Origin and Genetic Diversity of Pig Breeds

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Genetic and archaeological findings suggest that pig domestication began about 9000–10 000 YBP at multiple sites across Eurasia, followed by their subsequent spread at a worldwide scale. Development of local types throughout the centuries led to the foundation, mostly during the nineteenth century, of current modern breeds with defined phenotypes and production abilities. Extensive intercrossing markedly increased the gene pool of these founder populations. For instance, it is well known that many European pig breeds carry Far Eastern haplotypes at high frequencies because of an ancient introgression with Chinese swine. Since then, artificial selection, genetic bottlenecks and inbreeding have significantly modified the allelic diversity of pig breeds. In the next future, state-of-the-art scientific advances as well as conservation programmes will be fundamental to preserve the genetic reservoir of pig breeds as well as to exploit it in the context of artificial selection schemes.

Introduction

Wild and domesticated pigs are even-toed ungulates that belong to the Suidae family. Closely related species forming part of this family are babirusa (*Babyrousa babyrussa*, from Indonesia) and common warthog (*Phacochoerus africanus*), bushpig (*Potamochoerus larvatus*) and Giant Forest hog (*Hylochoerus meinertzbageni*) that are native to Africa (Jones, 1998). Noteworthy, most species of the genus *Sus* are exclusively located in South East Asia (i.e. *Sus verrucosus*, *Sus celebensis*, *Sus cebifrons* and *Sus philippensis*). In strong contrast, wild boars (*Sus scrofa*) have a much wider geographical distribution that encompasses Eurasia and North Africa (Jones, 1998). Domestic pigs can be found worldwide because of their extraordinary importance in the production of red meat, lard and cured products. In this way, pigs are the main source of meat in the world (40%, 93 million metric tons), China, European Union, United States, Brazil and Canada being the top main producers (Orr and Shen, 2006). The high adaptability of pigs to a wide range of management and feeding conditions and their fast growth, early sexual maturity and high prolificacy and feed conversion rate are the key factors explaining the prominence of pigs as a livestock species (Taverner and Dunkin, 1996).

A long road has been covered since the initial domestication of wild boars in the Neolithic to the development of hundreds of modern pig breeds with very distinctive phenotypes and production abilities. In this article, we discuss the main events that shaped this process as well as their influence on the extant patterns of swine genetic diversity.

Complex Process of Pig Domestication

Livestock domestication was one of the most decisive events in the history of mankind. Establishment of an enduring and mutualistic relationship between human and animal populations rendered priceless benefits for both partners. Whilst humans were granted with a sustained access to animal food supplies, domestic species received protection against potential predators and increased their numbers and geographical distribution far beyond their wild ancestors (Zeder *et al.*, 2006). Zooarchaeological

records suggest that domestication began about 9000 YBP promoting the transition from hunter-gatherer to agricultural and farming societies. Domestication was not an instantaneous process. On the contrary, changes in the morphology and behaviour of domesticates were gradual and cumulative (Zeder *et al.*, 2006). Analysis of ninth to seventh millenium pig remains at the early Neolithic site of Çayönü Tepesi (Eastern Anatolia) provides a clear picture of this slow change, evidencing a progressive shortening of the dental row, face, mandible and legs as well as a global reduction of body size (Porter, 1993; Dobney and Larson, 2006). **See also**: Evolution during Domestication

The classical view that pigs were fundamentally domesticated at the Fertile Crescent has been recently challenged by genetic studies suggesting the existence of additional domestication centres (Giuffra *et al.*, 2000; Larson *et al.*, 2005, 2010). In this way, mitochondrial and microsatellite-based analyses have consistently shown that Western and Far Eastern pigs were independently domesticated (Giuffra *et al.*, 2000; Larson *et al.*, 2005; SanCristobal *et al.*, 2006; Megens *et al.*, 2008). These two populations show a strong genetic differentiation and most deoxyribonucleic acid (DNA)-based estimates indicate that they might have split around 600 000–900 000 YBP, that is well before domestication took place (Alves *et al.*, 2003; Fang and Andersson, 2006). At a phenotypic level, Western and Far Eastern pigs are very different, with the latter displaying distinctive features such as short legs, dropping belly, prick ears, wrinkled skin and fatter appearance (Porter, 1993). Current evidences suggest that *Sus scrofa* originated in South East Asia (as other suid species) and dispersed into India and East Asia moving westwards until reaching Europe (Larson *et al.*, 2005, 2010; Ramírez *et al.*, 2009). Later on, the Eastern and Western gene pools became genetically isolated. The obvious consequence of this process would be a higher genetic diversity of *Sus scrofa* in Asia versus Europe. As a matter of fact, a series of genetic studies have compellingly demonstrated that this is the case (Larson *et al.*, 2005; Wu *et al.*, 2007; Ramírez *et al.*, 2009; Luetkemeier *et al.*, 2010).

