KOKOR04	ERX2360445	Korean Saanen	Y2B	[2]
IRCH04	IRA04	ERX286352	Iran	Y2A	[3]
IRCH06	IRA06	ERX286345	Iran	Y2A	[3]
IRCH10	IRA10	ERX286355	Iran	Y1AA	[3]
IRCH14	IRA14	ERX286363	Iran	Y2A	[3]
IRCH16	IRA16	ERX286347	Iran	Y2A	[3]
IRCH19	IRA19	ERX313213	Iran	Y1AB	[3]
IRCH20	IRA20	ERX313216	Iran	Y1AB	[3]

MCCH01	MOR01	ERX194212	Moroccan	Y2A	[3]
MCCH02	MOR02	ERX194211	Moroccan	Y2A	[3]
MCCH03	MOR03	ERX204035	Moroccan	Y2A	[3]
MCCH04	MOR04	ERX204033	Moroccan	Y2A	[3]
MCCH05	MOR05	ERX204019	Moroccan	Y2A	[3]
MCCH08	MOR08	ERX204026	Moroccan	Y2A	[3]
MCCH10	MOR10	ERX204034	Moroccan	Y2A	[3]
MCCH11	MOR11	ERX204027	Moroccan	Y2A	[3]
MCCH12	MOR12	ERX207043	Moroccan	Y2A	[3]
MCCH15	MOR15	ERX208812	Moroccan	Y2A	[3]
MCCH17	MOR17	ERX220684	Moroccan	Y2A	[3]
MCCH23	MOR23	ERX272615	Moroccan	Y1AB	[3]
MCCH24	MOR24	ERX286410	Moroccan	Y1AB	[3]
MCCH25	MOR25	ERX286408	Moroccan	Y2A	[3]
MCCH26	MOR26	ERX286419	Moroccan	Y2A	[3]
MCCH28	MOR28	ERX286420	Moroccan	Y2A	[3]
MCCH29	MOR29	ERX286403	Moroccan	Y1AB	[3]
MCCH31	MOR31	ERX288658	Moroccan	Y2A	[3]
MCCH33	MOR33	ERX288657	Moroccan	Y2A	[3]
MCCH37	MOR37	ERX288652	Moroccan	Y2A	[3]
MCCH38	MOR38	ERX288656	Moroccan	Y1AB	[3]
MCCH39	MOR39	ERX288926	Moroccan	Y2A	[3]
MCCH40	MOR40	ERX291909	Moroccan	Y2A	[3]
MCCH41	MOR41	ERX306478	Moroccan	Y2A	[3]
MCCH42	MOR42	ERX306471	Moroccan	Y2A	[3]
MCCH43	MOR43	ERX313276	Moroccan	Y2A	[3]
MCCH44	MOR44	ERX286409	Moroccan	Y2A	[3]

[1] Z. Zheng & Y. Jiang, unpublished
[2] Kim et al. (2019) doi: 10.3389/fgene.2019.00699
[3] Alberto et al. (2018) doi: 10.1038/s41467-018-03206-y

Table 4. Haplogroup distributions in breeds or populations, in ancient DNA and in the bezoar. Kasp, Kasp (Kompetitive allele specific PCR assay); ddSeq, dideoxy sequencing. Codes starting with ERX or SRX codes are from the Short Reads Archive

