Novel and known signals of selection for fat deposition in domestic sheep breeds from Africa and Eurasia

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31   **Short title:** Selection signatures for fat deposition in sheep

32

Abstract

34   Genomic regions subjected to selection frequently show signatures such as within-

35   population reduced nucleotide diversity and outlier values of differentiation among differentially

36   selected populations. In this study, we analyzed 50K SNP genotype data of 373 animals belonging

37   to 23 sheep breeds of different geographic origins using the Rsb and F_{ST} statistical approaches, to

38   identify loci associated with the fat-tail phenotype. We also checked if these putative selection

39   signatures overlapped with regions of high-homozygosity (ROH). The analyses identified novel

40   signals and confirmed the presence of selection signature in genomic regions that harbor candidate

41   genes known to affect fat deposition. Several genomic regions that frequently appeared in ROH

42   were also identified within each breed, but only two ROH islands overlapped with the putative

43   selection signatures. The results reported herein provide the most complete genome-wide study of

44   selection signatures for fat-tail in African and Eurasian sheep breeds; they also contribute insights

45   into the genetic basis for the fat tail phenotype in sheep, and confirm the great complexity of the

46   mechanisms that underlie quantitative traits, such as the fat-tail.

47

Introduction

49   Natural selection plays an important role in determining the individuals that are best adapted

50   to novel and existing environmental conditions. Besides natural selection, artificial selection has

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51   been widely applied to livestock species to achieve more desirable/profitable phenotypes [1]. For

52   instance, sheep (*Ovis aries*) have been selected since domestication, approximately 9,000 years ago

53   [2]. This process of selection resulted in divergent sheep breeds, reared in different geographic

54   regions due to their different adaptability. Among these, fat-tail are an important class of sheep

55   breeds and represent about 25% of the world's sheep population [3] mainly distributed in the

56   Middle East, North and East Africa and Central Asia. According to Xu et al. [4] fat tails represent

57   the energy reserve necessary to survive critical conditions such as drought seasons and food

58   shortage. This statement being emphasized by Mwacharo et al. [5] who confirmed that the fat-tails

59   are the predominant sheep across the deserts of northern Africa, and in the highlands, semi-arid and

60   arid environments of eastern and southern Africa while the thin-tails occur in Sudan and in the sub-

61   humid and humid regions of West Africa.

62   The unique genetic patterns inscribed in the genome of individuals by natural and/or

63   artificial selection are defined as signatures of selection, which are usually regions of the genome

64   that harbor functionally important sequence variants [6]. Although human consumption of animal

65   fat has dramatically reduced in preference of leaner meat, the investigation of the potential

66   candidate genes involved in the fat-tail might contribute to exploring the genetics of fat deposition,

67   energy storage and adaptation to climate changes [7-9]. With the aim to identify candidate genes

68   with a potential role in these traits, several authors performed studies targeting the fat-tail

69   phenotype contrasted with the thin-tail one. All authors used, for their comparisons, sheep of the

70   same geographic regions to prevent referring to the fat-tail differentiation signals arising from

71   different origins or isolation by distance. These studies included indigenous Chinese [4,8,10,11],

72   Mediterranean-North African [9,12], Iranian [3] and Ethiopian breeds [13]. Similarly, in this study,

73   the genomes of fat-tail sheep from different regions of Africa and Eurasia were contrasted with the

74   genomes of thin-tail sheep of the same geographical area. In order to improve the specificity of

75   signal detection, we combined two complimentary approaches (Rsb and F_{ST}); moreover, as

76   distinguishing false positive genes from candidate genes is not straightforward, selection signatures

77 of fat-tail were considered only when shared by two or more fat-tail breeds of different geographic

78 origin, and substantiated by verifying whether the candidate genes in proximity of the anonymous

79 markers of differentiation have a known, or assumed, role in fat deposition and adipogenesis in

80 mammals.

81

Materials and Methods

Samples, genotyping and quality control

84 A total of 373 animals belonging to 23 sheep breeds from different geographic regions were

85 selected (Table 1). For all the animals, genotype data from the Illumina OvineSNP50 BeadChip

86 array were collated for the analysis. Chromosomal coordinates for each SNP were obtained from

87 the latest release of the ovine genome sequence assembly Oar_v4.0. The dataset was filtered to

88 remove animals with more than 10% missing genotypes, SNPs with a call rate lower than 95% and

89 with a minor allele frequency (MAF) lower than 1%, and to exclude non-autosomal and unassigned

90 markers.

91

Genetic relationships amongst breeds

93 Pair-wise genetic relationships were estimated using identity-by-state genetic distances

94 calculated with PLINK 1.7 [14] and graphically represented by multidimensional scaling (MDS)

95 analysis.

96

Signatures of selection analysis

98 To analyze genome-wide selection signatures, the MDS results were used to categorize the

99 23 breeds into contrasting genetic groups for comparative analysis. Table 1 summarizes the

100 description of the breeds used in the pair-wise comparisons. The contrasting groups were as follow:

4

101   1. Ethiopian fat-tail breeds (11 breeds) vs. two thin-tail breeds from Sudan (Hammari and

102   Kabashi);

103   2. Ethiopian long fat-tail breeds (6 breeds) vs. the two thin-tail breeds from Sudan;

104   3. Arabian peninsula fat-tail (Naimi, Najdi, Omani and Huri) vs. the two thin-tail breeds from

105   Sudan;

106   4. Barbaresca vs. two Italian thin-tail breeds (Sardinian and Comisana);

107   5. Laticauda vs. the two Italian thin-tail breeds;

108   6. Libyan Barbary vs. Algerian Sidaoun.

