

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

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44

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46 **introgression**

47

48 **Abstract**

49

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

71

72 **1. Introduction**

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74 Because of its absence or recombination, the male part of the mammalian Y-chromosomes
75 is by far the longest haplotype that is stably transmitted across generations (Hughes et al.,
76 2015). Together with its inheritance from father to son, it is a highly informative marker for
77 the paternal origin of species, populations or individuals with a much stronger
78 phylogeographic differentiation than observed for mitochondrial or autosomal DNA. The
79 highly informative Y-chromosomal markers are now widely exploited in population-genetic
80 studies of humans (Jobling and Tyler-Smith, 2017; Kivisild, 2017), cattle (Edwards et al.,
81 2011; Xia et al., 2019), horse (Wallner et al., 2017; Wutke et al., 2018; Felkel et al., 2019a)
82 water buffalo (Zhang et al., 2016), sheep (Meadows and Kijas, 2009; Zhang et al., 2014),
83 camel (Felkel et al., 2019b), pigs (Guirao-Rico et al., 2018) and dogs (Natanaelsson et al.,
84 2006; Oetjens et al., 2018).

85

86 A preliminary analysis of the Y-chromosomal diversity in European and Turkish goats
87 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

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

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 98

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

105

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

106

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

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

115

116 **2. Methods**

117

118 **2.1 WGS data, filtering and tree construction.**

119

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

129

130 **2.2 Haplogroups in 132 goat breeds.**

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

- 134 (1) From the goat panel collected for the Econogene project, DNA samples of 353 male goats
135 from 38 European or southwestern Asian breeds were analyzed by PCR amplification and
136 dideoxy-sequencing of segments within the *DBY*, *SRY* and *ZFY* genes (Lenstra and
137 Econogene Consortium, 2005) as described previously for bovine samples (Nijman et al.,
138 2008; Edwards et al., 2011) and using the primers listed in Table 5.
- 139 (2) We used published data for 90 goats from 5 Portuguese breeds or from Morocco (Pereira
140 et al., 2009), for 211 goats from 10 Asian breeds (Waki et al., 2015), for 181 goats from 8
141 Turkish breeds (Cinar Kul et al., 2015) and for 270 goats from 26 Spanish or Swiss breeds
142 (Vidal et al., 2017).
- 143 (3) 362 DNA samples (57 breeds) from several sources, including the AdaptMap panel (Colli
144 et al., 2018) were genotyped by the KASP assay (Table 4).
- 145 (4) For 90 goats from 15 breeds genotypes were obtained by BLAST searching of the Short-
146 Read Archive (SRA).

147

148

149

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

151

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

152

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

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

162

163 **3. Results and Discussion**

164

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

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

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

181 - Haplogroup Y2B is absent in Europe, Africa and west Asia, but became a major haplotype
182 in east Asia and southeast Asian, where Y2A is not represented. In contrast, it is observed in
183 ancient goat from Medieval Georgia and Neolithic Iran (ca. 6,000 BCE), supporting an origin
184 of east Asian goat from regions east of Zagros Mountains.

185 - Y2A is in northern and central Europe only found in the crossbred AngloNubian (see
186 below), but is the predominant haplogroup in central, eastern and southern Africa.

187 - Haplogroup Y1B is predominant in northern Europe, but outside Europe and North African
188 has only been found in one Karamonja animal, in the Korean native breed and in exported

189 Saanen populations. The different Y2A and Y1B frequencies in north-central vs southern
190 Europe may reflect the Neolithic migrations following the Danube and the Mediterranean
191 routes, respectively (Cymbron et al., 2005; Tresset and Vigne, 2007; Rivollat et al., 2015)
192 with the strongest bottlenecks along the northernmost migrations.

193 - Y1AA is sporadic in Europe and has been observed also in Neolithic Serbia (ca. 6,000
194 BCE), but is present in Asia (Fig. 3).