					Y1A				
	Breed subpopulation	Method, ref., SRA code	code	N	Y1AA	Y1AB	Y1B	Y2A	Y2B
Europe									
Albania	Capore	ddSeq	CAP	9				9	
	Dukati	ddSeq	DUK	9		1	4	4	
	Hasi	ddSeq	HAS	7				7	
	Liqenasi	ddSeq	LIQ	9		4		5	
	Muzhake	ddSeq	MUZ	8		2	2	4	
	Mati	ddSeq	MAT	8			2	6	
Alp region	Alpine								
	Switzerland	ddSeq				12	3		
	Switzerland	Vidal				14	2		
	Germany	ddSeq				4	5		
	France	ddSeq				2	2		
	Italy	ddSeq				10			
	Austria	Kasp				5			
	Combined		ALP	59		47	12		
Austria	Blobe	Kasp	BLO	7			6		
	Pinzgauer	ddSeq	PIZ	6			6		
	Steirische Schecken	Kasp	SSG	7	4		3		
	Tauernschecken	ddSeq	TAS	6			6		
Croatia	Croatian Spotted	Kasp	CRO	5			5		
	Istrian	Kasp	IST	1			1		
Denmark	Danish Landrace	Kasp	DKL	3	1		2		
England	Bagot	Kasp	BAG	4			4		
	British Alpine	ERX2360400, ERX2360402	BRA	2			2		
	Cheviot	Kasp	CHV	7			7		
	AngloNubian								
	China	SRX5042650, SRX5042648, SRX5042661, SRX5042659[1]			2			2	
	Australia	ERX2360407[2]						1	
	Combined		ANB	5	2			3	
Finland	Finnish	Kasp	FIN	3			3		
France	Corsican	ddSeq	COR	9			6	3	
	Pyrenean	ddSeq	PYR	5				5	
	Rove	ddSeq	ROV	8		5		3	
Germany	Thuringian Forest	ddSeq	TWZ	9		7	2		
Greece	Greek	ddSeq	GRG	7		2	3	2	
	Skopelos	ddSeq	SKO	9			9		
Iceland	Icelandic Goat	Kasp	ICL	4	4				
Ireland	Arran	Kasp	ARR	4			4		
	Bilbery	Kasp	BLB	4			4		
	Mulranny	Kasp	MUL	11			11		
Italy	Argentata dell'Etna	ddSeq	ARG	7		2	4	1	
	Bionda dell'Amadello	ddSeq-, Kasp	BIO	10		3	7		
	Garganica	Vidal et al. 2017[4]	GAR	3			3		
	Girgentata	ddSeq	GGT	10		10			
	Grigia Molisana	ddSeq	GMO	2		2			
	Orobica	ddSeq	ORO	9		1	8		
	Sarda	ddSeq				5		4	
		Kasp						1	
		Vidal et al. 2017[4,5]				16	1	5	
		Combined	SAR	32		21	1	10	
	Teramo	Kasp	TER	2			1	1	
	Valdostana	ddSeq	VAL	9			9		
Malta	Maltese	Vidal et al. 2017[4]	MLT	3		3			