109   Inter-population analyses of the six fat- vs. thin-tail groups (Table 1) were performed using

110 the Extended Haplotype Homozygosity (EHH) – derived statistic Rsb [15], as in Bahbahani et al.

111 [16-17]. To identify statistically significant SNPs under selection in each of the six pair-wise

112 comparisons (positive Rsb value), one-sided P-values (fat- vs. thin-tail group) were derived as

113 $-\log10(1-\Phi(Rsb))$, where $\Phi(Rsb)$ represents the Gaussian cumulative distribution function. Inter-

114 population genome-wide F_{ST} and χ^2 analysis were also performed to corroborate the results obtained

115 with the Rsb analysis. The following constraints were introduced to define the fat-tail selection

116 signatures: 1) $-\log10$ (P-value) ≥ 3.2, equivalent to a P-value of 0.0005, was used as a threshold to

117 define significant Rsb; 2) candidate regions were retained if at least two SNPs, separated by ≤200

118 Kb, passed this threshold; 3) the candidate region was present in two or more pair-wise

119 comparisons.

120

Runs of homozygosity

122   Runs of homozygosity (ROHs) were estimated for each individual using PLINK 1.7 [14].

123 The minimum length that constituted the ROH was set to one Mb. The following criteria were also

124 used: (i) one missing SNP was allowed in the ROH, and up to one possible heterozygous genotype;

125 (ii) the minimum number of SNPs that constituted the ROH was set to 30; (iii) the minimum SNP

126 density per ROH was set to one SNP every 100 kb; (iv) maximum gap between consecutive

127 homozygous SNPs of 1000 Kb. The percentage of SNP residing within an ROH for a given breed

128 was estimated by counting the number of times that each SNP appeared in a ROH and by dividing

129 that number by the number of animals in each breed, allowing us to obtain a locus homozygosity

130 range (from 0 to 1). To identify the genomic regions of "high homozygosity", also called ROH

131 islands, the top 0.9999 SNPs of the percentile distribution of the locus homozygosity range within

132 each breed were selected.

133

Gene annotation

135 Candidate regions identified by different approaches were used to annotate genes, that were

136 either entirely or partially included within each selected region, using the NCBI Genome Data

137 Viewer (https://www.ncbi.nlm.nih.gov/genome/gdv/browser/?context=gene&acc=101104604).

138 Finally the biological functions of each annotated gene within the selection signatures was

139 investigated via a comprehensive search of literature.

140

Results

142 After quality control, 43,224 SNPs and 349 animals (6 to 39 per breed) were retained for the

143 analyses (Table 1). To examine and visualize the genetic relationships among the 23 sheep breeds,

144 we used a MDS plot of the pairwise identity-by-state distance. The results showed that most sheep

145 breeds formed non-overlapping clusters and were clearly separate populations (Fig 1). The first

146 dimension (C1) separated the Italian breeds from the Arabian Peninsula and African ones, likely

147 reflecting different breeding histories. The second dimension (C2) distinguished Barbaresca from

148 the other breeds. Therefore, with the exception of Barbaresca, the MDS grossly separated the breeds

149 according to their genetic origin and/or to geographical proximity between their breeding areas. The

150 Ethiopian breeds were separated into two groups: one including the three fat-rumped breeds and one

6

151 short fat-tail (Molale), and one group including the long fat-tail breeds and the other short fat-tail

152 breed (Gafera). Noteworthy, the MDS plot did not separate the breeds on the basis of the different

153 tail phenotypes.

154

155 **Fig 1. Genetic relationships among the 23 sheep breeds defined through multidimensional**

156 **scaling analysis**

157

158 In this study, selection signatures for fat-tail were identified using the *Rsb* approach, after

159 corroboration with F_{ST} approach. The markers with a significant inter-population *Rsb* are shown in

160 S1-S6 Tables, corresponding to the six comparisons described in the Material and methods.

161 Likewise, in S7-S12 Tables, genome-wide F_{ST} and χ^2 values, with the corresponding Bonferroni

162 corrected χ^2 *P*-values, are shown. A summary of the number of significant SNPs obtained with the

163 different statistical methods in the six pair-wise comparisons is reported in Table 2.

164 The genome-wide Manhattan plots where significant signals of differentiation between the fat-tail

165 breed/group and the thin-tail of the corresponding region were shared by two or more fat-tail

166 breed/group are reported in S1-S14 Figs. The y axis shows the probability of *Rsb* values for each

167 marker across the genome ($-\log 10(1-\Phi(Rsb))$). Below each plot, the positions of the significant

168 SNPs, with their corresponding probability values, are reported for each fat-tail breed/group. F_{ST}

169 values and Bonferroni corrected χ^2 *P*-values are reported only when achieved by significant SNPs

170 located in the candidate region, or at distance $\leq$ 0.2 Mb up- and down-stream of the candidate

171 region boundaries.

