Genome-wide SNP data unravel the ancestry and signatures of divergent selection in Ghurrah pigs of India

Arnav Mehrotra¹, Bharat Bhushan¹, Karthikeyan A¹, Akansha Singh¹, Snehasmita Panda¹, Meenu Bhati², Manjit Panigrahi¹, Triveni Dutt¹, Bishnu P. Mishra¹, Hubert Pausch², Amit Kumar¹

¹Division of Animal Genetics, ICAR – Indian Veterinary Research Institute, Izatnagar, Bareilly – 243122, UP, India

²Animal Genomics, ETH Zürich, Zürich, Switzerland. (Email: meenu.bhati@usys.ethz.ch)

Corresponding author : Amit Kumar: Division of Animal Genetics, ICAR – Indian Veterinary Research Institute, Izatnagar, Bareilly – 243122, UP, India (Corresponding author Email: vetamitchandan07@gmail.com; ORCID ID: <http://orcid.org/0000-0002-4423-7881>)

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28 **Summary**

29 The evolution and domestication of pigs is a complex and ongoing process. Despite its rich
30 biodiversity and proximity to the geographical origins of *Sus scrofa domesticus*, the place of Indian
31 pigs in the global phylogeny is unclear. Using microarray-derived (porcine 60K SNP chip)
32 genotypes of 11 Ghurrah pigs from North-Western India and a public dataset comprising 2113 pigs
33 of 146 breeds, we determined the genomic ancestry of Ghurrah pigs and compared their genetic
34 constitution to European and Asian breeds to ascertain signatures of divergent selection. Results
35 showed that Ghurrah pigs contain genes of Asian and European ancestry with signs of inter-species
36 introgression. Using Admixture LD – decay statistics, the European admixture event was dated to
37 the recent past, coinciding with the start of cross-breeding efforts in India. The complex Asian
38 ancestry pattern of the breed resembled that of wild boars of South – Central China and Thailand,
39 possibly suggesting introgression from an Indian wild boar relative. F_{ST} and XP – EHH
40 comparisons with Asian breeds highlighted divergent selection in genomic regions associated with
41 odontogenesis and skeletal muscle development. Comparisons with European commercial breeds
42 revealed that genomic regions governing olfaction and response to sensory stimulation were under
43 selection in Ghurrah pigs. QTL for meat and carcass traits also showed divergent selection between
44 European breeds and Ghurrah pigs. Our results present the first genomic characterization of an
45 Indian pig breed using dense microarray-derived genotypes and highlight the importance of further
46 genomic characterization of Indian domestic and wild pigs.

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48 **Keywords;** Admixture; Introgression; Phylogeny; Tropical; *Sus Scrofa*

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53 **Introduction**

54 Within the last decade, the implementation of high throughput SNP genotyping and whole-genome
 55 sequencing has provided an in-depth insight into the demographic history of the domestic pig.
 56 The origins of the *Sus scrofa* species have been traced to the Mainland South East Asia (MSEA) and
 57 Island South East Asia (ISEA), about 5 million years ago (Mya) (Frantz *et al.*, 2013). Subsequently,
 58 pigs dispersed all over Eurasia and the divergence between the European and Asian wild boars has
 59 been dated back to around 1 Mya, with independent domestication events taking place in the two
 60 continents about 10,000 years ago (Groenen 2016). The geographical differences, diverse
 61 domestication practices and more recently, commercial breeding have resulted in remarkable
 62 morphological and physiological differences between pig breeds. Studies carried out in European
 63 and Chinese pig breeds have identified selective sweeps in the genomic regions related to teeth,
 64 bone and nervous system development (Frantz *et al.*, 2015)□, olfactory and immune response
 65 pathways (Paudel *et al.*, 2015)□ and feed intake and fat deposition (Wilkinson *et al.*, 2013).
 66
 67 Geographically and ecologically, India occupies a unique position in the world with its four
 68 biodiversity hotspots, and proximity to South-East Asia which has been the origin of the pig and
 69 home to several other extant *Sus* species (Dobney *et al.*, 2008; Myers *et al.*, 2000)□. India also
 70 possesses three sub-species of the *S. scrofa* (*cristatus*, *davidi* and *affinis*) (Meijaard *et al.*, 2011). So
 71 far, the only studies attempting to place the Indian pig breeds in a global phylogenetic context have
 72 been based on mitochondrial DNA (Singh *et al.*, 2016)□. However, mtDNA based studies are less
 73 suited to resolve the phylogeny due to a limited number of loci involved (Frantz *et al.*, 2013)□.
 74 In this study we characterize the Indian Ghurrah pig breed using a genome wide panel of markers.
 75 Ghurrah is a lightly built breed with adult weight about 48 kg. The black coated Ghurrah pigs are
 76 native to the Rohilkhand region of North – Western India (Ghurrah Pig, NBAGR breed profiles).

