- 1 Supplementary Information
- 2
- **3 Genomic analysis on pygmy hog (***Porcula salvania***) reveals**
- 4 multiple interbreeding during wild boar expansion
- 5
- 6 Liu et al.
- 7



Supplementary Fig. 1

Maximum likelihood phylogenetic tree constructed on concatenated coding
sequences using the supermatrix method (Optimization Likelihood: -42825135.3).
The numbers on the nodes represent bootstrap values based on 100 non-parametric
bootstrap replications. *Babyrousa babyrussa* was used as out group. See
Supplementary data 1 for name abbreviation.



- 16
- 17 Supplementary Fig. 2

0.02

18 Maximum likelihood phylogenetic tree based on supertree method.

Among the 1,0142 coding sequences that are used for generating gene trees, 2,659 gene trees with highest average bootstrap values (minimum 40) were used to build a consensus species tree. The numbers on nodes represent concordance factors (ranges from 0 to 1), which represent the proportion of the genome supporting the branch. *Babyrousa babyrussa* was used as out group. See Supplementary data 1 for name abbreviation.



0.01 Supplementary Fig. 3 27

28 Mitochondrial phylogeny

A bayesian phylogeny of the 38 samples using complete mitochondrial genomes 29 30 (16,613 bp). Pygmy hogs are the sister taxon of Sus species, with sub-Saharan suids as outgroup and the mitochondria replacement found by L.A.F Frantz et al 2014 and 31 S.M. Funk et al 2007 is also supported^{1,2}. See Supplementary data 1 for name 32 33 abbreviation. 34



36 Supplementary Figure 4

37 Phylogenetic time tree

38 Species tree with mean posterior age (in millions of years). Blue bars indicated 95%

39 confidence intervals. Red dots indicated the calibration points. We used a float prior

40 and a maximum bound age, with a scale parameter of c=2. For the root divergence,

41 we set the prior to (tU=2 [20 Mya], p=0.1, c=2). For MRCA of Suinae and Sus, we

42 used the same fossil calibration as in Frantz et al. 2013 (tL=0.55 [5.5 Mya], p=0.9,

43 c=0.5 and tL=0.2 [2 Mya], p=0.1, c=0.5, respectively).

a) rejected tree model



b) graph with 2 migration edge





46

47 Supplementary Fig. 5

48 Admixture graph inferred using Treemix

a) A simple tree-like model without admixture fits the data poorly, as can be seen from
the matrix of residuals between empirical and modelled allele frequency covariance
on the right. b) The optimal placement of two admixture event are from the common
ancestor of Eurasian wild boar to pygmy hog, as well as from ISEA Sus to common
ancestor of Asian wild boar.

































































93 Supplementary Fig. 6

94 The D-statistic and fd for testing introgression for 100-kb windows on each 95 chromosome with the tree topology (((ISEA, Pygmy hog), X), warthog), X=European 96 wildboar (EU), Northern China wildboar (NC) or Southern China wildboar (SC). We 97 also calculated DNA sequence divergence (dxy) between X and pygmy hog for each 98 window and color the windows red whose dxy is in the lower 25% distribution of all the 99 windows and D-value>0. Chr = chromosome, ISEA = Island of South east Asia pigs 100



102 Supplementary Fig. 7

103 Observed fraction of X chromosome read depth compared to the average read depth

104 of autosomes in all individuals in this study.



0.02

108 Supplementary Fig. 8

109 X chromosome topology

110 The maximum likelihood tree of the whole X chromosome (Optimization Likelihood:

-223197633.0). The topology of the whole X chromosome tree was inconsistent with

the topology of autosomal phylogenetic trees (Supplementary Fig. 1&2). The numbers

113 represent node support inferred from 100 non-parametric bootstrap repetitions.

114 B.babyrussa is the outgroup. See Supplementary data 1 for name abbreviation.



Distribution of chromosomal segments supporting the 12 most frequent tree
topologies assigned by SAGUARO to segments along the autosomes and the X
chromosome. The numbers given next to phylogenies indicate chromosome IDs. See
Supplementary data 3 for further details.