172 The majority of shared fat-tail signals were observed for the two groups of Ethiopian breeds

173 on chromosomes (OAR) 5, 6, 10, 18 and 19 (S3, S5, S9, S13 and S14 Figs, respectively) and by the

174 two breeds of Barbary sheep origin (Laticauda and Libyan Barbary) on OAR 3, 10, 12, 13 (S2, S9,

175 S10 and S11 Figs, respectively). It is interesting to note that all the regions shown in S1-S14 Figs

176 registered the presence of at least one marker attaining highly significant *Rsb* values, i.e. > 4,

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177   equivalent to a *P*-value of 0.0001. Moreover, in all the regions, except the one on OAR12 that is

178   shared between Laticauda and Libyan Barbary (S10 Fig), at least one significant $\chi 2$ value was also

179   registered in either one or both of the fat-tail breed/groups.

180   Several genomic regions that frequently appeared in a ROH were identified within each

181   breed (S15 and S16 Figs, for fat- and thin-tail sheep breeds, respectively). Table 3 provides the

182   chromosome position, and the start and end of the ROH islands. The top 0.9999 SNPs of the

183   percentile distribution of locus homozygosity values led to the use of different thresholds for each

184   breed (from 0.11 to 0.83), and a total of 15 genomic regions of high-homozygosity across breeds

185   were identified. Although the distribution of the ROH was relatively balanced and the signals were

186   moderate in height, we found a few outstanding peaks with a high occurrence of ROH, especially in

187   the Barbaresca breed (S15 Fig).

188

Discussion

190   In studies aiming to detect genomic signals for specific traits, for instance signals directly

191   associated with fat deposition and adipogenesis, the major drawback is to detect strong differences

192   (viz. between fat-tail and thin-tail breeds) that are due either to different origins or to reproductive

193   isolation, and not obviously involved in the trait (fat deposition). In this work, the fat-tail breeds

194   from Ethiopia, Algeria, Arabian peninsula and southern Italy were pair-wise compared with their

195   thin-tail counterparts from the closest geographical region. The signals that are detected between

196   any two or more simultaneous pair-wise comparisons might consequently be considered more

197   reliable, also because they are shown by geographically distant sheep breeds. While the fat-tail

198   sheep of Algeria, Arabian peninsula and southern Italy were all long or semi-long fat-tail breeds,

199   the Ethiopian fat-tail breeds included long-tail, short-tail and fat-rumped sheep breeds (Table 1).

200   Therefore, for the Ethiopian sheep, two different pair-wise comparisons were performed, the first

201   including all the 11 fat-tail breeds, the second including only the 6 long fat-tail breeds. The

202 assumption here was that the first comparison might elucidate the genes involved with

203 adipogenesis, irrespective of the shape of the tail, while the second comparison would reveal

204 findings that are more comparable to those observed in the breeds from the other regions, and are

205 therefore possibly more likely to be linked to the fat-tail phenotype.

206 We used two different, but complementary, statistical approaches to identify putative

207 selection signatures across the phenotypically different breeds. The F_{ST} index of differentiation is

208 among the most widely used statistic to detect signals of selection in differentially-selected

209 populations, where usually a locus is putatively considered under differential selection if its pair-

210 wise F_{ST} has a rank percentile value of 0.01 or less. Because the level of genetic differentiation

211 between each pair of breeds/groups of the six comparisons highly varied, the decision "*a priori*" of

212 a rank percentile to accept significant F_{ST} may disfavor the pairs presenting the highest genetic

213 diversity. Therefore, following Moioli et al. [12] who showed that F_{ST} and $\chi 2$ are highly correlated,

214 in order to confirm with a statistical test which markers were significant, we calculated inter-

215 population locus-specific $\chi 2$ values and considered significant the markers reaching a Bonferroni-

216 adjusted $\chi 2$ P-values ≤ 0.05. Doing so, the different numbers of significant markers in each pair-

217 wise comparison allows to appreciate their global genetic difference. However, since F_{ST} and χ^2

218 values are based on allele frequencies and might represent an isolated event occurring by chance,

219 and not necessarily associated with fat-tail signals, in this case, the extended haplotype

220 homozygosity derived statistic, *Rsb*, was preferentially used. This statistic in fact considers the

221 whole haplotype region around one marker, or group of markers, and the larger is the region in

222 which the homozygous haplotype was maintained in the first breed in contrast with the second

223 breed, the more reliable is the probability of carrying a fat-tail signal. The number of significant

224 SNPs for inter-population *Rsb* is smaller than the number of significant SNPs for χ^2 (Table 2)

225 confirming that the first method is more stringent. In most cases, the number of SNPs that are

226 significant with one method showed some correlation with the number of SNPs that were obtained

227 with the second method: the higher was the number of the significant *Rsb* values, the higher was

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228 also the number of significant F_{ST} values. The highest number of significant signals obtained with

229 both methods was observed in the Barbaresca breed – 1.5 % for inter-population Rsb and 5.6 % for

230 F_{ST}/χ^2, while the lowest number was in the Arabian peninsula breeds: 0.15 and 0.25% with the two

231 methods, respectively. In accordance with our results, Yuan et al. [11], in a selection signature

232 analysis for tail type in sheep, identified seven and twenty-six regions using the extended haplotype

233 homozygosity and F_{ST} approaches, respectively, and only six small regions using both approaches.

234 Bahbahani et al. [18] showed that the two common approaches (inter-population Rsb and F_{ST}), used

235 to identify signatures of positive selection in East African Shorthorn Zebu, did not produce

236 overlapping signals. Although the authors interpreted the observed absence of overlaps between Rsb

237 and F_{ST} analyses as a possible consequence of the selection time-scale, with Rsb being considered

238 more suitable for detecting signatures of recent selection, it may also be hypothesized that false

239 positives may occur when using both Rsb and F_{ST}. As the aim of this study was to identify loci most

240 likely associated with fat-tail, we established that the candidate region(s) should be present in two

241 or more pair-wise comparisons (Table 4). Therefore only the signatures satisfying these criteria and

242 encompassing annotated genes will be subsequently discussed.