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

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

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

207

208 **Conflict of Interest**

209

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

212

213 **Authors' contributions**

214

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

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231

232 **Availability of data**

233 The SRA data are in the public domain.

234 **Members of the Econogene Consortium:**

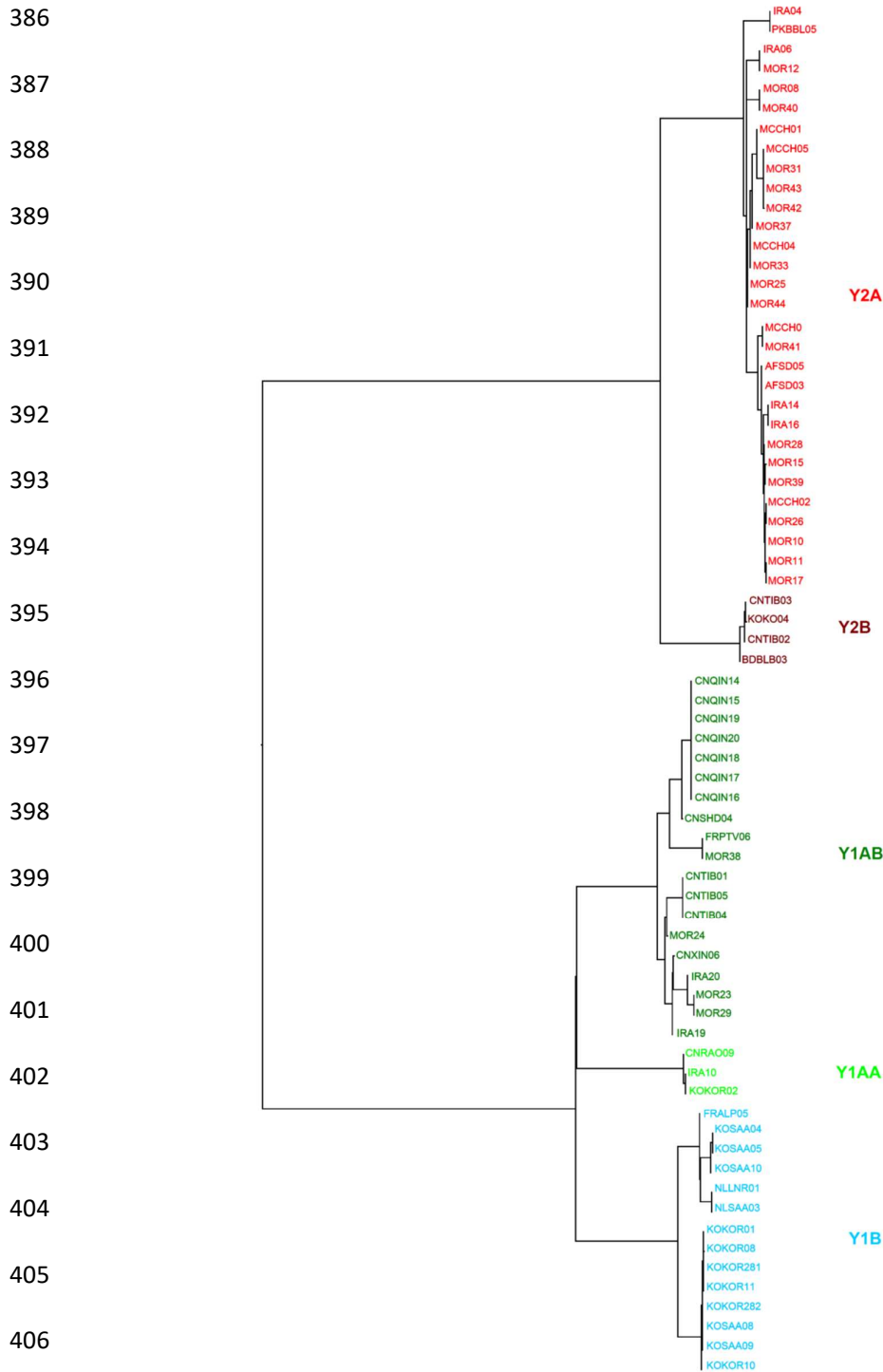
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385



