

Biodiversity and Origin of Pig Breeds

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Abstract: Worldwide analysis of *Sus scrofa* genetic diversity with a wide variety of autosomal, mitochondrial and Y-chromosome markers has allowed to establish that this species was independently domesticated at multiple sites in Eurasia. Exploratory and commercial journeys favored the geographical dispersion of pigs from one geographical area to another, being the transportation of pigs from the Iberian Peninsula to the New World during the 15-17th centuries one of the most compelling cases. Besides population admixture, selection of morphological, behavioral and production traits has been another major force shaping the gene pool of current porcine breeds. In the next years to come, the availability of powerful genomic tools such as high throughput genotyping and next generation sequencing platforms will be instrumental to decipher the impact of demographic, migratory and selection processes on the pig genome.

Keywords: pig, domestication, genetic diversity, mitochondria

INTRODUCTION

Currently, pig breeds display an enormous amount of phenotypic diversity in terms of shape, color, size, production and reproduction abilities. How was this diversity generated and enhanced by pig breeders is a question of paramount importance in order to fully understand the history of this species and to be able to make inferences about past events related with two essential processes: domestication and breed formation. Importantly, genetic information can be also used in conservation programmes devoted to prevent the decline and extinction of local endangered breeds.

The predominant view in the middle of the 20th century was that pigs were domesticated in the Near East and brought abroad by Neolithic farmers, being the hypothesis of a pig domestication event in Asia clearly minority. In fact, archaeological findings in the Crescent Fertile geographical area, and particularly at Eastern Anatolia, supported a role for pigs as an important component of the Neolithic economy together with cattle, sheep and goats. Analysis of a unique stratigraphic sequence (10,200-7,500 YBP) at the site of Çayönü Tepesi revealed that pigs, as a consequence of domestication, suffered important morphological changes such as molar teeth and snout shortening (Larson *et al.*, 2011). The establishment of a dependent relationship between pigs and human might have been rather slow and possibly reached completion by the beginning of the Pottery Neolithic (Larson *et al.*, 2011). Archaeological findings, however, not only pointed out the Fertile Crescent as an important center of pig domestication. As early as the beginning of the 20th century, very substantial evidences about the occurrence of an ancient pig domestication event at China were found. Pig bones and paintings of swine dated 5,000-7,000 YBP have been discovered from then to present at archaeological sites at Hemudu, Banpo, Yangshao and Luojiajiao, to cite a few (Yuan *et al.*, 2008). From a genetic point of view, the existence of at least two independent domestication sites for pigs was strongly supported by mitochondrial data contributed by Giuffra *et al.* (2000). These authors evidenced the existence of two highly

divergent Far Eastern and Western porcine mitochondrial lineages, with an estimated time of divergence of at least 500,000 years before present (YBP). Of course, the existence of these two highly differentiated lineages was much more consistent with a scenario of two independent domestication sites, one at the Far East and the other one with a Western location, than with a single domestication site and subsequent migration to other geographical areas. Data obtained through the analysis of microsatellites clearly supported this conclusion by showing a strong genetic differentiation between Chinese and European pigs (Fan *et al.*, 2002), a result that has been confirmed by subsequent studies focused on genetic variation at the pig autosomal genome (Megens *et al.*, 2008). A worldwide survey of mitochondrial diversity gave further insights into the complexity of pig domestication by highlighting the existence of multiple domestication sites in the Old World (Larson *et al.*, 2005). Moreover, and by the first time, it was proposed that European pigs might have been locally domesticated. This hypothesis was supported by the fact that modern European pig breeds and Near Eastern wild boars do not share mitochondrial alleles, meaning that the former are not likely to descend from the latter. However, analysis of ancient European remains challenged this view by demonstrating the presence of Near Eastern mitochondrial alleles in porcine samples from Romania, Croatia, Germany and France (Larson *et al.*, 2007). Current data indicate that Near Eastern pigs entered Europe through the Danube and Mediterranean corridors but that in a short time frame they were replaced by pigs domesticated locally (this would explain the absence of a Near Eastern footprint in the genetic pool of European breeds). In summary, Near East and China, but not Europe, would be primary domestication sites for pigs. India, South East Asia and Taiwan have been also proposed as cryptic domestication sites but their status is still contentious because of a lack of archaeological evidence (Larson *et al.*, 2010).