243   Another method for detecting signatures of positive selection based on intra-population

244 analysis is the identification of high-homozygosity regions [6]. Since ROHs are normally abundant

245 in regions under positive selection, their accumulation at specific loci, or islands, has been used to

246 identify genomic regions that reflect directional selection in cattle [19], sheep [20], horse [21] and

247 goat [22]. We therefore checked if such regions of high-homozygosity overlapped with putative

248 selection signatures in the sheep breeds considered in this study.

249   The region in OAR3:104.2-105.9 Mb (S1 Fig and Table 4) was identified in two

250 comparisons: fat-tail sheep of the Arabian peninsula vs. Sudanese thin-tail sheep, and Libyan

251 Barbary vs. Algerian Sidaoun. Out of the ten genes found in this region, only *ANAPC1* has been

252 associated with obesity-related traits by Comuzzie et al. [23] in a Genome-Wide Association Study

253 (GWAS) on Hispanic children. The signature on OAR3:154.0-155.6 Mb (S2 Fig and Table 4),

254 detected in the Laticauda and the Libyan Barbary breeds, had already been reported for the

255 Barbaresca, Laticauda and Chios breeds [9]. Yuan et al. [11], in a GWAS on seven indigenous

256 Chinese sheep, by contrasting fat-tail versus thin-tail phenotypes, detected a signature in this region

257 encompassing the *MSRB3*, that has been identified as a candidate gene associated with adaptation

258 [24]. In a study on world sheep breeds, *MSRB3* was highlighted to have experienced high selection

259 pressure [25]. However, Yuan et al. [11] warned on the possibility of distinguishing, through

260 GWAS, false positive genes from candidate genes. On the other hand, Wei et al. [10] analyzed

261 Chinese native sheep by contrasting thin-tail (Tibetan group) and fat-tail (Mongolian and Kazakh

262 group) types and suggested that the genes encoded by the signal on OAR3, *i.e. MSRB3* and *LEMD3,*

263 would be best considered as candidates for ear size. This hypothesis is supported by the fact that

264 *MSRB3* and *LEMD3* were identified as candidate genes for ear morphology in dogs [26] and pigs

265 [27]. Therefore, despite these genes having not been associated with the ear size [28], doubts on

266 ascribing this signal to the fat-tail are obvious. A large region on OAR5:47.0-49.0 Mb (S3 Fig and

267 Table 4) turned out here to encode putative fat deposition genes in the two groups of Ethiopian

268 sheep: the one composed only by the long fat-tail, and the one including all the eleven Ethiopian

269 fat-tail breeds. Although Fariello et al. [29] reported that this region encoded a signature

270 differentiating prolific and non-prolific Asian sheep, the involvement of a signature in this region in

271 the fat-tail phenotype had been previously reported [9,12]. This involvement is corroborated by

272 genetic studies of body mass index in humans, describing a role played in obesity by the *CXXC5*

273 gene in Americans [30] and the *PSD2* gene in the Japanese population [31]. Moreover, this

274 selection signature overlapped with the ROH island identified in the Ethiopian fat-tail breeds, which

275 include 17 and 29 homozygous markers respectively for the two groups of breeds (the eleven

276 Ethiopian fat-tail, and the six Ethiopian long fat-tail). The signal on OAR6:38.1-39.6 Mb (S4 Fig

277 and Table 4) was detected in Barbaresca and Laticauda and was previously reported as selection

278 signature for fat-tail in these two breeds, also when compared with 13 Italian thin-tail breeds [9]. It

279 includes the *SLIT2* gene, a potential candidate for internal organ weights in Simmental beef cattle

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280   [32] and therefore possibly connected with fat deposition. This signal is worth investigating further,

281   because it encompasses a large region (1.5 Mb) where the Barbaresca showed 27 SNP markers with

282   allele frequency patterns that are highly differentiated from the Italian thin-tail breeds, 15 of which

283   exceeded the significant threshold of *Rsb* *P*-value < 0.0001. Moreover, this genomic region partially

284   overlapped with the ROH island on OAR6 detected in Barbaresca and shared by more than 80% of

285   the individuals of this breed. The Laticauda showed less significant signals in the same region, with

286   the exception of a highly significant one (-log10(*P*-value) = 7.68) at position 38,345,613 bp.

287   Moreover, several markers attained high F_{ST} values and significant $\chi2$ values in the pair-wise

288   comparisons of both breeds. However, because the two breeds have Barbary origin, it is also

289   possible that this signature encodes loci inherited from North-African breeds. The selection

290   signature on OAR6:55.6-55.7 Mb (S5 Fig and Table 4) was shown in this study to be present in the

291   two groups of Ethiopian breeds; it has never been reported before as a fat-tail signal and the only

292   gene included in the region (*DTHD1*) does not appear to have any connection with fat deposition.