We explore the ancestry of Ghurrah pigs, assess admixture patterns with global breeds and attempt to place the breed in a global phylogenetic tree using a public dataset consisting of 146 pig breeds. Moreover, we compare it to a subset of Asian and European breeds using F_{ST} and XP - EHH to discover regions of diversifying selection.

Materials and Methods

Samples and data

Blood samples were collected from the jugular vein of 11 Ghurrah pigs kept at the AICRP farm at IVRI, Izatnagar in Bareilly according to regulations of the Institute Animal Ethics Committee (IAEC). The pigs were procured from the surrounding regions of Bareilly (28.3670° N, 79.4304° E). Genomic DNA was extracted using standard protocols and genotyped on the Illumina PorcineSNP60 BeadChip comprising 62,163 SNPs.

To place the Ghurrah breed in a global phylogenetic context, we also retrieved the data that were gathered by Yang *et al.*, (2017) containing the genotypes of 2113 pigs belonging to 146 domestic, wild and commercial breeds. This dataset also contained genotypes of 39 animals from 5 *Sus* species other than *Sus scrofa*. Detailed information about the breeds is provided in Supplementary file 1 of Yang *et al.*, (2017).

SNP coordinates based on the newer Sscrofa11.1 genome assembly were assigned to the dataset using the UCSC liftOver function. Using PLINK 1.9 (Chang *et al.*, 2015), we removed SNPs which were unmapped, on sex chromosomes, had a minor allele frequency less than 0.05 (--maf 0.05) and a call rate below 90% (--geno 0.1). 11 individuals with more than 10% missing genotypes (--mind 0.1) were also removed, leaving a combined dataset of 2113 individuals and 45,323 SNPs, including Ghurrah (n = 2113).

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104 **Principal component analysis and population admixture**

105 We pruned the data for SNPs in linkage disequilibrium using the PLINK v1.9 command *-indep-*
106 *pairwise 50 5 0.2*, leaving 10,211 independent SNPs. The genomic relationship matrix among the
107 samples was built and the too 20 principal components were extracted using GCTA 1.93 (Yang *et al.*,
108 2011).

109 To infer the global ancestry of the Ghurrah pig, we ran an analysis using the ADMIXTURE v1.3
110 SOFTWARE (Alexander & Lange 2011). Initially, the analysis was run with all 147 breeds, followed
111 by a subset of 24 breeds belonging to the different breed clusters outlined by Yang *et al.*, (2017).
112 This subset included South Chinese domestic breeds (CNDH, CNLU, CNWZ), East and Central
113 Chinese domestic breeds (CNMS, CNEH, CNJH), Asian wild boars (CNWB1, CNWB2, CNWB3,
114 CNWB4, THWB, RUWB1, RUWB2), European commercial breeds (PIT1, LDR1, LWT1),
115 European wild boars (NEWB, ITWB1), other *Sus* species (BABA, SBSB, SCEL, SVSV, PHAF) and
116 Ghurrah (GHUR). Abbreviations and sample sizes of the 24 breeds considered are listed in Table
117 S1.

118 ADMIXTURE was run for K values ranging from 2 – 24 with cross validation. Each run was repeated
119 5 times with a random seed to gain accurate estimates (Liu *et al.*, 2020). The results were
120 visualized using PONG (Behr *et al.*, 2016).

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122 **TREEMIX analysis**

123 To complement the ADMIXTURE analysis we used TREEMIX 1.13 (PICKRELL & PRITCHARD 2012) to
124 analyze the 24 breed subset. This approach draws a maximum likelihood phylogram which
125 facilitates to depict ancestral divergence and admixture between the breeds. We ran TREEMIX fitting
126 up to 10 migration pathways, choosing the African Warthog (PHAF) as the root of the tree.