China might have been one of the most important pig domestication sites in the Far East (Yuan *et al.*, 2008). Pig bones and paintings of swine have been discovered at distant Neolithic sites located at Yangshao (Henan, 5000–6800 YBP), Banpo (Shaanxi, 5600–6640 YBP), Hemudu (Zhejiang, 6780 YBP) and Luojiajiao (7040–7170 YBP). Although precise domestication times and locations remain to be defined accurately (Larson *et al.*, 2010), Wu *et al.* (2007) have suggested that the Mekong and Yangtze regions might have played a prominent role in this process. *Sus scrofa* from India, South East Asia and Japan have also very distinctive genetic backgrounds suggesting the existence of additional domestication sites (**Figure 1**; Larson *et al.*, 2005, 2010; Wu *et al.*, 2007). This is supported by recent evidence showing that Far Eastern pigs have multiple origins (Luetkemeier *et al.*, 2010). However, these genetic signatures should be interpreted with caution because their existence does not necessarily imply the

occurrence of local domestication events (Zeder *et al.*, 2006). In consequence, primary domestication sites should be defined not only on the basis of genetic data but also according to archaeological and historical evidences.

The origin of European domestic pigs is still unclear. The analysis of mitochondrial markers has evidenced the absence of Near Eastern haplotypes in modern European swine breeds (**Figure 1**; Larson *et al.*, 2005; Ramírez *et al.*, 2009). This finding might suggest that pigs would have been independently domesticated in Europe. However, investigations based on autosomal and Y-chromosome markers have revealed that European and Near Eastern *Sus scrofa* populations are closely related (**Figure 2** and **Figure 3**; Ramírez *et al.*, 2009). Moreover, the analysis of ancient pig remains has evidenced the presence of Near Eastern mitochondrial haplotypes in Europe (Larson *et al.*, 2007). These results suggest that pig domestication in Europe would have not been truly independent, and that Near Eastern pigs entered Europe in the Early Neolithic and spread westwards through the Danubian and Mediterranean corridors (Larson *et al.*, 2007). This Fertile Crescent footprint might have been fully erased by the accelerated replacement of Near Eastern pigs by their European counterparts (Larson *et al.*, 2007).

Development of Pig Breeds around the World

In the Neolithic, primitive pigs might have been confined in crude stockades or styes (Baxter, 1984), although intentional or accidental backcrossing with their wild ancestors would have not been uncommon (Porter, 1993). This feature might have contributed to recover part of the genetic diversity lost as a consequence of domestication. The low to moderate genetic divergence between pigs and wild boars (F_{ST} around 0.07) supports this interpretation (Scandura *et al.*, 2008; Ramírez *et al.*, 2009). Archaeological findings at the pre-Dynastic site of Merimde and at Tell el-Amarna suggest that pigs were produced at a large scale in the ancient Egypt (Blench, 2000). Pigs were also spread along North Africa playing a significant role in the economy of Neolithic populations of Tangier (Morocco, 6000–3000 YBP; Blench, 2000). In the Roman Empire, pigs were widely used not only for domestic consumption but also for hunting and religious ceremonies (Baxter, 1984). With regard to the Far East, pig breeding was well established in China more than 5000 years ago (Porter, 1993), representing not only a mean of sustenance but also a symbol of power and prestige (Kim, 1994).