293   On the same chromosome, at position 76.5-77.5 Mb (S6 Fig and Table 4), we identified another

294   signal in the Ethiopian group (eleven breeds) and the Laticauda, which has been reported previously

295   in the Barbaresca but not in the Laticauda [9]. Although the thin-tail breeds analyzed in the

296   aforementioned study for the pair-wise comparison with the Barbaresca and the Laticauda were not

297   the same as those used here, and the methodology used to detect the signatures was also different, it

298   is likely that this is merely a suggestive fat-tail signal. Moreover, for the only annotated gene in this

299   region (*ADGRL3*), to the best of our knowledge, no association with adipogenesis has been

300   reported. Another candidate region identified on OAR6:80.6-81.0 Mb (S7 Fig and Table 4), shown

301   by the Ethiopian group (eleven breeds) and the Libyan Barbary and including the *EPHA5* gene, was

302   also detected in a GWAS for wool production traits in a Chinese Merino sheep population and

303   reported to be significantly associated with fiber diameter [33]. Moreover, it has been identified

304   through GWAS as a candidate gene for feed conversion ratio in Nellore cattle [34]. The signal on

305   OAR7:33.5-33.9 Mb (S8 Fig and Table 4) was detected in the Barbaresca and Laticauda, as well as

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306 in a previous study [9]. While these authors could not assign an obvious role of any of the genes

307 located in this region, Lirangi et al. [35] suggested that the *CHP1* gene is involved in cellular fat

308 storage. Inoue et al. (2014) revealed that *OIP5* promotes proliferation of pre- and mature-adipocytes

309 and contributes adipose hyperplasia; moreover, an increase of *OIP5* may associate with

310 development of obesity. A common candidate region located on OAR10:40.2-45.0 Mb (S9 Fig and

311 Table 4) observed in the two groups of Ethiopian sheep, Libyan Barbary and Laticauda, includes

312 the *PCDH9* gene. The same signature was detected by Kim et al. [37] who contrasted the Egyptian

313 Barki sheep with British breeds, and referred to it as signal of adaptation to arid environments.

314 However, the Barki is a fat-tail sheep while the British are all thin-tail breeds. We would then

315 propose the idea that this is a signal of fat-deposition, this being corroborated by the presence of

316 *PCDH9*, reported by Wang et al. [38] as a candidate gene for obesity in humans. The signal on

317 OAR12:43.0-43.3 Mb, shared by the Laticauda and the Libyan Barbary (S10 Fig and Table 4) has

318 not been reported previously as a fat-tail signal and the two genes (*RERE* and *SLC45A1*) included in

319 the region do not appear to have any connection with fat deposition. *RERE* has been identified as

320 candidate for embryonic growth and reproductive development, whereas *SLC45A1* plays an

321 important role in immunity related to tropical adaptation [39]. On OAR13:45.5-48.4 Mb, a selection

322 signature shared by the Laticauda and the Libyan Barbary was identified (S11 Fig and Table 4). The

323 region was also reported as a fat-tail signature in several studies [9-11]. The strong linkage

324 disequilibrium between the SNPs in this OAR13 region with a missense mutation in exon 1 of the

325 *BMP2* gene (OAR13:48,552,093-48,897,111 bp) was demonstrated by Moioli et al. [12] in the

326 Laticauda fat-tail and Altamurana thin-tail sheep. Yuan et al. [11] emphasized that *BMP2* may play

327 important roles in fat tail formation. However, here *BMP2* does not appear to be the only candidate

328 gene. This signature spans a size > 3Mb, and Laticauda showed a very high *Rsb* value (-log10-

329 Pvalue=7.96) at position 46,582,744 bp. A transcriptome profile analysis of adipose tissues from

330 fat- and short-tailed Chinese sheep identified *CDS2* among the differentially expressed genes [40].

331 This gene which spans 46,560,029 to 46,605,239 bp of OAR13, encompasses the significant marker

332 mentioned above. Another candidate region on OAR17:61.0-61.6 Mb, shared by the Ethiopian

333 group (eleven breeds) and the Libyan Barbary (S12 Fig and Table 4) has not been detected

334 previously as a fat-tail signal in sheep. However, Fox et al. [41] associated the *OAS2* gene found in

335 this region to body fat distribution. Finally, the candidate regions on OAR18:1.8-2.2 Mb, and

336 OAR19:51.6-51.8 Mb, shared by the two groups of Ethiopian breeds (S13 and S14 Figs,

337 respectively) have not been reported previously as fat-tail signals and the five genes included in the

338 two regions (*ATP10A* on OAR18, and *CDC25A, MAP4, DHX30, SMARCC1* on OAR19) do not

339 appear to have any obvious connection with fat deposition. However, other studies also reported

340 genes mapped in the same two regions with no obvious roles in sheep tail type or fat deposition

341 [3,11]. The complexity of the fat-tail phenotype [10] may partly justify the high number of signals

342 detected in the pair-wise comparisons.

343 As reported above, only two ROH islands identified in fat-tail breeds overlapped with the

344 selection signatures. One reason for the little overlap is that ROH might detect selection related to

345 any trait, while contrasting thin and fat tail breeds is more likely to detect signal related to this trait.

346 However, Purfield et al. [20] reported a significant moderate correlation between the occurrence of

347 SNPs in a ROH and two different statistical approaches (F_{ST} and HapFLK) for identifying putative

348 selection signatures, and showed two ROH islands that overlapped with selection signatures.