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129 **Timing of admixture**

130 We ran ALDER 1.03 (Loh *et al.*, 2013) □ □ to estimate the time since the admixture event occurred.

131 In brief, ALDER estimates the rate of LD decay as a result of the admixture between the populations

132 through a weighted LD statistic. There are two additional advantages to using this approach. First, it

133 is robust against the effect of SNP array ascertainment bias, and second, it can detect the false

134 positive admixture signals arising due to non-admixture LD caused by events such as population

135 bottlenecks. For this analysis, we set Ghurrah as the admixed population, and all the European and

136 Chinese breeds as surrogates for the admixing populations. The program initially computed a one-

137 reference curve for each breed to determine signals of admixture – i.e. whether a lineage

138 represented by that breed was involved in admixture of Ghurrah, then it used the breeds detected to

139 be involved in admixture, in a two-reference test to estimate the timing of admixture.

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141 **Signatures of divergent selection**

142 The Indian Ghurrah pigs were compared with the three major European commercial breeds -

143 Landrace (LDR1), Large White Yorkshire (LWT1) and Pietran (PIT1), and three Asian domestic

144 breeds - Guangdonghuabai (CNDH), Diannanxiaoer (CNDN) and Luchuan (CNLU). These three

145 Asian breeds were chosen as they belonged to the south-central Chinese population which had the

146 least introgression from European breeds (Yang *et al.*, 2017). Two different approaches were

147 employed to assess signatures of selection, i.e., F_{ST} (Weir & Cockerham 1984) and Cross

148 Population Extended Haplotype Homozygosity (XP-EHH) (Sabeti *et al.*, 2007). The pairwise F_{ST}

149 calculations were carried out using VCFTOOLS (Danecek *et al.*, 2011), with a sliding window of 500

150 Kb and a 250 Kb step size. The F_{ST} values were assigned Z-scores in the R package SCALE to

151 facilitate selection for significant regions. Separately, for both the breed groups (Asian and

152 European), the average Z-score for each 500 kb region was calculated. Regions with an average Z-

153 score four standard deviations above the mean ($Z \geq 4$), were retained for further analysis. For

calculation of XP-EHH, haplotypes were inferred using BEAGLE v5.1 (Browning *et al.*, 2018) and analyzed through the R-package REHH (Gautier *et al.*, 2017) to calculate the p_{XP-EHH} statistic between Ghurrah and each of the six breeds under comparison. Average p_{XP-EHH} values were derived for each SNP within both the breed groups. To avoid false positives, we scanned the genome in 500 Kb windows with 250 Kb overlap and retained the regions with at least two markers with a p_{XP-EHH} value greater than the 99.97th percentile as suggested by Gautier *et al.*, (2017) and Sabeti *et al.*, (2007). Genes within the regions identified by the F_{ST} and XP-EHH statistic were obtained from Ensembl Biomart (Cunningham *et al.*, 2019). Functional profiling of the selected genes was done using g:PROFILER (Raudvere *et al.*, 2019). Enrichment of GO terms and pathways was determined at a FDR adjusted p -value of 0.05.

Results and Discussion

Principal component analysis and population admixture

To place the Ghurrah breed in a global context, we performed a PCA on a dataset containing samples from Ghurrah and 146 other breeds. Each breed was marked as a single point on the plot by averaging the eigenvectors of all individuals within a breed for each principal component. The top principal components (PC) revealed three distinct clusters containing Asian, European and other Suid species. PC1 separated the Asian from European breeds while PC2 separated the wild from domestic breeds (Fig. 1a). Ghurrah was placed in the middle of the two clusters along with CNST, CSLM, CNLC and RUMS. All these Asian breeds have been reported to contain significant (> 20%) European admixture (Yang *et al.*, 2017), suggesting that the ancestral pattern is similar for Ghurrah. PC3 separated the *S. scrofa* animals from the other Suid species, with Ghurrah being one of the prominent outliers of the *S. scrofa* cluster (Fig. 1b).