Netherlands	Dutch Nordic Goat	Kasp					20		
		SRX2982490[3]					1		
		Combined	DUL	21			21		
	Dutch Pied Goat	Kasp	DPG	5			5		
	Dutch Saanen	SRX2982490[3]	DSA	1			1		
Norway	Norwegian Dairy	Kasp	NDG	9	1		8		
	Norwegian Coastal	Kasp	NCG	6			6		
Poland	Polish Fawn Colored	ddSeq	BUK	7		7			
Portugal	Algarve	Pereira et al. 2009[6]	ALG	1				1	
	Bravia	Pereira et al. 2009[6]					8	6	
		ddSeq					3	3	
		Combined	BRV	20			11	9	
	Charnequeira	Pereira et al. 2009[6]	CHQ	8			3	4	
	Serpentina	Pereira et al. 2009[6]	SRP	7			7		
	Serrana	Pereira et al. 2009[6]	SER	14			14	33	
Romania	Carpathian	ddSeq				4		4	
		Vidal et al. 2017[4,5]				10	1	8	
		Combined	CRP	27		14	1	12	
Slovenia	Dreznica	Kasp	DRZ	14	3		11		
Spain	Balearic	Vidal et al. 2017[4]	BAL	25				25	
	Bermeya	Vidal et al. 2017[4]	BEY	9				9	
	Blanca Andaluzza	Vidal et al. 2017[4]	BLA	2	1			1	
	Florida	ddSeq, Kasp	FLR	11			8	3	
	Guadarrama	ddSeq						7	
		Vidal et al. 2017[4]						10	
		Combined	GDR	17				17	
	Malagueña	ddSeq				2		9	
		Vidal et al. 2017[4]						4	
		Combined	MLG	15		2		13	
	Murciano Granadina	Vidal et al. 2017[4]	MUG	23				23	
	Payoya	ddSeq	PYY	10		1		9	
	Rasquera	Vidal et al. 2017[4]	RAS	5				5	
	Verata	ddSeq	VRT	11				11	
Switzerland	Appenzell	Vidal et al. 2017[4]	APP	8			8		
	Grisons Striped	ddSeq				1	8		
		Vidal et al. 2017[4]					9		
		Combined	GRS	18		1	17		
	Peacock	ddSeq				2	9		
		Vidal et al. 2017[4]					9		
		Combined	PCG	20		2	18		
	Saanen	Vidal et al. 2017[4]	SAA	18			18		
	St Gallen Booted	ddSeq				12			
		Vidal et al. 2017[4,5]				9			
		Combined	SGB	21		21			
	Toggenburg	Vidal et al. 2017[4]	TOG	8			8		
	Valais Blackneck	ddSeq				4	12		
		Vidal et al. 2017[4]					9		
		Combined	VBN	25		4	21		
	Verzasca	Vidal et al. 2017[4]	VZC	8			8		
Asia									
Southeast Asia	Cambodja	Waki et al., 2015	CAM	36	30				6
	Myanmar	Waki et al., 2015	MYA	34	26				8
	Laos	Waki et al., 2015	LAO	14	11				3
	Vietnam	Waki et al., 2015	VIE	7	6				1
	Philippines	Waki et al., 2015	PHI	16	15				1
	Indian	Waki et al., 2015	IND	7	7				0
	Bhutan	Waki et al., 2015	BHU	24	2				22
Mongolia	Mongolian	Waki et al., 2015	MGL	32	15			16	1

Japan	Shjiba	Waki et al., 2015	JPA	11						11
	Saanen	Waki et al., 2015	JSA	30			30			
China	Qinhai	SRX2982487, SRX2982502, SRX2982503, SRX2982504, SRX2982507, SRX2982511, SRX2982537[3]	QHI	7		7				
	Tibetan	SRX1011417, SRX1011436, SRX1011437, SRX1011440, SRX1011441, SRX1011443, SRX1011672[7]				1			6	
		SRX2982520, SRX2982521, SRX2982513, SRX2982514, SRX2982515[3]				3			2	
		Combined	TIB	12		4		8		4
	Shaanbei Cashmere	SRX3472906, SRX3472909, SRX3472910, SRX3472913, SRX3472914	NCA	5		5				
	North China									
	Xinjiang	SRX2982522[3]				1				
	Henan Raoshan White	SRX2982486[3]			1					
	Shandong	SRX2982510[3]				1				
	Combined		CHN	3	1	2				
Bangladesh	Black Bengal	SRX5002284, SRX5057038, SRX5058418[8]			2					1
		SRX2982563[3]								1
		Combined	BBG	4	2					2
Iran	Iran	SRA (see Table 2)	IRA	7	1	2		4		
	Lori-Bakhtiari		LBA	10	10					
	Esfahan		ESF	10	8			2		
Pakistan	Beetal Black Pakistan	SRX2982568[3]	BBL	1				1		
South Korea	Korean Native	ERX2360430, ERX2360431, ERX2360437, ERX2360439, ERX2360440, ERX2360442, ERX2360443, ERX2360445[2]	KON	8	1		6			1
	Korean Saanen	ERX2360419, ERX2360420, ERX2360423, ERX2360424, ERX2360425[2]	KSA	5			5			
Turkey	Abaza	ddSeq						9		
		Cinar-Kul et al., 2015[9]			1			11		
		Combined	ABA	21	1			20		
	Angora									
	Turkey	Cinar-Kul et al., 2015[9]						31		
	Turkey	ddSeq						6		
	Turkey	Kasp						10		
	Combined	Combined	ANK	47				47		
	Gurcu	ddSeq						9		
		Cinar-Kul et al., 2015[9]						12		
		Combined	GUR	21				21		
	Hair	Cinar-Kul et al., 2015[1,9]				6	1	29		
		ddSeq				4		2		
		Combined	HAI	42		10	1	31		
	Honamli	Cinar-Kul et al., 2015[9]	HNM	24			3	21		
	Kil	Cinar-Kul et al., 2015[9]	KIL	7	5			2		
	Kilis	Cinar-Kul et al., 2015[9]			24			1		
		Kasp			2					
		Combined	KLS	27	26			1		
	Norduz	Combined	NDZ	24	1			23		
Africa										
Algeria	Arabia	Kasp	ARA	5	2			3		