After domestication and throughout the ages, Europe and China became the two major pig-breeding centres of the Old World, developing a large variety of local types perfectly adapted to the environmental conditions where they were raised. These local types were independently selected for certain traits (mostly behavioural and morphological) during many centuries providing the
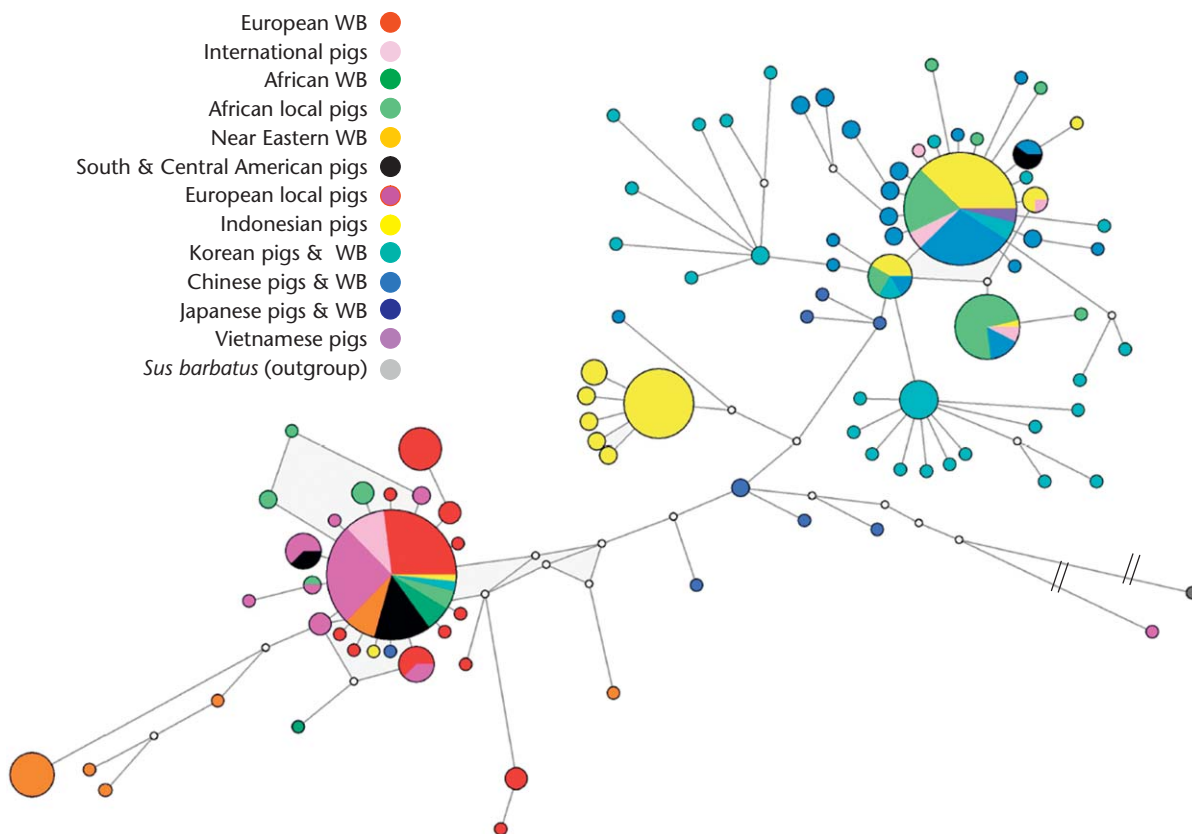
Figure 1 Median joining network of 440 mitochondrial D-loop sequences corresponding to worldwide pig and wild boar (WB) populations. It can be seen that Far Eastern *Sus scrofa* display higher levels of genetic diversity than their European counterpaarts (most European haplotypes are grouped in a single cluster). It is also worth to highlight that European and Near Eastern mitochondrial haplotypes in general do not cluster together suggesting that both populations have distinct origins.
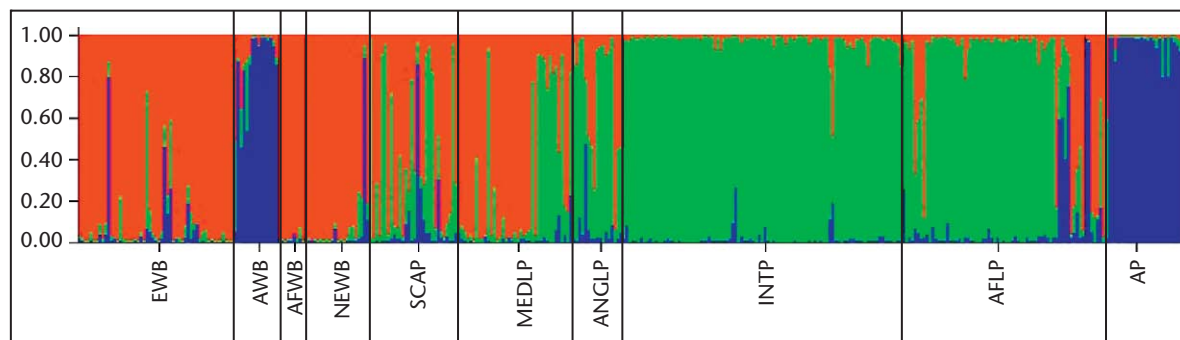

Figure 2 Genetic dissection of the relationships between several *Sus scrofa* population based on the structure analysis of microsatellite data. It can be observed that there are three major groups with European (red), Far Eastern (blue) and mixed (green) ancestry. EWB, European wild boar; AWB, Far Eastern wild boar; AFWB, African wild boar; NEWB, Near Eastern wild boar; SCAP, South and Central American local pigs; MEDLP, Mediterranean and Slav local pigs; ANGLP, Anglo-Saxon local pigs; INTP, International pig breeds; AFLP, African local pigs and AP, Far Eastern local pigs. Reproduced from Ramírez *et al.* (2009) with permission from Oxford University Press.

foundations for the creation of modern breeds. Global spread of European and Far Eastern swine populations was an unavoidable consequence of the ever-increasing network of commercial and exploratory routes reaching the most remote boundaries of the world. The Age of