122



125 The D-statistic for testing introgression for 100-kb windows on chromosome 1-18 and 126 X. For the tree topology (((ISEA, EUWB), pygmy hog), warthog). The ABBA-BABA 127 method and its related statistics compute the excess of shared derived mutation 128 between two taxa compared to a control not connected by gene flow to the others. 129 The outgroup allows mutations to be polarized. A mean D value of 0 is expected if the 130 two taxa are not connected by gene flow. Red shaded areas show the introgression 131 regions inferred by Saguaro using the same quadruplet. ISEA=Island of South Asia 132 pigs, EUWB = European wild boar. 133



136 The D-statistic for testing introgression for 100-kb windows on chromosome 1-18 and

137 X. For the tree topology (((ISEA, EUD), pygmy hog), warthog). Red shaded areas

138 show the introgression regions inferred by Saguaro using the same quadruplet.

139 ISEA=Island of South Asia pigs, EUD = European domesticated pig.

140



144 The D-statistic for testing introgression for 100-kb windows on chromosome 1-18 and

145 X. For the tree topology (((ISEA, NCWB), pygmy hog), warthog). Red shaded areas

146 show the introgression regions inferred by Saguaro using the same quadruplet.

147 ISEA=Island of South Asia pigs, NCWB = North Chinese wild boar.

148



152 The D-statistic for testing introgression for 100-kb windows on chromosome 1-18 and

153 X. For the tree topology (((ISEA, NCD), pygmy hog), warthog). Red shaded areas

154 show the introgression regions inferred by Saguaro using the same quadruplet.

155 ISEA=Island of South Asia pigs, NCD = North Chinese domesticated pig.



159 The D-statistic for testing introgression for 100-kb windows on chromosome 1-18 and

160 X. For the tree topology (((ISEA, SCWB), pygmy hog), warthog). Red shaded areas

161 show the introgression regions inferred by Saguaro using the same quadruplet.

162 ISEA=Island of South Asia pigs, SCWB = South Chinese wild boar.



166 The D-statistic for testing introgression for 100-kb windows on chromosome 1-18 and

167 X. For the tree topology (((ISEA, SCD), pygmy hog), warthog). Red shaded areas

168 show the introgression regions inferred by Saguaro using the same quadruplet.

169 ISEA=Island of South Asia pigs, SCD = South Chinese domesticated pig.



171 0.02

172 Supplementary Fig. 16

173 X chromosome topology for the two introgression regions.

174 Maximum likelihood tree for the two genealogical discordant regions on chromosome X. A. Maximum likelihood tree using the first discordant region spanning 52.0~57.8Mb 175 176 on X chromosome (Optimization Likelihood: -18385084.9). B. Maximum likelihood 177 tree built using the second discordant region spanning 57.8~91.5Mb on X 178 chromosome (Optimization Likelihood: -50166590.1). Meishan (North China domestic 179 breed) was marked with asterisk (*) to highlight that this breed has different 180 haplotypes in the two regions. See Supplementary data 1 for name abbreviation. The 181 numbers at the nodes represent bootstrap values based on 100 non-parametric 182 bootstrap replications



185 Supplementary Fig. 17

186 The Venn diagram shows shared autosomal segments with 'ghost' introgression 187 signal in sliding-window ABBA-BABA analysis among different swine populations. For 188 European pigs, we calculated the average D-value for the clear 'ghost' introgression 189 region on X chromosome and any autosomal windows with D-value lower than this 190 will be regarded as introgression region. Numbers in parentheses refer to the total 191 amount of introgression windows in each population. SCWB = South Chinese wild 192 boar, SCD = South Chinese domesticated pig, NCWB = North Chinese wild boar, NCD = North Chinese domesticated pig, EUWB = European wild boar, EUD = 193 194 European domesticated pig.