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

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415 (A)

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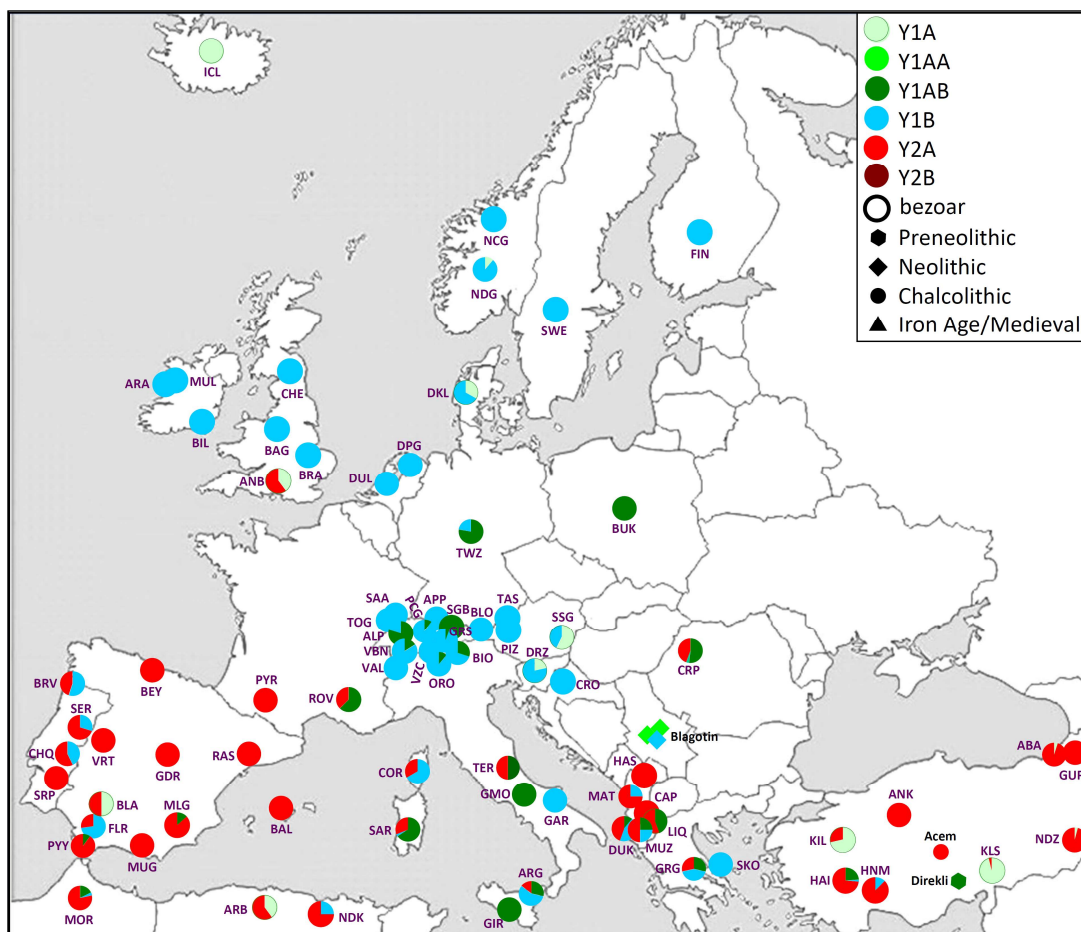
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433 (B)