Discoveries (fifteenth to seventeenth centuries) was particularly important in this regard, resulting in the colonisation of a new continent, America, the circumnavigation of Africa and the exploration of the Indian and Pacific oceans by European nations. The Eastern coast of Africa
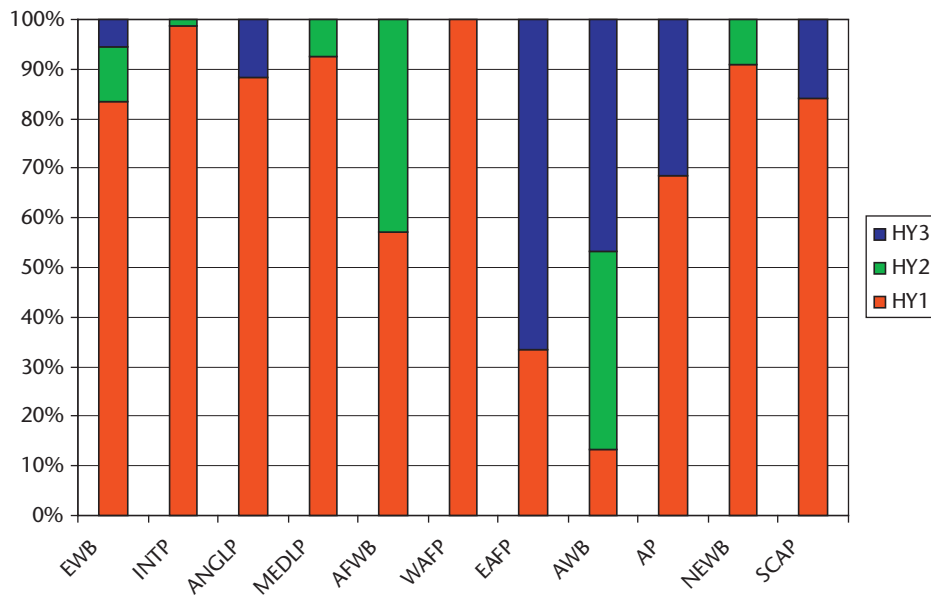
Figure 3 Three Y-chromosome haplotypes have been identified in *Sus scrofa* so far, being distributed in two major lineages (HY1+HY2 and HY3) that diverged around 1.27 Mya. In this picture, Y-chromosome haplotype frequencies at diverse *Sus scrofa* populations are shown. Abbreviations are indicated in the legend of **Figure 2**, with the exception of WAFP (West African pigs) and EAFP (East African pigs). Noteworthy, in these two latter populations differences in haplotype frequencies are dramatic, suggesting that EAFP pigs were strongly introgressed with Far Eastern blood at the paternal level while WAFP did not.
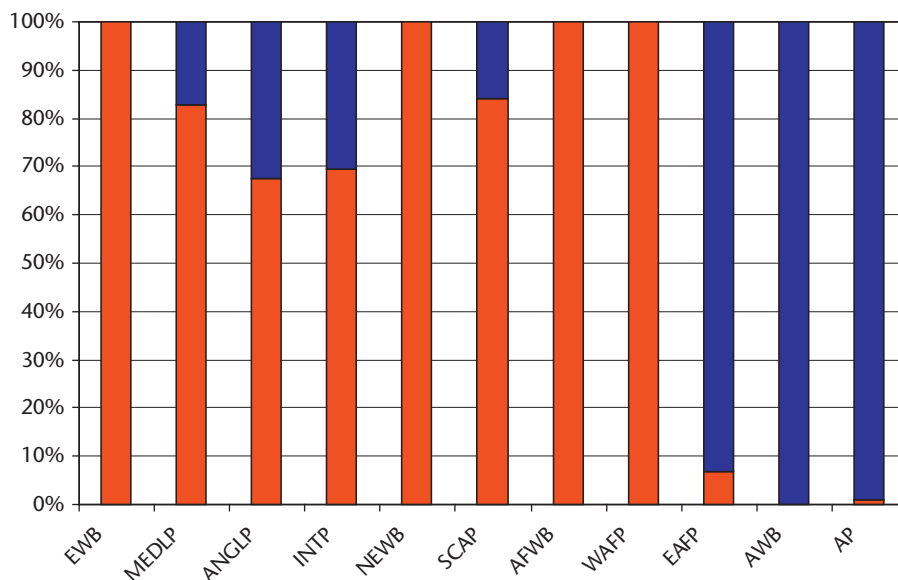
Figure 4 Frequencies of European (in red) and Far Eastern (in blue) mitochondrial cytochrome *b* haplotypes in diverse *Sus scrofa* populations (abbreviations as indicated in the legends of **Figure 2** and **Figure 3**). It is worth to highlight the strong Far Eastern genetic signature in Anglosaxon, International and East African pig breeds.

was also explored by the Chinese five centuries ago (Levathes, 1994). These historical events have had an enormous impact on the genetic diversity of pig breeds, leaving a footprint that can be recognised nowadays. In this way, the combined analysis of mitochondrial, autosomal and Y-chromosome markers has revealed two clearly distinct genetic patterns in Africa (**Figure 3** and **Figure 4**;

Ramírez *et al.*, 2009). In Western Africa, pigs do not display Far Eastern alleles suggesting that they descend from the admixture of indigenous populations and exotic breeds with an European ancestry (i.e. Iberian pigs brought by the Portuguese in the fifteenth century as well as swine introduced by the European colonisers in the nineteenth to twentieth centuries). In strong contrast, East African pigs

harbour Far Eastern alleles at significant frequencies evidencing that they have a mixed European/Chinese origin (Ramírez *et al.*, 2009).