198 Violin plot representing the length of autosomal 'ghost' introgression region in different

199 population inferred by Saguaro. Numbers on top of each violin are the total length of

200 introgression region. Dash lines indicated the average length. SCWB = South

201 Chinese wild boar, SCD = South Chinese domesticated pig, NCWB = North Chinese

wild boar, NCD = North Chinese domesticated pig, EUWB = European wild boar, EUD

203 = European domesticated pig.

204



0.01

206 Supplementary Fig. 19

207 Y chromosome topology

The maximum likelihood tree of the non- recombining Y chromosome (Optimization
Likelihood: -21216029.3). The topology of Y chromosome tree was consistent with the
topology of autosomal phylogenetic trees (Supplementary Fig. 1&2). The numbers
represent node support inferred from 100 non-parametric bootstrap repetitions.
B.babyrussa is the outgroup. See Supplementary data 1 for name abbreviation.



215 Supplementary Fig. 20

216 Heatmap showing the comparation of the Bayes factors for all model pairs. |K|>3 is

217 considered as the significant threshold. Coordinates of the scale indicated the internal

- code for each model.
- 219



222 23 most well supported models (based on K) used for ADMIXTUREGRAPH. Strings
223 on top of each diagram indicated the internal code for each model. (AF=
224 *Phacochoerus africanus*; LIB=pygmy hog; ISEA_SVSV=*Sus verrucosus*;
225 EUWB=European wildboar; NCWB=North Chinese wildboar; SCWB=South Chinese
226 wildboar)



229 Supplementary Fig. 22

Demographic Models used for G-Phocs analyses. Two-way arrows indicated the migration band designated in each model. Gray dashed arrow indicated the migration band which ghost population involved. Green dot in Null model shows the fossil calibration. ISEA=Island of South Asia pigs, SC = South Chinese pig, NC = North Chinese pig, EU = European pig.



236

238 Migration bands are shown in blue, red and gray (see Supplementary Fig. 23) with 239 associated values indicating estimates of total migration rates, which equal the 240 probability that a lineage will migrate through the band during the time period when 241 the two populations co-occur. Thig figure only show a subset of models tested and 242 only significant migration signals were delineated (See Supplementary data 4 for 243 further details). G-Phocs result is consistent with our admixture analysis between 244 pygmy hog and Sus scrofa. In our model with ghost population, European pigs 245 appeared to have more introgression from ghost population than other pigs, which 246 supports the hypothesis that European pig used to hybrid with other species. Notably, 247 G-Phocs always estimated a migration signal from Sus scrofa to other species. A 248 possible reason is that Sus scrofa population remain the biggest effective population 249 size and genetic diversity, which may overweight ILS. ISEA=Island of South Asia pigs, 250 SC = South Chinese pig, NC = North Chinese pig, EU = European pig.251



253 Supplementary Fig. 24

254 NJ tree based on selected 10,000 neutral loci used in G-PhoCS. Node labels show

255 bootstrap values. The result is accordance with our main topology in consensus and

256 concatenation tree. . ISEA=Island of South Asia pigs, SCWB = South Chinese wild

boar, NCWB = North Chinese wild boar, EUWB = European wild boar.



259

261 Supplementary Fig. 25

Null distributions of D. a) Each density curve corresponds to the D values (((ISEA, Pygmy hog), X), warthog) obtained under null models without gene flow, and the dash vertical line corresponds to the threshold value for the introgression fragments in the real data. b) Each density curve corresponds to the D values (((ISEA, X), pygmy hog), warthog) obtained under null models without gene flow, and the dash vertical line corresponds to the D values observed in the read data. All observed D values are significant (P < 0.001).