To further explore the findings presented by PCA, we ran ADMIXTURE. An initial analysis that considered all 147 breeds outlined the complex ancestry of the Ghurrah pig. To facilitate the interpretation of the ancestry, we then ran the analysis on a subset of 24 breeds belonging to different wild and domestic breed clusters (see Methods). The lowest cross-validation error was obtained for $K = 19$ (Fig. S1). The barplots of the 19

admixture runs can be found in supplementary Fig. S2. $K = 3$ divided the populations in distinct clusters belonging to Asian and European pigs, and other suid species (Fig 2). Ghurrah pigs had 45.5% Asian, 33.8% European and 20.6% inheritance from the other suid species. Ghurrah had the highest level of interspecies introgression, followed by the Thai and Chinese Wild boars (7-9%). $K = 4$ divided the Asian ancestry into distinct Southern and Eastern Chinese clusters with Ghurrah showing a pre-dominant South Chinese ancestry (36.4 %). At higher level of $K = 8$, the increasingly complex ancestry of the Ghurrah pig resembled that of the South Chinese and Thai wild boars, which coalesced into a distinct ancestral block at $K = 11$ and Ghurrah shared more than 59.4% of its ancestral proportion with the aforementioned Asian wild boars with the rest coming from European (~28%) and other suid species (12%). Ghurrah was separated into its own cluster at $K = 14$.

TREEMIX analysis

The admixture results were further supported by the phylogram constructed by TREEMIX (Fig. 3a and 3b). The northern (RUWB1, RUWB2, CNWB2) and southern (CNWB1, CNWB3, CNWB4) wild boars of Asia were assigned different branches in the Asian clade, as were the southern and central-eastern Chinese domestic breeds. The European clade had similar distinct branches for the wild and commercial breeds. Ghurrah was not placed within these two clades, but instead was a sister group to the Chinese and European breeds. This tree explained 98.8 % of the covariance observed between populations. A complex history of admixture of *Sus scrofa* was suggested when migration edges were added to the graph. The addition of 10 migration paths explained 99.8% of the observed covariance between populations and allowed us to recapitulate the phylogenetic tree created by Frantz *et al.*, (2013) who used sequence data to correctly group different suid species. Admixture between Ghurrah and European commercial breeds as well as South Chinese breeds was represented by two migration edges. The admixture among the Chinese and European breeds over the last two centuries, which has been well documented in the literature (Groenen 2016), has also been captured in our phylogram. However, the effect of ascertainment bias of the SNP chip markers is also visible in the relatively shorter branch lengths of Asian pigs compared to their European counterparts in Fig 3b.

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210 **Timing of admixture**

211 In the pairwise testing involving all European and Asian breeds using ALDER, we got 118 significant
 212 combinations (Table S2). A number of European wild boars were the surrogates for the European lineage,
 213 and several Eastern and Central Chinese domestic breeds and Asian wild boars represented the Asian lineage.
 214 The strongest signal ($z = 15.33$, $p = 1.3e-49$) was obtained when the Iberian Wild Boar (IBWB) and Chinese
 215 Jinhua pig (CNJH) were taken as surrogates for the two lineages, respectively. The estimated time of
 216 admixture by ALDER's weighted LD statistic was 13.52 ± 0.88 generations. Taking the average generation
 217 interval of a pig as 1.5 years, this equates to the admixture event taking place approximately 20 years ago.
 218 Similar time frames were drawn from the pairwise comparisons of different surrogate breeds, although with
 219 varying standard errors. The relatively recent admixture detected in our study corresponds with the initiation
 220 of cross-breeding efforts in India in the late eighties and nineties through the introduction of European
 221 germplasm, with Large White and Landrace being the predominant exotic breeds (Rajkhowa *et al.*, 2018)□.
 222 Even though we could reconcile the European inheritance found in our analysis with the records of cross-
 223 breeding in the region, we can only hypothesize about the origin of the complex Asian inheritance of
 224 Ghurrah pig. Our admixture results show the resemblance between the genomic ancestry patterns of Ghurrah
 225 and the Asian wild boars (Fig. 2 and Fig. S2). This pattern of the ancestry in Ghurrah may have been derived
 226 from a wild relative such as the Indian wild boar or *Sus scrofa cristatus* which is indigenous to North –
 227 Western India (Meijaard *et al.*, 2011). Due to the migratory and backyard rearing system under which
 228 Ghurrah is kept, an introgression of genes from wild boars may happen frequently. Such mobile domestic
 229 herding systems have been shown to be responsible for gene flow between domestic and wild boars
 230 elsewhere (Frantz *et al.*, 2011). The wild boar inheritance could also explain the fraction of ancestry from
 231 other ISEA suid species in Ghurrah, as we could detect similar signals of interspecies introgression in the
 232 admixture blocks of other Asian wild boars. However, any definitive conclusion would require genotype data
 233 for the other Indian pig breeds including *Sus scrofa cristatus*.