South America was completely devoid of pigs until its colonisation by the Spanish and the Portuguese in the fifteenth to seventeenth centuries. Consistently, European alleles are neatly predominant in creole breeds (Ramírez *et al.*, 2009; Souza *et al.*, 2009). Iberian pigs were transported at many Spanish expeditions including the second trip of Columbus (1493) as well as in the exploration of Perú (1526–1531) and Mexico (1526) by Pizarro and Montego respectively (Rodero *et al.*, 1992). This practice was motivated by several circumstances. In the first place, pigs were cheap and became very abundant (particularly in the Antilles) because of their hardiness and high fecundity (Zadik, 2005). Moreover, they occupied little space in boats and provided a considerable percentage of usable meat (Zadik, 2005). Recent studies have confirmed these historical records by demonstrating the existence of an Iberian genetic signature in South American creole breeds (Ramírez *et al.*, 2009; Souza *et al.*, 2009).

Throughout the centuries, the sustained development of local types crystallised in the establishment of well-defined pig breeds around the nineteenth century. Large White was recognised as a genuine breed in England in 1868 and the first herd book was published in 1884 (Jones, 1998). The Duroc or Jersey Red Swine Club, an association of nine Wisconsin breeders, was founded in 1882 and a national Large White and 'land pig' breeding scheme was established in Denmark at the end of the nineteenth century (Jones, 1998). The current number of pig breeds might fluctuate around 200–300 (Porter, 1993; Jones, 1998). Historically, the three main centres of breed development have been England, China and the United States (Jones, 1998). Breeds were often created by admixing diverse swine local types with different production aptitudes and genetic backgrounds. Piétrain, for instance, is a Belgian pig breed that, according to Jones (1998), might have as many as six putative ancestors (Berkshire, Normand, Large White, Tamworth, Limousin and local Belgian breeds). Duroc pigs also seem to descend from multiple genetic sources including Berkshire, Iberian, Tamworth and Red Guinea Hog (Porter, 1993). This extensive process of genetic admixture is convincingly illustrated by the introgression of British breeds with Chinese sows that took place 2–3 centuries ago with the intention of increasing fatness and achieving an earlier maturity (Jones, 1998). The impact of this gene flow was subsequently amplified by the fact that British swine participated in the foundation of many other breeds. As a consequence of these events, Far Eastern mitochondrial haplotypes can be found at high frequencies in a wide array of European populations (**Figure 4**; Clop *et al.*, 2004; Fang and Andersson, 2006; Ramírez *et al.*, 2009).

Whilst certain pig breeds have a single well-defined ancestry, others were formed by crossbreeding populations with distinct origins. Subsequently, pig breeds became closed genetic pools modelled by the chisels of artificial selection and genetic drift. This process was very effective and current estimates of genetic differentiation among European breeds yield F_{ST} values between 0.21 and 0.27 (SanCristobal *et al.*, 2006). Microsatellite-based studies of European pigs have also shown that individuals from the same breed tend to cluster together when subjected to phylogenetic analysis, evidencing the existence of a notable level of genetic structure (SanCristobal *et al.*, 2006). Similar conclusions can be reached for Chinese breeds, although F_{ST} values tend to be somewhat lower ($F_{ST} = 0.07$–0.14) suggesting the existence of a higher level of genetic exchange (Li *et al.*, 2004). **See also**: Drift: Introduction; Drift: Theoretical Aspects

Notably, the geographical distribution of pig breeds differs dramatically depending on the population under consideration. Although certain breeds (e.g. Large White, Landrace, Hampshire, Duroc, etc.) have been extraordinarily sucessful spreading all over the world and becoming widely predominant in modern intensive systems (the so-called International breeds), others (Iberian, Normand, Sicilian, Mangalitsa, Tamworth, Taihu, Jinhua, etc.) have remained confined to specific geographical areas (local breeds).

Impact of Evolutionary Forces on Pig Genetic Diversity

Artificial selection is but adaptation although at an accelerated rate. The amazing diversity of pig breeds, as in other domestic animals and plants, as well as how rapidly animal species have responded to artificial selection is a convincing proof of how DNA variability is responsible for phenotypic plasticity. Therefore, the same evolutionary forces that shape nucleotide variability in natural populations operate in domestic species. Their relative importance, though, is not necessarily the same as in wild species. Two important phenomena are of particular relevance in livestock: domestication and artificial selection (Porter, 1993). Both episodes involve strong bottlenecks/founder effects and dramatic selective sweeps decreasing the levels of nucleotide diversity. The footprints of these two processes can be differentiated because adaptation or selection is usually restricted to small genome regions (only a subset of genes is affected), whereas demographic events (i.e. bottlenecks, founder effects) leave a whole-genome signature (Bamshad and Wooding, 2003). Localised reduced diversity has been reported in several instances in the pig but, to date, the absence of comprehensive genome-wide studies together with the scarcity of known causal mutations has made the interpretation of these findings difficult (Ojeda *et al.*, 2008). In fact, disentangling selective from purely demographic forces is a very challenging problem from both theoretical and experimental points of view (Nielsen *et al.*, 2007). In pigs, it is worth to mention the identification of a strong selective sweep signature in the insulin-like growth factor 2 gene (Van Laere *et al.*, 2003).