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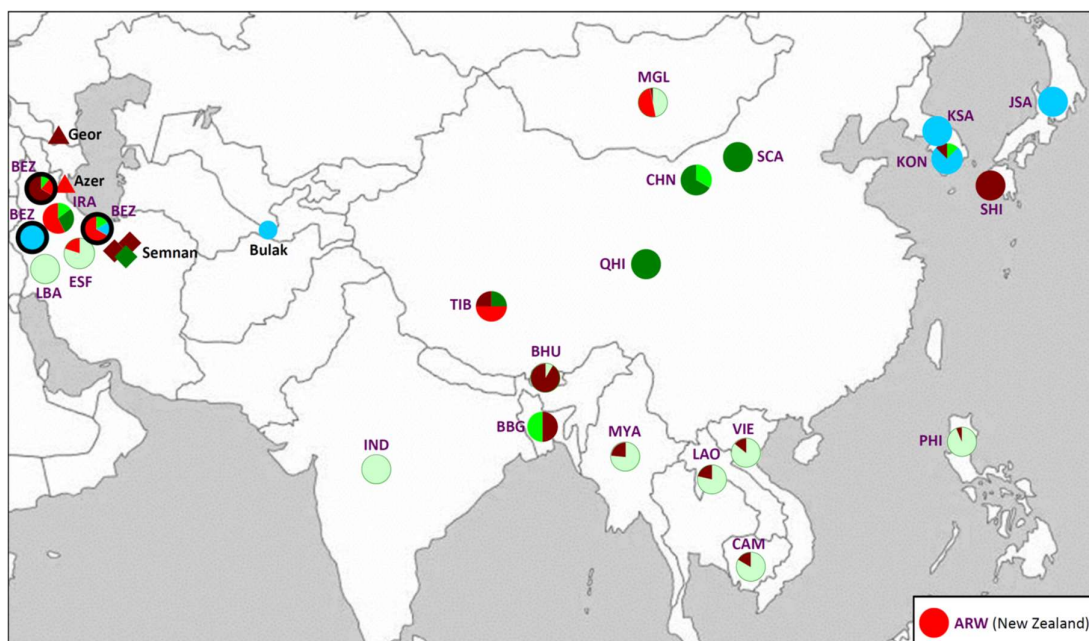
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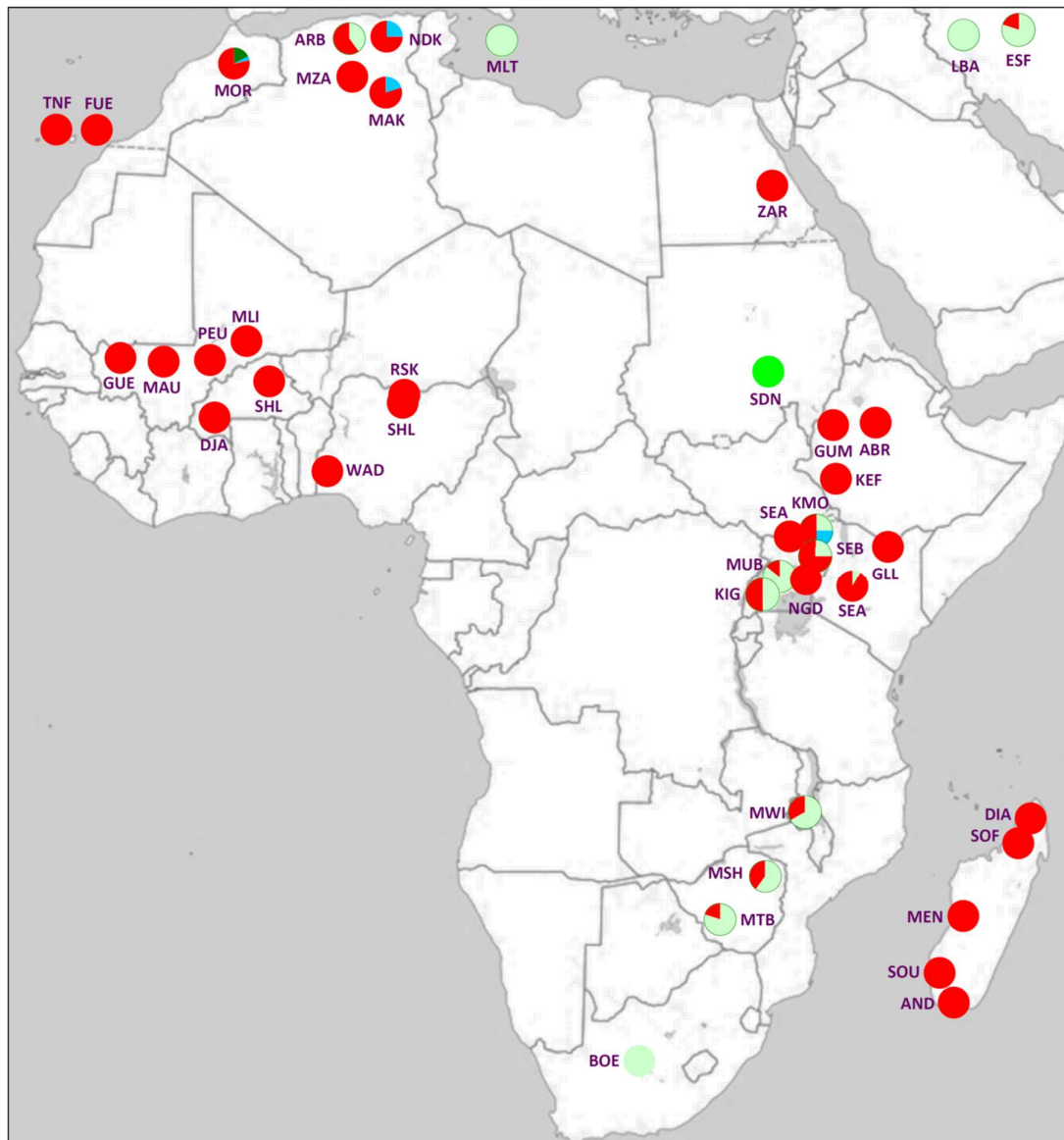
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446 (C)