349 Moreover, the ROH island on OAR5 identified in the Ethiopian breeds was also identified in the

350 Lori Bakhtiari fat-tail breed [10]. The authors reported that this increase in homozygosity would be

351 consistent with selection for mutations affecting fat-tail size several thousand years following

352 domestication. Therefore, although the existence of ROH islands has been attributed to several

353 factors (recombination events, demography) [42], our results corroborate the hypothesis that regions

354 of high-homozygosity may indeed harbor targets of positive selection, as also observed in previous

355 studies [20,22,43].

356 In this study, we report so far the most complete genome-wide study of selection signatures

357 for fat-tail in sheep. We identified novel signals and confirmed the presence of selection signatures

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358   in the genomic regions that harbor candidate genes that are known to affect fat deposition. These

359   findings also confirm the great complexity of the mechanisms underlying quantitative traits, such as

360   the fat-tail, and further confirm the hypothesis that many different genes are involved in the

361   phenotype. However, it is important to highlight that among the candidate genomic regions, false

362   positives may still be a possibility. Therefore, further studies using different populations and the

363   new ovine high-density SNP chip will be required to confirm and refine our results and investigate

364   the role of specific genes. Notwithstanding, the selection signatures reported here provide

365   comprehensive insights into the genetic basis underlining the fat tail phenotype in sheep.

366

Conflict of interest

368   The authors declare that they have no competing interests.

369

Data Availability Statement

371   This article reports no new genotyping data. All relevant data are within the paper and its

372   Supporting Information files.

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485   adaptation of goats. Genet Select Evol. 2018;50:59.

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487 **Table 1. Breeds, number of animals (N), tail type, country and origin of genotyping data of**

488 **the breeds used in the contrasting groups (fat- vs. thin-tail).**

Breed	N	Tail type	Country	Comparison	Data origin
Bonga	9	long fat-tail	Ethiopia	1, 2	[13]
Doyogena	15	long fat-tail	Ethiopia	1, 2	[13]
Gesses	10	long fat-tail	Ethiopia	1, 2	[13]
Kido	10	long fat-tail	Ethiopia	1, 2	[13]
Loya	15	long fat-tail	Ethiopia	1, 2	[13]
Shubi Gemo	15	long fat-tail	Ethiopia	1, 2	[13]
Kefis	14	rumped	Ethiopia	1	[13]
Arabo	10	rumped	Ethiopia	1	[13]
Adane	12	rumped	Ethiopia	1	[13]
Molale (Menz)	15	short fat-tail	Ethiopia	1	[13]
Gafera (Washera)	15	short fat-tail	Ethiopia	1	[13]
Huri	7	fat-tail	Arabian peninsula	3	[13]
Naimi	7	fat-tail	Arabian peninsula	3	[13]
Najdi	6	fat-tail	Arabian peninsula	3	[13]
Omani	10	fat-tail	Arabian peninsula	3	[13]
Barbaresca	30	fat-tail	Italy	4	[9]
Laticauda	24	fat-tail	Italy	5	[12]
Libyan Barbary	23	fat-tail	Algeria	6	[9]
Hammari	7	thin-tail	Sudan	1,2,3	[13]
Kabashi	8	thin-tail	Sudan	1,2,3	[13]
Sardinian	24	thin-tail	Italy	4,5	[12]
Comisana	24	thin-tail	Italy	4,5	[12]
Sidaoun	39	thin-tail	Algeria	6	This study

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492 **Table 2. Number of significant single nucleotide polymorphisms (SNPs) obtained with the two**

493 **selection signature approaches in the six pair-wise comparisons.**

Pair-wise comparison		No. significant SNPs	
Fat-tail group	Thin-tail group	Rsb $P<0.0005$	Bonferroni corrected $\chi2$ P-value ≤ 0.05
Ethiopian fat-tail	Hammary and Kabashi	99	754
Ethiopian long fat-tail	Hammary and Kabashi	106	1,114
Arabian peninsula fat-tail	Hammary and Kabashi	64	108
Barbaresca	Sardinian and Comisana	638	2,402
Laticauda	Sardinian and Comisana	158	328
Libyan Barbary	Sidaoun	185	302

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496 **Table 3. Run of homozygosity (ROH) islands identified within each breed**. The chromosome

497 (OAR), the number of single nucleotide polymorphisms (SNPs) within each ROH island and the

498 positions of the genomic regions (in base pairs, bp) are reported.

Breeds/groups	OAR	N of SNPs	Start (bp)	End (bp)
Ethiopian fat-tail (11 breeds)	5	17	48,278,057	49,199,542
	10	34	36,757,445	39,446,610
Ethiopian long fat-tail (6 breeds)	5	29	47,692,576	49,199,542
Arabian peninsula fat-tail	2	8	131,264,212	131,695,396
	2	11	135,482,289	136,005,787
	4	25	26,305,564	27,655,062
Barbaresca	6	48	34,851,127	38,495,020
Laticauda	3	7	13,571,685	13,899,340
Libyan Barbary	2	12	113,637,672	114,513,743
	7	76	94,404,153	98,581,328
Sudan (Hammary and Kabashi)	1	9	198,471,933	198,933,003
Sidaoun	2	5	38,190,022	38,368,173
	2	35	38,827,516	40,453,440
	13	17	35,563,319	36,504,021
Italian thin-tail (Comisana and Sardinian)	2	64	71,595,057	75,092,467

500 **Table 4. Candidate regions and genes identified in two or more pair-wise comparisons (see material and methods). Start/end positions are**

501 **based on the ovine genome sequence assembly Oar_v4.0**.