This locus contains an intronic mutation with effects on muscle growth and fat deposition. Breeds that have been intensively selected for leanness (e.g. Piétrain) display a reduced number of haplotypes because most of the variability has been erased by artificial selection favouring the A-allele (Ojeda et al., 2008). The complex interplay between artificial selection and genetic variability of pig breeds has also been explored in the framework of quantitative trait loci (QTL) analyses. In this way, whole-genome scans with microsatellite markers have revealed that commercial pig populations still retain a considerable amount of genetic variation affecting production traits that have been selected for many generations (Vidal et al., 2005). This observation might be explained by factors, such as the existence of multiple breeding goals (that might change with time), pleiotropy, past introgression events and limited selection pressure on females, that diminish the probability of QTL allele-fixation (Vidal et al., 2005). **See also**: Quantitative Genetics

Given that European pig breeds were domesticated from local wild boars, it is expected that domestic pigs harbour much less nucleotide diversity than their wild counterparts due to the occurrence of founder effects. Paradoxically, both nuclear and mitochondrial DNA studies suggest rather the opposite (**Figure 1**; **Table 1**). The reason for this unexpected observation is probably 2-fold. First, European wild boar has itself undergone strong bottlenecks, for example, during the last glaciation (Scandura et al., 2008). Even recently, wild boars were eradicated from several countries, like Great Britain during the Middle Ages, only to be reintroduced later (Porter, 1993). Currently, European wild boar populations are under exponential growth as is evident from mtDNA phylogenies (**Figure 1**). But more importantly, and as mentioned in the previous section, Far Eastern pigs were imported and crossed with European domestic pigs during the eighteenth to nineteenth centuries (Porter, 1993). In so doing, European breeders were unconsciously increasing the nucleotide diversity of pigs that made up later the germplasm of most well-known International breeds like Large White and Landrace (Porter, 1993). A recent estimation suggests that the genetic flow between Chinese and European swine breeds has been very large and fundamental to increase genetic variability in the latter (**Figure 4**; Ojeda et al., 2010). This feature also explains why levels of genetic diversity are similar in highly selected and unselected European pig populations, since the former have been mostly introgressed with Far Eastern alleles while the latter in general were spared from this admixture process (Clop et al., 2004).

In addition to nucleotide diversity, linkage disequilibrium, that is the degree of co-transmission between alleles at different loci is also important to assess the genetic structure of a given population. Unfortunately, there is as yet relatively scarce information on the extent of linkage

Table 1 Microsatellite variability in diverse pig and wild boar populations

Population	H	H_o	A	N	n	References
African wild boar	0.65	0.58	3.83	9	12	Ramírez et al. (2009)
Asian wild boar	0.81	0.55	8.50	15	12	Ramírez et al. (2009)
European wild boar	0.64	0.54	7.83	51	12	Ramírez et al. (2009)
Near Eastern wild boar	0.71	0.60	6.92	22	12	Ramírez et al. (2009)
Berkshire	0.43	0.44	3.14	46	49	SanCristobal et al. (2006)
Chenghua	0.83	0.51	12.77	60	27	Yang et al. (2003)
Daweizi	0.87	0.67	14.46	56	27	Yang et al. (2003)
Duroc	0.56	0.54	3.52	199	13	Boitard et al. (2010)
Fuyuandahe	0.86	0.59	14.27	60	27	Yang et al. (2003)
Guanling	0.88	0.63	11.85	33	27	Yang et al. (2003)
Hampshire	0.54	0.48	5.12	53	50	SanCristobal et al. (2006)
Iberian	0.70	0.58	7.20	173	36	Fabuel et al. (2004)
Landrace	0.64	0.61	4.46	120	13	Boitard et al. (2010)
Large Black	0.51	0.50	4.24	48	49	SanCristobal et al. (2006)
Large White	0.69	0.64	4.77	71	13	Boitard et al. (2010)
Min	0.83	0.46	12.92	60	27	Yang et al. (2003)
Neijiang	0.84	0.63	13.31	60	27	Yang et al. (2003)
Ningxiang	0.85	0.68	14.23	60	27	Yang et al. (2003)
Piétrain	0.68	0.65	4.56	925	13	Boitard et al. (2010)
Tamworth	0.47	0.47	3.10	40	50	SanCristobal et al. (2006)
Wuzhishan	0.50	0.52	3.44	22	16	Kim et al. (2005)
Xiang	0.78	0.63	12.54	60	27	Yang et al. (2003)
Yorkshire	0.64	0.58	5.13	32	16	Kim et al. (2005)

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

disequilibrium between and within breeds in pigs. In agreement with expectations, Far Eastern pigs seem to harbour shorter haplotype blocks than their European counterparts, as a consequence of smaller effective population sizes in the latter populations (Amaral *et al.*, 2008). Nevertheless, this evidence stems from genotyping rather than sequencing, and single nucleotide polymorphism (SNP) ascertainment might have strongly biased these results. Other authors have reported a more complex pattern based on full resequencing data, although for smaller regions (Ojeda *et al.*, 2006; **Figure 5**). An important remark is that the disequilibrium pattern can vary dramatically according to the population under analysis. This is simply a consequence that coalescence has a very large variance, especially in structured populations with low effective size (Hein *et al.*, 2005). **See also**: Coalescent Theory; Linkage Disequilibrium