271 Supplementary Fig. 26

272 Functional enrichment result for pygmy hog/Sus scrofa introgression gene set

273 Analysis by gene ontology terms and pathways. The number of horizontal axis is the

274 number of enriched genes. The bubble size indicates the ratio of genes in each term

275 or pathway, and different colours correspond to different adjusted p-values. The

- 276 p-values are adjusted by Benjamini-Hochberg method.
- 277

278 Supplementary Note

279

280 Phylogenomic analysis

281 We characterized the evolutionary history of pygmy hog by using one-to-one 282 autosomal orthologous genes (1:1 - pig:cow). We applied both supermatrix and 283 supertree phylogenomic methods based on maximum likelihood (ML) using Babyrousa babyrussa as an outgroup^{3,4}. The concatenation and consensus methods 284 285 resulted in same main topology (Fig. 2a, Supplementary Fig. 1, Supplementary Fig. 2). 286 The phylogenetics analyses clearly show that Suinae consists of three separate 287 clades, sub-Saharan suids, pygmy hog (Porcula salvania) and the genus Sus. The 288 most basal split within the Suinae are sub-Saharan suids followed by a highly 289 supported split of pygmy hogs (BS=100 in supermatrix and CF=1 in supertree) from 290 all Sus species. There has been a longstanding taxonomic debate over the 291 classification of pygmy hog as either basal to or nested inside the genus Sus^{5,6}. Up to 292 now, only one case of molecular classification has been reported for pygmy hog 293 based on a short fragment of mitochondrial genome². To compare our phylogenetics 294 results to an earlier study using fragments of mitochondrial DNA, we carried out a 295 Bayesian phylogenetic analysis using complete mitochondrial genomes 296 (Supplementary Fig. 3). The resulting topology is consistent with previous studies 297 confirming pygmy hog as basal to Sus and showing mitochondrial replacements 298 between Sundaland Sus species'.

299

300 Estimation of divergence time

301 We selected autosomal genomic loci supporting the main topology to obtain the basal 302 divergence between the studied taxa (Fig. 2a, Supplementary Fig. 4). The divergence 303 between Babyrousa and the other Suidae (sub-Saharan suids, pygmy hog and Sus) 304 took place during middle Miocene ~14.2 Mya (95% HPD = 17.1-11.6). The basal split 305 of Suinae, between extant sub-Saharan African Suidae and the Pygmy-Sus clade, 306 took place during the late Miocene ~10.2 Mya (95% HPD = 12.7-7.9). This split was 307 followed by the initiated diversification of the ancestors of extant sub-Saharan suids^{8–} 308 ¹¹. Our results show that the divergence between *Phacochoerus* and *Potamochoerus* 309 during ~ 6.2 Mya (95% HPD = 7.7-4.5). Our divergence time estimates suggest that 310 the initial divergence of the pygmy hog and Sus during Miocene/Pliocene boundary 311 ~6.1Mya (95% HPD = 7.8-4.2). Within the Sus genus, DNA analysis suggests the two 312 major groups of extant species (Sus scrofa and ISEA sus) diverged from a common 313 ancestor in early Pliocene ~4.1Mya (95% HPD = 5.5-2.7).

314

315 Admixture between pygmy hogs and Sus

We used D-statistics (D) to test whether pygmy hogs had autosomal introgression from some present-day *Sus* species. We measured the difference in the percent matching by D (P1, P2, Pygmy hog, sub-Saharan suids) that does not differ significantly from zero when the derived alleles in the pygmy hog match alleles in the two Sus species/breeds equally often. If D is positive, pygmy hog alleles match alleles in the second Sus species (P2) more often, while if D is negative, pygmy hog alleles match alleles in the first Sus species (P1) more often. We performed this test using 11 Sus populations (Supplementary data 2). We found that pygmy hogs have a clear overrepresentation of derived autosomal alleles with *Sus scrofa* compared to the Sus species from Island of south east Asian (ISEA) (Fig. 2b), suggesting that some admixture between pygmy hog and Sus scrofa may have occurred.

327 To further examine this autosomal genome-wide patterns of admixture between 328 Pygmy hog and Sus scrofa, we calculated the D-statistics and fd-statistics in (ISEA, 329 Pygmy hog, Sus scrofa, warthog) for every 100 kb non-overlapping window across 330 the autosomal genome separately and used D and fd both >0 as a minimum threshold 331 for introgressed intervals. In order to distinguish between introgression and ancestral 332 variation, we also calculated DNA sequence divergence (dxy) for each candidate 333 introgression interval and compared this with the autosomal chromosomal mean dxy, 334 because introgressed regions generally show lower genetic divergence¹². We 335 compared the result between Sus scrofa from Europe, Northern China and Southern 336 China. We identified 636 intervals of which 427 (67.1%) were shared among Sus 337 scrofa (Supplementary Fig. 6), which suggested an ancestral gene flow between 338 pygmy hog and the common ancestor of Sus scrofa.