	Pair-wise comparison group						
	1	2	3	4	5	6	Genes
OAR	start/end (bp)	start/end (bp)	start/end (bp)	start/end (bp)	start/end (bp)	start/end (bp)	
3			104,333,496 105,210,346			104,291,439 105,909,563	ZNF2, ZNF514, MRPS5, MALL, NPHP1, ACOXL, BUB1, BCL2L11, ANAPC1, MERTK
3					154,458,718 156,011,304	155,014,204 155,055,875	MSRB3, WIF1, LEMD3, TBC1D30, GNS, RASSF3, TBK1, SRGAP1, TMEM5
5	482,26,104 48,526,532	46,925,830 49,273,852					EGR1, ETF1, HSPA9, CTNNA1, SIL1, MATR3, PAIP2, SPATA24, SLC23A1, PROB1, MZB1, DNAJC18, TMEM173, ECSCR, UBE2D2, CXXC5, PSD2, NRG2, PURA, IGIP, PFDN1, HBEGF, CYSTM1, SLC4A9, TMCO6, WDR55, HARS2, NDUFA2
6				38,104,576 39,576,650	38,179,178 39,639,829		TRNASTOP-UCA, LOC106991224
6	55,697,868 55,794,685	55,697,868 55,811,685					DTHD1
6	75,842,854 76,599,033				75,533,914 75,941,134		ADGRL3
6	80,325,742 80,531,786					80,878,591 80,912,095	EPHA5
10	40,258,505 45,063,369	40,594,254 45,416,672			40,957,582 45,416,672	42,194,236 45,155,143	PCDH9, LOC101121526, KLHL1
12					43,000,381 43,168,807	43,168,807 43,297,179	RERE, SLC45A1
13					46,565,715 49,137,513	47,583,113 49,208,171	CDS2, PROKR2, GPCPD1, CHGB, TRMT6, CRLS1, LRRN4, FERMT1, BMP2
17	61,094,671 61,631,272					61,496,170 61,658,381	OAS2, OAS1, RPH3, PTPN11, RPL6, HECTD4
18	1,895,285 2,129,462	1,980,832 2,243,903					ATP10A
19	51,617,073 51,789,681	51,649,648 51,819,178					MAP4, DHX30, SMARCC1

Supporting information

S1 Table. Significant markers for *Rsb* in Ethiopian fat-tail breeds (eleven breeds) contrasted with two thin-tail breeds from Sudan (Hammari and Kabashi).

S2 Table. Significant markers for *Rsb* in Ethiopian long fat-tail breeds (six breeds) contrasted with two thin-tail breeds from Sudan (Hammari and Kabashi).

S3 Table. Significant markers for *Rsb* in Arabian Peninsula fat-tail breeds (Naimi, Najdi, Omani and Huri) contrasted with two thin-tail breeds from Sudan (Hammari and Kabashi).

S4 Table. Significant markers for *Rsb* in Barbaresca fat-tail breed contrasted with two Italian thin-tail breeds (Sardinian and Comisana).

S5 Table. Significant markers for *Rsb* in Laticauda fat-tail breed contrasted with two Italian thin-tail breeds (Sardinian and Comisana).

S6 Table. Significant markers for *Rsb* in Libyan Barbary fat-tail breed contrasted with Sidaoun thin-tail breed.

S7 Table. Significant markers for F_{ST} / *χ2* in Ethiopian fat-tail breeds (eleven breeds) contrasted with two thin-tail breeds from Sudan (Hammari and Kabashi).

S8 Table. Significant markers for F_{ST} / *χ2* in Ethiopian long fat-tail breeds (six breeds) contrasted with two thin-tail breeds from Sudan (Hammari and Kabashi).

S9 Table. Significant markers for F_{ST} / *χ2* in the Arabian Peninsula fat-tail breeds (Naimi, Najdi, Omani and Huri) contrasted with two thin-tail breeds from Sudan (Hammari and Kabashi).

S10 Table. Significant markers for F_{ST} / *χ2* in Barbaresca fat-tail breed contrasted with two Italian thin-tail breeds (Sardinian and Comisana).

S11 Table. Significant markers for F_{ST} / *χ2* in Laticauda fat-tail breed contrasted with two Italian thin-tail breeds (Sardinian and Comisana).

527   **S12 Table. Significant markers for F_{ST} / $\chi2$ in Libyan Barbary fat-tail breed contrasted with**

528   **Sidaoun thin-tail breed.**

529   **S1 Fig. Manhattan plot of OAR 3 depicting signals of fat-tail shared between Arabian**

530   **Peninsula breeds (Naimi, Najdi, Omani and Huri) and Libyan Barbary.**

531   **S2 Fig. Manhattan plot of OAR 3 depicting signals of fat-tail shared between Laticauda and**

532   **Libyan Barbary.**

533   **S3 Fig. Manhattan plot of OAR 5 depicting signals of fat-tail shared between the two groups**

534   **of Ethiopian breeds.**

535   **S4 Fig. Manhattan plot of OAR 6 depicting signals of fat-tail shared between Barbaresca and**

536   **Laticauda.**

537   **S5 Fig. Manhattan plot of OAR 6 depicting signals of fat-tail shared between the two groups**

538   **of Ethiopian breeds.**

539   **S6 Fig. Manhattan plot of OAR 6 depicting signals of fat-tail shared between Ethiopian fat-**

540   **tail breeds and Laticauda.**

541   **S7 Fig. Manhattan plot of OAR 6 depicting signals of fat-tail shared between Ethiopian fat-**