Once domesticated, pigs were independently and simultaneously selected at many distinct geographical areas in the world for specific phenotypes related with morphology, color, tameness and productive and reproductive performance. This process led to the creation of swine populations that were progressively differentiated at a genetic level as a consequence of both geographical isolation and strong differences in selection goals. For instance, estimates of coefficients of genetic differentiation between European breeds range between 0.21-0.27 (SanCristobal *et al.*, 2006), a value that is remarkably high, while in Chinese breeds is somewhat lower (Li *et al.*, 2004). Moreover, current pig breeds display remarkable levels of genetic diversity (Tab. 1).

With no doubt, Europe and China were the main centers of pig breed development around the world, leaving a genetic footprint that can be recognized nowadays. For instance, it has been demonstrated that European breeds such as Large White, Berkshire, Tamworth and British Saddleback carry Far Eastern mitochondrial alleles at high frequencies (Fang and Andersson, 2006). The likely reason for this extensive Far Eastern introgression is the massive importation of Chinese sows into England during the 18th-19th centuries and their subsequent crossbreeding with local types in order to improve fatness and reproductive maturity (Jones, 1998). Analysis of Y-chromosome markers has also allowed to establish the participation of European and Far Eastern pigs in the foundation of African and South American swine breeds (Ramírez *et al.*, 2009). Particularly revealing was the case of Africa, with the Western part of the continent devoid of Far Eastern mitochondrial or Y-chromosome variants that, in contrast, were remarkably frequent in the Eastern coast (Fig. 1).

Ancient commercial relationships between China and Africa existed as soon as 863 AD, and there was an active trade between Portuguese colonies of Macao, Zimbabwe and Mozambique a few centuries ago. In summary, there was an ample window of opportunity to introduce Far Eastern pigs into Africa. The presence, at very low frequencies, of a Far Eastern

Y-chromosome haplotype in Nicaraguan and Argentinean creole pigs is more enigmatic. In fact, South American pigs have fundamentally a European genetic background since they descend from Iberian breeds brought by the Portuguese and Spanish sailors (Ramírez *et al.*, 2008). The existence of trading routes linking Macao and Brazil as well as Philippines and Mexico combined with the arrival of Chinese immigrants in Nicaragua at the end of the 19th century might explain these findings. As a whole, we can conclude that population admixture between distant geographical areas has been a major force shaping and enriching pig genetic diversity.

Tab. 1

Microsatellite variability in diverse pig populations¹

Population	H	H _o	A	N	n
Asian breeds					
Chenghua	0.83	0.51	12.77	60	27
Daweizi	0.87	0.67	14.46	56	27
Fuyundahe	0.86	0.59	14.27	60	27
Guanling	0.88	0.63	11.85	33	27
Min	0.83	0.46	12.92	60	27
Wuzhishan	0.50	0.52	3.44	22	16
Xiang	0.78	0.63	12.54	60	27
European breeds					
Berkshire	0.43	0.44	3.14	46	49
Duroc	0.56	0.54	3.52	199	13
Hampshire	0.54	0.48	5.12	53	50
Iberian	0.70	0.58	7.20	173	36
Landrace	0.64	0.61	4.46	120	13
Large Black	0.51	0.50	4.24	48	49
Large White	0.69	0.64	4.77	71	13
Piértrain	0.68	0.65	4.56	925	13
Tamworth	0.47	0.47	3.10	40	50