339

340 X chromosome analysis

341 We reconstructed a phylogenetic tree based on the whole X chromosome and found 342 remarkable inconsistency between the phylogenetic topology of the X chromosome 343 and the autosomes, more specific in that pygmy hog significantly group with European 344 and North Chinese Sus scrofa to the exclusion of Southern Sus scrofa and ISEA Sus 345 species (Supplementary Fig. 8). To investigate this discrepancy, we used SAGUARO, 346 which combines a hidden Markov model and a self-organizing map to infer both the 347 trees and window boundaries. We mapped occurrences of the six most frequently 348 observed unrooted ML topologies of six Suidae species along the 19 chromosomes 349 (Fig. 3, Supplementary data 3, Supplementary Fig. 9). SAGUARO identified a 350 ~40.6Mb (46.2-86.8 Mb) region in X chromosome, where pygmy hog clustered with 351 ISEA and South China Sus scrofa breeds, while the European Sus scrofa clade 352 appeared to be outgroup to this cluster. In the meantime, Northern Chinese domestic 353 pig shows a splicing pattern, which clustered with European pig/North China pig in 354 46.2-57.1 Mbp and clustered with South China pig in 57.1-86.8 Mbp. To further 355 confirm this observation, we carried out D-statistic analysis in sliding windows, 356 expecting symmetry (D = 0) under the null hypothesis corresponding to no gene flow 357 derived from the chromosomes (ISEA Sus, Sus scrofa, Pygmy hog, warthog) 358 (Supplementary Fig. 10-15). Since the fixed frame-size sliding-window test may 359 over-estimating the length of introgression region, for each quadruplet, we also ran 360 individual SAGUARO analysis. The results suggest that within this genomic region, 361 sequences of European/North China pigs have an ancient origin from a ghost lineage 362 older that the split of pygmy hogs but younger than Sub-saharan suids. Due to the 363 distinct haplotype between northern and southern Chinese Sus scrofa population in X 364 chromosome, there are two prominent topologies draw in the putative introgression 365 region. For those two genetic regions, we reconstructed phylogenetic tree separately

and obtained the same phylogenetic relationship among *Suinae* as SAGUARO
estimated (Supplementary Fig. 16). We also identified the autosomal regions which
support the introgression event found in the X chromosome. The sliding-window
D-statistic analyses suggest a nearly equal amount of introgressed windows among
different population (Supplementary Fig. 17). Similar average length of introgression
region was estimated by the quadruplet SAGUARO analyses present (Supplementary
Fig. 18).

373

374 D statistic under models of no gene flow

- We used the divergence time estimated from MCMCtree. We assumed an effective population size of 100,000 individuals and a generation time of 5 years, a
- 377 recombination rate 0.8 cM/Mb (0.8×10^{-8} per bp per generation) and a mutation rate
- 1.25×10^{-8} . All simulations were done in a msprime-based software momi2¹³. We simulated 10000 loci with length of 100kb:
- 380 #an simplify model for Suidae phylogeny without geneflow
- 381 model = momi.DemographicModel(N_e=1e5, gen_time=5,muts_per_gen=1.25e-8)
- 382 model.add_leaf("PYGMY", N=1e5)
- 383 model.add_leaf("EU", N=1e5)
- 384 model.add_leaf("NC", N=1e5)
- 385 model.add_leaf("SC", N=1e5)
- 386 model.add_leaf("ISEA", N=1e5)
- 387 model.add_leaf("AF", N=1e5)
- 388 model.move_lineages("NC","SC",t=800000)
- 389 model.move_lineages("EU","SC",t=900000)
- 390 model.move_lineages("SC","ISEA",t=4100000)
- 391 model.move_lineages("ISEA","PYGMY",t=6100000)
- 392 model.move_lineages("PYGMY","AF",t=10200000)