	Makatia	Kasp	MAK	5			1	4	
	M'Zabite	Kasp	MZA	5				5	
	Naine de Kabylie	Kasp	NKA	4			1	3	
Burkina Fasso	Djallonke	Vidal et al. 2017	DJA	5				5	
	Shahel	Vidal et al. 2017	SHL	9				9	
Canadian Isles	Fuenteventura	Kasp							
	Ajuy							8	
	Majorera							11	
	Combined		FUE	19				19	
	Tinerfena	Kasp							
	Norte							7	
	Sud							8	
	Combined		TNF	15				15	
Egypt	Zaraiba	Vidal et al. 2017[4]	ZAR	15				15	
Ethiopia	Ethiopian	Kasp							
	Abergelle							10	
	Gumez							1	
	Keffa							1	
	Combined		ETH	12				12	
Kenya	Galla	Kasp	GAL	9				9	
Kenya, Uganda	Small East African	Kasp	SEA	12	1			11	
Madagascar	Androy	Kasp	AND	3				3	
	Diana	Kasp	DIA	6				6	
	Menabe	Kasp	MEN	3				3	
	Sofia	Kasp	SOF	6				6	
	Southwest	Kasp	SOU	6				6	
Mali	Guéra	Kasp	GUE	5				5	
	Maure		MAU	4				4	
	Naine+Soudanaise+Targui		MLI	4				4	
	Peulh		PEU	5				5	
Malawi	Malawi	Kasp							
	Balaka-Ulonge				1				
	Dedza				1				
	Lilongwe							1	
	Combined		MLW	3	2			1	
Morocco		SRA (see Table 2)				4		23	
		Pereira et al. 2009[6], Kasp				9	2	35	
		Combined	MOR	73		13	2	58	
Nigeria	Nigerian Maradi (Red Sokoto)	Kasp	RSK	11				11	
Nigeria	Nigerian Sahel	Kasp	SHL	12				12	
Nigeria	West African Dwarf	Vidal et al. 2017[4]						2	
		Kasp						13	
		Combined	WAD	15				15	
South Africa	Boer	Kasp, Var							
	Zimbabwe				5				
	Uganda				2				
	Combined		BOE	7	7				
Sudan	Sudan	SRX5417025, SRX5417026	SDN	2				2	
Uganda	Karamonja	Kasp	KMO	4	1		1	2	
	Kigezi	Kasp	KIG	2	1			1	
	Mubende	Kasp	MUB	7	6			1	
	Nganda	Kasp	NGD	2				2	
	Sebei	Kasp	SEB	4	1			3	
Zimbabwe	Mashona	Kasp	MSH	6	4			2	
	Matebele	Kasp	MTB	10	8			2	
New World									
New Zealand	Arapawa	Kasp	ARW	7				7	
all 132 extant domestic breeds or populations:				**1534**					
Ancient DNA		Daly et al. 2019[10]							
Turkey	Direkli 9500 BCE			1		1			
Serbia	Blagotin 6100 BCE			3	2		1		