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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; ICL, 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.

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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

	Breed subpopulation	Method, ref., SRA code	code	N	Y1A				
					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 SRX2982490 ³ Combined	DUL	21		20 1			
	Dutch Pied Goat	Kasp	DPG	5			21 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 ddSeq Combined				8 3	6 3		
		Charnequeira	Pereira et al. 2009 ⁶	BRV	20			11	9
		Serpentina	Pereira et al. 2009 ⁶	CHQ	8			3	4
	Serrana	Pereira et al. 2009 ⁶	SRP	7			7		
			Pereira et al. 2009 ⁶	SER	14			14	33
Romania	Carpathian	ddSeq				4		4	
		Vidal et al. 2017 ^{4,5} Combined				10	1	8	
			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 Vidal et al. 2017 ⁴ Combined						7 10	
			GDR	17					17
		Malagueña	ddSeq Vidal et al. 2017 ⁴ Combined				2	4	
			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 Grisons Striped	Vidal et al. 2017 ⁴ ddSeq	APP	8			8		
		Vidal et al. 2017 ⁴ Combined				1	8 9		
			GRS	18		1		17	
	Peacock	ddSeq Vidal et al. 2017 ⁴ Combined					2	9 9	
			PCG	20		2		18	
	Saanen St Gallen Booted	Vidal et al. 2017 ⁴ ddSeq	SAA	18				18	
		Vidal et al. 2017 ^{4,5} Combined					12	9	
			SGB	21		21			
	Toggenburg Valais Blackneck	Vidal et al. 2017 ⁴ ddSeq	TOG	8			4	12	8
		Vidal et al. 2017 ⁴ Combined						9	
			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 Saanen	Waki et al., 2015 Waki et al., 2015	JPA JSA	11 30				30		11
China	Qinhai Tibetan Shaanbei Cashmere North China Xinjiang Henan Raoshan White Shandong Combined	SRX2982487, SRX2982502, SRX2982503, SRX2982504, SRX2982507, SRX2982511, SRX2982537 ³ SRX1011417, SRX1011436, SRX1011437, SRX1011440, SRX1011441, SRX1011443, SRX1011672 ⁷ SRX2982520, SRX2982521, SRX2982513, SRX2982514, SRX2982515 ³ Combined SRX3472906, SRX3472909, SRX3472910, SRX3472913, SRX3472914 SRX2982522 ³ SRX2982486 ³ SRX2982510 ³ Combined	QHI TIB NCA CHN	7 12 5 1 3 3		7 1 3 1 1			30	11
Bangladesh	Black Bengal	SRX5002284, SRX5057038, SRX5058418 ⁸ SRX2982563 ³ Combined	BBG	4		2 2				1 1 2