We compared these simulations with read data from our study. D-statstics were calculated using quadruplets (((ISEA, Pygmy hog), X), warthog) and (((ISEA, X), pygmy hog), warthog). Comparing the D values to the simulations under the null

396 model, we find that the observed D statistics are in the extreme tail, with p < 0.001 for 397 all comparisons. Thus, these simulations suggest that it is very unlikely that D values 398 that low are due to incomplete lineage sorting in the ancestral population, consistent 399 with our claim of introgression. However, we need to be aware that this method 400 requires a very detailed and precise demographic model to get a better assessment. 401 The historical demographic information of pygmy hog and the ancestral population of 402 Suinae species are still deficient. Here, we can only fit in a simplified model. 403 Inaccurate of effective ancestral population size and bottleneck event may led to 404 over-/underestimation of ILS.

405 406

407 Demographic model for Pygmy hog and Sus

408 To better assess the demographic implications of a separate species origin, rather 409 than one due entirely to admixture, we performed demographic inference by applying 410 G-PhoCS (Generalized Phylogenetic Coalescent Sampler) to simple branching 411 models. G-PhoCS analyses are computational demanding, thus, due to 412 computational constraints, we focused on 12 individuals, from the following different 413 population or species: pygmy hog, ISEA (represented by S. verrucosus which has 414 little detectable admixture with Sus scrofa), European wild boar, North and South 415 China wild boar. Our objective was to infer rates of gene flow from between pygmy 416 hog and Sus scrofa in the context of a complete demographic model that includes 417 population divergence and changes in ancestral population sizes. We applied 418 G-PhoCS to a multiple sequence alignment of neutral genome fragments of the 12 419 genomes. From this neutral dataset, we first constructed a NJ tree which is 420 concordance with the main topology of the used population (Supplementary Fig. 24). 421 We therefore assumed a plausible topology based on the main phylogenetic tree for 422 the population phylogeny and fitted a variety of different gene flow models 423 (Supplementary Fig. 22). G-PhoCS models' migration bands allow a test of admixture 424 from D-statistic. Under the assumed branching structure, we inferred high probability 425 of gene flow between the common ancestor of Sus scrofa and pygmy hog. Using 426 G-PhoCS, we were also able to examine signatures of admixture in the ISEA 427 population, and found significant gene flow between the ISEA Sus and Asian wild boar. 428 which is consisted with former research⁷. Furthermore, we also applied a model with a 429 basal ghost population to test the results obtained from the X-chromosome analysis. 430 This model confirmed a post-speciation gene flow between the common ancestor of 431 wild boar and the ghost population (Supplementary data 4, Supplementary Fig. 23). 432 Also, European wild boar shows a secondary gene flow from the ghost population. 433 We interpret this pattern as isolation by distance, as mainland Asia is the start point of 434 Sus scrofa expansion, which allow the ancestor of extant Asian pig have more chance 435 to hybrid with non-introgression population. As we can't properly match a 436 non-introgression population into our model, G-PhoCS may assign the exceeding 437 introgression allele in European wild boar as a potential gene flow signal.

438

439 Enrichment analysis

We applied a functional annotation analysis using PANTHER v.11¹⁴ on the candidate 440 441 introgressed genes (Supplementary data 5). Genes from the pygmy hog/Sus scrofa 442 introgression and the Sus scrofa/ghost lineage introgression were analyzed separately. Gene-enrichment analyses were performed using clusterProfiler¹⁵. False 443 444 discovery rate (FDR) was performed to adjust P-values using the Benjamini and 445 Hochberg method. A P-value of <0.05 was used as the cut-off criterion. For the pygmy 446 hog/Sus scrofa introgression gene set, significant enriched KEGG pathway was 447 showed in Supplementary Fig. 27. For the Sus scrofa/ghost lineage introgression, we 448 only identified a limited number of candidate genes we identified, and no significant 449 enrichment was found. 450

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