Recently, a 60 k high-density SNP genotyping assay covering all autosomes and sex chromosomes has been developed (Ramos *et al.*, 2009). This tool will allow a genome-wide estimate of linkage disequilibrium, among other important parameters, in the porcine species. As of today, there are no published data using this approach although the sequence of the pig genome and a whole-genome survey of SNP variation in diverse breeds are expected to be brought to light during 2010. Our own results in local Mediterranean (e.g. Iberian pig), European

and Far Eastern wild boar and South American creole populations show that the largest genetic distance lies between Far Eastern and European *Sus scrofa*, with local Mediterranean pigs being closely related to European wild boars. South American populations show a complex genetic ancestry, being closer to European rather than Far Eastern populations, and occupying an intermediate position between Iberian and International breeds, a logical outcome of their synthetic origin. Population structure is remarkably high, with F_{ST} in the order of 10% between European or South American populations and in the order of 30% between European and Far Eastern pigs. Overall, adaptive signals seem to be weak, contrary to what has been found in other species, like humans or dogs. Moreover, we have not found an excess of genic SNPs among the most extreme SNPs in terms of genetic differentiation (Souza *et al.*, 2010).

Genetic Conservation of Pig Breeds

In the second half of the twentieth century, several European and US pig breeds were subjected to high selection pressures for production traits, its management was intensified and industrialised, and its geographical localisation, expanded at a worldwide scale. This had a huge impact on local breeds, which felt out of use and were either
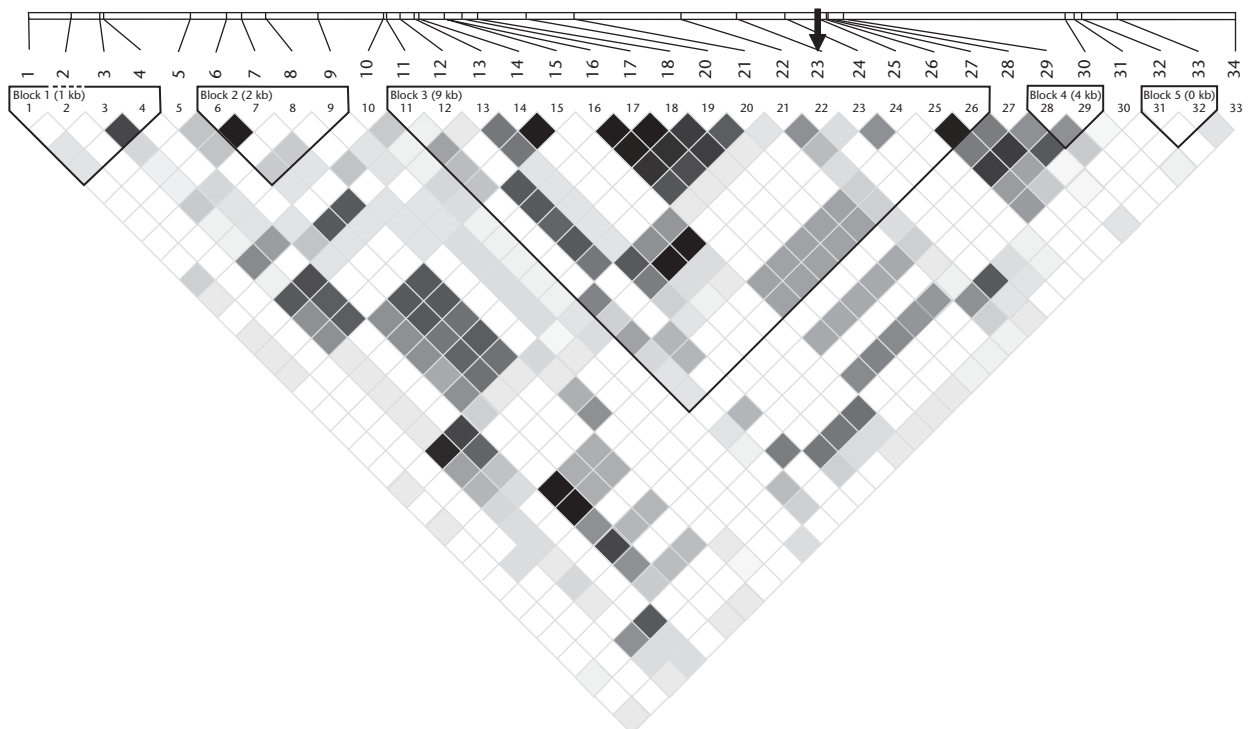
Figure 5 Haplotype structure around an intron 3 mutation at the insulin-like growth factor 2 gene with causal effects on muscle growth and leanness. This plot shows the squared correlation (r^2) between pairs of loci (colour intensity augments proportionally to r^2 values). Haplotype blocks are underlined and the arrow points at the causative intron 3 mutation. Five haplotype blocks were detected, spanning 1, 2, 9, 4 and 0.8 kb respectively. The third block was the largest and contained the causative mutation. From Ojeda *et al.* (2008) with permission from the Genetics Society of America.