542   **tail breeds and Libyan Barbary.**

543   **S8 Fig. Manhattan plot of OAR 7 depicting signals of fat-tail shared between Barbaresca and**

544   **Laticauda.**

545   **S9 Fig. Manhattan plot of OAR 10 depicting signals of fat-tail shared between the two groups**

546   **of Ethiopian breeds, Laticauda and Libyan Barbary.**

547   **S10 Fig. Manhattan plot of OAR 12 depicting signals of fat-tail shared between Laticauda and**

548   **Libyan Barbary.**

549   **S11 Fig. Manhattan plot of OAR 13 depicting signals of fat-tail shared between Laticauda and**

550   **Libyan Barbary.**

551   **S12 Fig. Manhattan plot of OAR 17 depicting signals of fat-tail shared between Ethiopian fat-**

552   **tail breeds and Libyan barbary**

553 **S13 Fig. Manhattan plot of OAR 18 depicting signals of fat-tail shared between the two**

554 **groups of Ethiopian breeds.**

555 **S14 Fig. Manhattan plot of OAR 19 depicting signals of fat-tail shared between the two**

556 **groups of Ethiopian breeds.**

557 **S15 Fig. Regions of homozygosity in the fat-tail group/breeds. The threshold used to detect**

558 **high-homozygosity regions is indicated with a black line.**

559 **S16 Fig. Regions of homozygosity in the thin-tail group/breeds. The threshold used to detect**

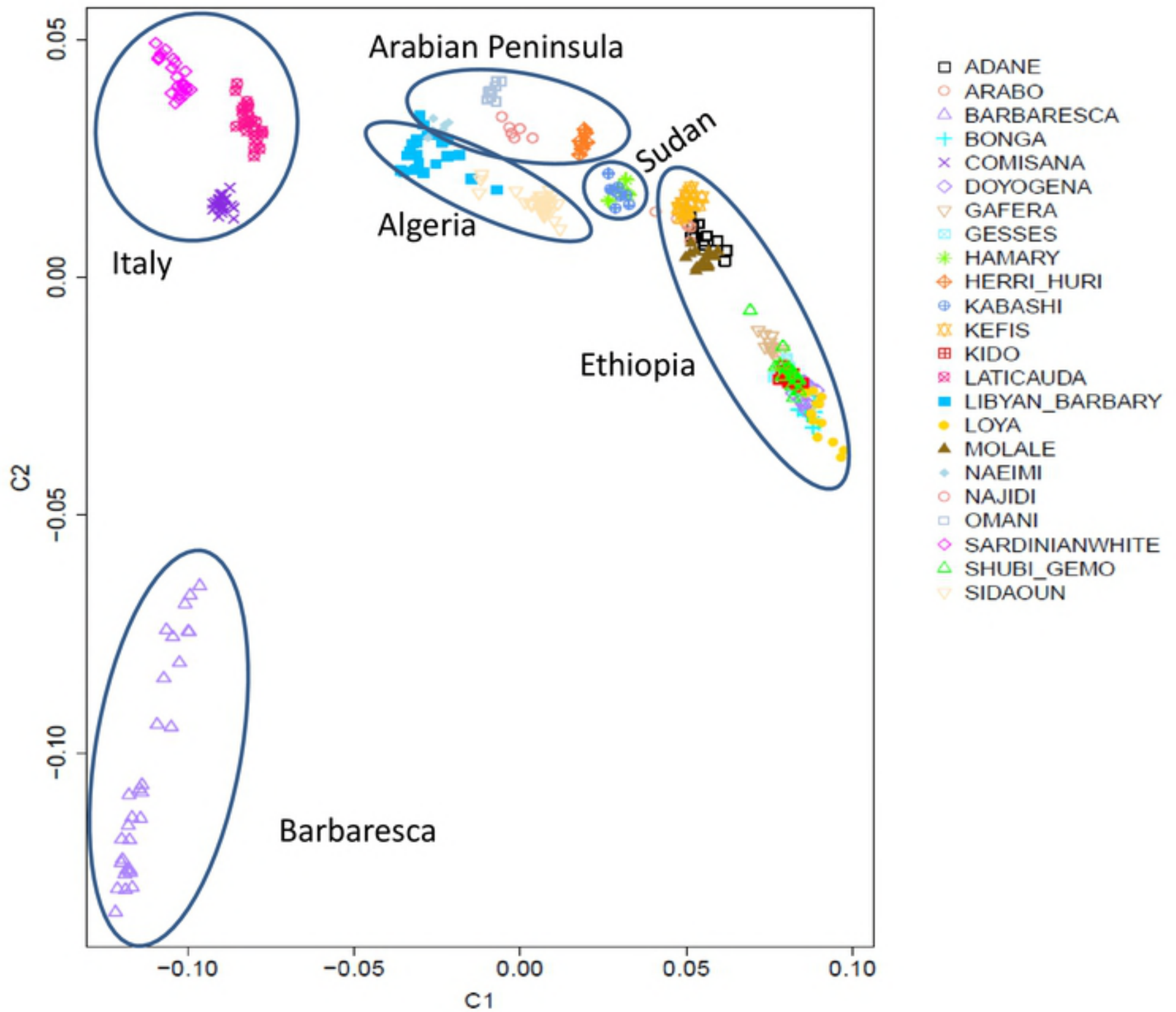560 **high-homozygosity regions is indicated with a black line.**

Figure 1