Iran	Semnan 6000 BCE			3		1			2
Uzbekistan	Bulak 1850 BCE			1		1			
Turkey	Acem 1700 BC							1	
Azerbaijan	Azer 440 BCE			1				1	
Georgia	Geor 1000-1500			1					1
	all ancient			**10**					
Wild ancestor		Cumer, T., unpublished.							
	Bezoar								
	North Iran				1			2	6
	Central Iran						5		
	Iran, Caspian				1		1	4	
	Combined		BEZ	**20**	2		6	6	6

[1] Cao et al., 2019, doi.org/10.3389/fgene.2019.00145

[2] Kim et al., 2019, doi.org/10.3389/fgene.2019.00699

[3] Zheng & Jiang, unpublished

[4] Vidal et al., 2017, doi.org/10.1038/s41598-017-15593-1

[5] The absence of Y1AA in this breed has been inferred from dideoxy sequencing and/or WGS data for samples from the same breed

[6] Pereira et al., doi.org/10.1093/molbev/msp200

[7] Wu et al., 2019, doi.org/10.1101/743955

[8] Siddiki et al., 2019, doi.org/10.1186/s13104-019-4400-3

[9] Cinar-Kul, 2015, doi.org/10.1111/jbg.12154

[10] Daly et al., 2018, doi.org/10.1126/science.aas9411

Table 5. Primers for amplification and dideoxy sequencing of DBY, SRY and ZFY fragments and genomic coordinates of sequence covered by the sequence reads excluding the primer sequences.

Primer	Primary PCR	Nested PCR with M13 tags	Coverage
M13F		TGTAAAACGACGGCCAGT	
M13R		AGGAAACAGCTATGACCAT	
DBY1F	AGCAGTTTGGRTCTCGWGA	M13F-GTGTGTATAATATAGSATTTCAG	NW_017189685.1: 43044-43499
DBY1R	CCAACGACTATGWCCACT	M13R-GTAACCTTCAAAGATGCTAGT	
SRY2F	GACTGAGTGACTAAACTGAACTG	M13F-TAAAGGTTCTTATCTTCCC	NW_017189563.1: 277335-278711; 278905-280806
SRY2R	TATACTGAGCCACTTCAAAGCA	M13R-TGGAGAAAATTGAAAAGTAAGG	
SRY3F	AGCCTTTGAAGTTTCTACTGTC	M13F-ACAATATACAGTTATTACTCCCA	
SRY3R	CCCCAATACCTCCCCTCAATAC	M13R-CAGAATTTGTGAAGGCGC	
SRY4F	GTCTGCTGCACCTTCATC	M13F-AAATAACTTCACAATGACACCT	
SRY4R	CTTATTGTGGCCCAGGCTTGTC	M13R-TGTGAGCGGCTTAATTGGCTT	
SRY5F	CCGGGCTATAAATATCGACCTC	M13F-CCACAGAAATCGCTTGATGC	
SRY3R	GATGAAACCTTGGGTCTCACAG	M13R-CAGAATTTGTGAAGGCGC	
SRY6F	CTCACAAATTCATGGTACAGAG	M13F-GAAAAAACCTCGTACTTGGA	
SRY6R	GATCTTGTTTATCCCATCCC	M13R-GCCACATAGTCTGAATAGG	
ZFY1F	CAGGTGAGGGCACATGAG	M13F-GCTCTCAGAAGAAATTCCAGTA	NW_017189885.1: 10983-12149
ZFY1R	ATCACATTCGATGGCCTTC	M13R-GATTGTGTAAACTTATCTTCTT	
ZFY2F	ATATGCTTGAAGAGACGACAAC	M13F-TTCATTTGATCACTCATGCTC	
ZFY2R	AGTCAGAAGACAAATGTCACA	M13R-TATGGATTCGCATGTGCTT	