largely replaced by or intercrossed with International breeds. For instance, most of lard pig breeds disappeared from the United States during the second half of the twentieth century because consumers were concerned with fats of animal origin and vegetable oils were successfully marketed as a healthier alternative. Today, only a few lard breeds (e.g. Guinea hog, Mulefoot and Choctaw) have managed to survive in the United States, although their census is really low (http://www.albc-usa.org/cpl/wtchlist.html#pigs). In Spain, one of the main pig producers of the EU, several breeds have been brought to extinction (e.g. Chato Vitoriano and Batzanesa) and many others (e.g. Cerdo Canario, Torbiscal, Chato Murciano and Dorado Gaditano) only have a few hundred individuals at best (http://www.uco.es/organiza/departamentos/genetica/serga). Similarly, diverse British breeds have an endangered (e.g. British Lop and Middle White) or vulnerable (e.g. Berkshire, Large Black, Tamworth and Welsh) status (http://www.bamfield.eu/rare_breeds.php). These are not isolated cases but the reflection of a general and worrying situation, with 20% of pig breeds at risk of extinction (Hammond and Leitch, 1998). Fortunately, in the past 20 years many breed conservation programmes have been initiated. Their main goals are to decrease inbreeding, while implementing, if possible, animal breeding and selection infrastructures. This course of action is complemented by *ex situ* conservation programmes that rely on the criogenic conservation of germplasm from minimally related animals and the maintenance of endangered populations at protected reservations (e.g. farm parks).

Finally, it should be stressed that even breeds with large population sizes (e.g. International breeds) have suffered a strong genetic erosion in the past decades. Now, pig production is dominated by a few transnational companies that are vertically integrated and that rely on three way crosses between a reduced number of highly selected pig lines. Estimation of mean inbreeding coefficients and effective sizes in five US pig breeds (Berkshire, Duroc, Hampshire, Landrace and Yorkshire) have yielded values of 3.2–7.8% and of 74.18–113.12 respectively (Welsh *et al.*, 2010). These numbers reflect that genetic variation of these populations, formed by hundreds of thousands of individuals, has been severely reduced by the increasing rate of inbreeding and artificial selection. Design of appropiate mating and restocking strategies would be crucial to limit the negative impact of these two factors. **See also**: Inbreeding

Future Prospects in the Analysis of Pig Genetic Variability

The study of DNA variability has suddenly come to a new age: that of complete genome population genetics. The advent of next generation sequencing technologies has truly revolutionised genomics research (Metzker, 2010).

These technical advances have democratised genomic resources and will provide fast and complete data *à la carte* in any species, allowing to catch up with model or human species. For instance, the latest Illumina's technology at this time (May 2010) provides a $30 \times$ coverage of a mammalian genome in a single run (8 days) at a consumable's cost of $10 000. And this is only the beginning. **See also**: High-Throughput Single Nucleotide Polymorphisms Genotyping Technologies; Next Generation Sequencing Technologies and Their Applications

But after all the fuss, do we *really* need more sequence? What are the implications from a population genetics point of view? Although a categorical *yes* is a response to the first question, it is a bit early to respond accurately to the second one. As for having complete sequence, the most immediate advantages are the removal of SNP ascertainment bias and the identification of structural, and not only sequence, variants. Ascertainment bias occurs because SNPs contained in high-density genotyping chips are usually chosen from a very limited number of sequenced individuals and often a criterion of either minimum allele frequency or segregation in different breeds is established. This results in a biased site frequency spectrum towards intermediate allele frequencies. For diversity studies, the main consequence of this practice is a biased estimate of DNA diversity. If the genotyped panel is close genetically to the discovery panel, the estimate will be biased upwards, because most of the SNPs will also be segregating at intermediate frequencies. On the contrary, if both panels are very distant, diversity measures will be severely underestimated because many SNPs (reflecting the true levels of genetic variation) are systematically ignored. With regard to structural variants, their identification is much more difficult computationally and requires much higher coverage than the discovery of point mutations (Medvedev *et al.*, 2009). No guarantee exists yet that all structural variants can be uncovered with short read sequencing technologies.

Thus far, applications of next generation sequencing methods to pig genomics have been limited to SNP discovery in reduced representation libraries of pools (Amaral *et al.*, 2009a; Ramos *et al.*, 2009). This has been a very cost-effective approach compared to traditional Sanger sequencing. However, the more interesting applications are yet to come. For instance, and following the avenues of studies performed in chicken (Rubin *et al.*, 2010), the partial resequencing of pools pertaining to highly divergent populations, for example wild ancestor and domestic breeds, will allow to characterise the footprint of domestication and artificial selection at a genome-wide level. A similar approach to that of Rubin and coworkers has allowed to identify, in the wild boar, regions with either low or high variability that are potential targets of selection (Amaral *et al.*, 2009b). But, as mentioned, this is only the very beginning because we will witness the deliverance and detailed description of complete pig genomes very soon. Not only the bioinformatics challenges are daunting, many of the questions we might answer are still to be formulated.

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