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Signatures of divergent selection between Ghurrah and Chinese pigs

In the pairwise comparisons between Ghurrah and three Chinese breeds (CNDN, CNDH, CNLU), we found 11 regions (5 Mb) through F_{ST} and 2 regions (2 Mb) through XP-EHH analyses (Fig. 4a and 4b), which met their respective significance thresholds of $Z \geq 4$ and $p_{XP-EHH} \geq 2.09$. There was no overlap between the significantly identified regions by the two methods. The detected genomic regions contained 69 genes (Table S3). Through these genes, six significantly enriched (FDR adj. $P < 0.05$) GO:BP terms were identified by g:Profiler, all of which related to Odontogenesis (Table S4).

The F_{ST} analysis pointed towards a 750 Kb region on SSC8 (67.25 – 68 Mb) which contained the most significantly differentiated markers ($Z \geq 5.11$). This region contains the *AMTN*, *AMBN* and *ENAM* genes, which code for the amelotin, ameloblastin and enamel proteins, respectively, involved in the formation and maturation of tooth enamel (Gasse *et al.*, 2015). Genes involved in biomineralization of dental tissue have been reported as candidates for diversifying selection in several mammals including pigs, humans and canines (Machado *et al.*, 2016). Dental morphometry in pigs show a systematic variation with changing geographical location and domestication status, with distinct phenotypes found across the breeds (Evin *et al.*, 2015), and our findings in the Indian pig further supports this notion.

Another divergently selected region includes a gene poor segment on SSC15 (98.5 – 99.25) which is in the vicinity of the *MSTN* gene (94.62 Mb) that is associated with skeletal muscle growth. We also identified other regions flanking this gene which showed significant differentiation ($Z \geq 3$) between the breeds, but fell below our set threshold. Divergent selection between the Asian domestic and wild boars has been attributed to this region previously (Zhu *et al.*, 2017). XP-EHH analysis revealed a region on SSC15 (25 – 26 Mb) which overlapped QTLs for lean meat and fat percentage (Rothhammer *et al.*, 2014).

Signatures of divergent selection between Ghurrah and commercial European pigs

Comparisons with the three European breeds (LWT, LDR, PIT), 14 significant ($Z \geq 4$) regions amounting to a combined non-overlapping length of 6 Mb were identified by F_{ST} (Fig. 4C; Table S5). Several regions around the *MSTN* gene (SSC15: 89 – 99 Mb) were also detected in this comparison. A search on the PigQTLdb (<https://www.animalgenome.org/QTLdb/pig/>) showed this region overlapping with QTLs for

meat and carcass traits namely, backfat percentage, muscle protein percentage and meat tenderness, all of which under strong artificial selection in commercial breeds.

The strongest F_{ST} signal for divergence was observed in a 5.25 Mb region on SSC8 (45.75 – 51 Mb). This region contains *GLRB*, *GRIA2* and *GSX2* genes, the human orthologs of which are involved in synaptic transmission and nervous system development (Lueken *et al.*, 2017; Salpietro *et al.*, 2019). Further evidence of neurological and behavioral divergence between the breed groups was found by the results of the XP-EHH analysis ($p_{XP-EHH} \geq 2.40$, Fig. 4d). Two regions of 3 Mb cumulative length on SSC2 (14-15 Mb, 16-18 Mb) containing a cluster of genes coding for olfactory receptors were detected to be under selection in the Ghurrah pigs. The indigenous pigs of India are reared in a free – range scavenging system (Rahman *et al.*, 2020) and depend on their olfactory abilities to find feedstuff and mating partners, which may be a reason for these genes to be under selection in the Ghurrah breed compared to the commercial breeds which are reared and fed in captivity. These results were underlined by the functional profiling of the 103 genes present in the 16 regions detected by F_{ST} and XP-EHH analysis, where 23 GO:BP terms were found significantly enriched (Table S6). The GO terms pertaining to response to sensory stimuli and olfaction had the lowest FDR adjusted p -values ($p_{adj} < 10^{-6}$). KEGG and REACTOME pathways related to olfactory signaling and G protein-coupled receptor transduction were also significantly ($p_{adj} < 10^{-2}$) enriched.