Iran	Iran Lori-Bakhtiari Esfahan	SRA (see Table 2)	IRA LBA ESF	7 10 10		1 10 8	2			4 2
Pakistan	Beetal Black Pakistan	SRX2982568 ³	BBL	1						1
South Korea	Korean Native Korean Saanen	ERX2360430, ERX2360431, ERX2360437, ERX2360439, ERX2360440, ERX2360442, ERX2360443, ERX2360445 ² ERX2360419, ERX2360420, ERX2360423, ERX2360424, ERX2360425 ²	KON KSA	8 5		1		6		1
Turkey	Abaza Angora Gurcu Hair Honamli Kil Kilis Norduz	ddSeq Cinar-Kul et al., 2015 ⁹ Combined Cinar-Kul et al., 2015 ⁹ Turkey Turkey ddSeq Turkey Kasp Combined ddSeq Cinar-Kul et al., 2015 ⁹ Combined Cinar-Kul et al., 2015 ^{1,9} ddSeq Combined Cinar-Kul et al., 2015 ⁹ Cinar-Kul et al., 2015 ⁹ Cinar-Kul et al., 2015 ⁹ Kasp Combined Combined	ABA ANK GUR HAI HNM KIL KLS NDZ	1 21 47 21 42 24 7 27 24		1 1 6 4 10 5 26 1			9 11 20 31 6 10 47 9 12 21 29 2 31 21 2 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				1		
	Balaka-Ulonge					1		
	Dedza					1		
	Lilongwe					1		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				5		
	Zimbabwe					2		
	Uganda		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	1			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-GTGTGTATAATATAGSATTTTCAG	NW_017189685.1:
DBY1R	CCAACGACTATGWCCACT	M13R-GTAACCTTCAAAGATGCTAGT	43044-43499
SRY2F	GACTGAGTGACTAAACTGAACTG	M13F-TAAAGGTTCTTATCTTCCC	
SRY2R	TATACTGAGCCACTTCAAAGCA	M13R-TGGAGAAAATTGAAAAGTAAGG	
SRY3F	AGCCTTTGAAGTTTCTACTGTC	M13F-ACAATATACAGTTATTACTCCCA	
SRY3R	CCCAATACCTCCCCTCAATAC	M13R-CAGAATTTGTGAAGGCGC	
SRY4F	GTCTGCTGCACCTTCATC	M13F-AAATAACTTCACAATGACACCT	NW_017189563.1:
SRY4R	CTTATTGTGGCCAGGCTTGTC	M13R-TGTGAGCGGCTTAATTGGCTT	277335-278711;
SRY5F	CCGGGCTATAAATATCGACCTC	M13F-CCACAGAAATCGCTTGATGC	278905-280806
SRY3R	GATGAAACCTTGGGTCTCACAG	M13R-CAGAATTTGTGAAGGCGC	
SRY6F	CTCACAAATTCATGGTACAGAG	M13F-GAAAAACCTCGTACTTGGA	
SRY6R	GATCTTGTTTATCCCATCCC	M13R-GCCACATAGTCTGAATAGG	
ZFY1F	CAGGTGAGGGCACATGAG	M13F-GCTCTCAGAAGAAATTCAGTA	
ZFY1R	ATCACATTCGATGGCCCTTC	M13R-GATTGTGTAACCTTATCTTCTT	NW_017189885.1: 10983-12149
ZFY2F	ATATGCTTGAAGAGACGACAAC	M13F-TTCATTTGATCACTCATGCTC	
ZFY2R	AGTCAGAAGACAAATGTCACA	M13R-TATGGATTCGCATGTGCTT	