¹H and H_o=expected and observed heterozygosities; A=allelic diversity (mean number of alleles per locus); N=sample size; n=number of microsatellite loci

The recent advent of next-generation sequencing platforms and high throughput single nucleotide polymorphism (SNP) genotyping techniques has opened a new era in the analysis of pig genetic diversity. Combination of these two technologies has allowed to generate huge SNP panels and genotype them in a costly-effective way. Massive parallel sequencing of pooled DNA from Landrace x Piértrain pigs allowed to obtain around 70 million short sequences that, after alignment, enabled to discover 17,489 SNPs of which 3,142 were successfully validated (Amaral *et al.*, 2009). Similarly, massive sequencing of a reduced representation library corresponding to an Iberian sow allowed retrieving 680,778 SNPs (Esteve-Codina *et al.*, 2011) in spite of the fact that this porcine breed is highly inbred. Even more, sequencing of 19 reduced representation libraries derived from four swine breeds (Duroc, Landrace, Large White, Piértrain) and a wild boar population made possible to identify as much as 372,000 SNPs. A total of 64,232 SNPs were selected from the whole SNP dataset to construct the Illumina Porcine 60K+SNP iSelect Beadchip (Ramos *et al.*, 2009), a tool that will be fundamental to carry out the high-resolution genetic characterization of worldwide pig breeds in the framework of the Pig HapMap Project. Moreover, genome-wide signals of domestication and selection have been recently detected in the pig genome, paving the way to the discovery of genes targeted by these processes (Amaral *et al.*, 2011).

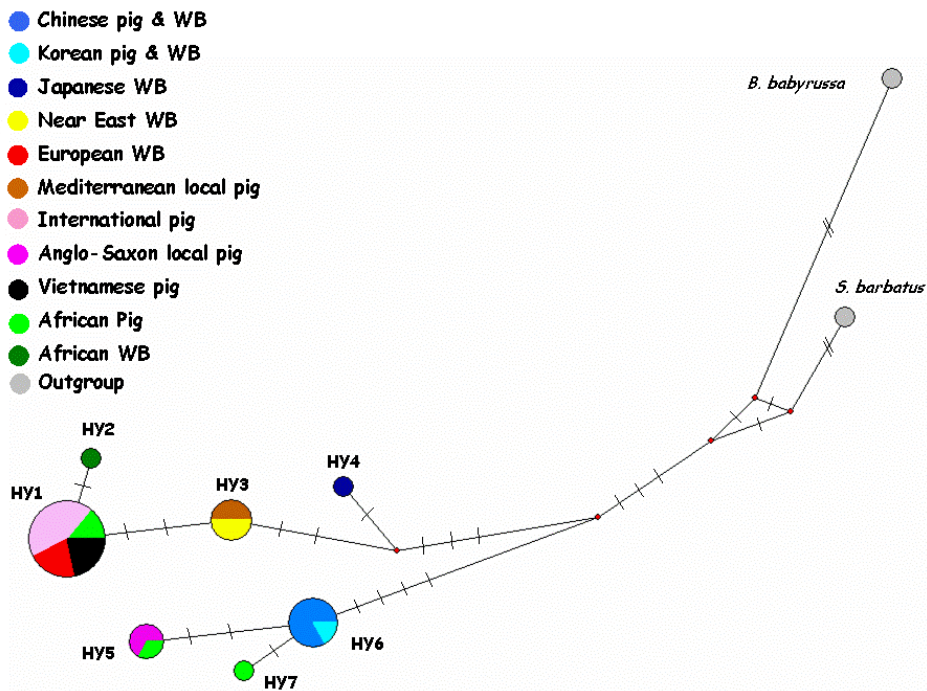


Fig. 1. Median joining network of pig and wild boar (WB) Y-chromosome haplotypes. West African pigs cluster in HY1, together with pigs and wild boars from Europe, while East African pigs group in HY5 and HY7 together with individuals from the Far East.

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