To conclude, many of the extant pig breeds in the world show a complex inheritance drawing from European and Asian lineages, and the Indian Ghurrah pig is no exception. However, it is unique with respect to the relatively high proportion of inter-species introgression and a pattern of inheritance resembling those of the Asian wild boars. In this study, we had the constraints of a limited sample size and the ascertainment bias arising from the design of the Porcine60K SNP array. Also, the rather low resolution of the porcine SNP array is a limitation to comprehensively identify genomic regions responsible for divergence within and between the breeds. However, our results provide a first genomic characterization of the Ghurrah breed and revealed putative targets of selection. We took into account the constraints of the current dataset by employing complementary approaches to arrive at our results. Yet, validating our findings using whole genome sequence data from a larger set of animals is required. Our study also suggests that genomic

291 characterization of other Indian pig breeds, especially the Indian wild boar, is important to develop a
292 thorough understanding of the evolution and domestication of *Sus scrofa*.

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298 **Data availability**

299 The public dataset used in the analysis is available from the Dryad Repository at
300 <http://dx.doi.org/10.5061/dryad.30tk6>. The data for Ghurrah pigs is available at
301 10.6084/m9.figshare.12204671

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303 **Conflict of interest**

304 The authors declare that there are no competing financial interests.

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Figure 1a. Separation of the 147 pig breeds along the first and second principal components.

CNWB, Chinese Wild Boar; CNDH, Guangdonghahubai; GHUR, Ghurrah; CNST, Sutai; RUMS, Russian Minisibs; CSLM, Large White x Meishan; CNLC, Lichahei; LWT, Large White Yorkshire; LDR, Landrace; HRWB, Croatian Wild Boar; ITWB, Italian Wild Boar.

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434 Figure 1b. Principal component analysis of all 147 pig breeds (PC3 and PC4 shown)

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445 Figure 1c. A Ghurrah sow at IVRI, Izatnagar

Fig 2. Admixture barplots with selected values of K. The fractions on the left describe the number of identical runs out of five, as calculated by PONG. For all values of K, see supplementary Figure S2. Breed abbreviations are provided in supplementary table S1.

Fig 3a. Maximum likelihood phylogram with 10 migration edges. Admixture is shown among Chinese (Red) and European breeds (Green), between Ghurrrah and European commercial breed and Ghurrrah and South Chinese breeds.

Fig 3b. The phylogram in Fig 3a presented as a conventional phylogenetic tree.

Figure 4a. - Manhattan plot of Z-transformed F_{ST} values for Ghurrah's comparison with 3 Chinese breeds.

Blue line indicates threshold of $Z \geq 4$.

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495

496 Figure 4b. – Plot of XP – EHH statistic for Ghurrah’s comparison with 3 Chinese breeds. Positive value
 497 indicates selection in Ghurrah; negative value indicates selection in Chinese pigs. Dotted lines indicate
 498 threshold corresponding to $p_{XP-EHH} \geq 2.09$.

510

511 Figure 4c. - Manhattan plot of Z-transformed F_{ST} values for Ghurrah's comparison with 3 European breeds.

512 Blue line indicates threshold of $Z \geq 4$.

513 Figure 4d. – Plot of XP – EHH statistic for Ghurrah's comparison with 3 European breeds. Dotted lines

514 indicate threshold corresponding to $p_{XP-EHH} \geq 2.40$.

515

516 Supplement Legend

517 Table S1 – Abbreviation definitions and sample sizes of selected breeds included in the analysis.

518 Table S2 – Alder admixture results

519 Table S3 – List of regions and genes showing divergent selection between Ghurrah and Chinese pigs

520 Table S4 – List of significantly enriched GO terms for genes diverging between Ghurrah and Chinese pigs

521 Table S5 – List of regions and genes showing divergent selection between Ghurrah and European pigs

522 Table S6 – List of significantly enriched GO terms and pathways for genes diverging between Ghurrah and

523 European pigs

524 Figure S1 – Plot of ADMIXTURE cross validation errors with increasing K value

525 Figure S2 – Admixture plots of K = 2 to 19.