The Origin of the Domestic Pig: Independent Domestication and Subsequent Introgression


Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala Biomedical Centre, S-751 24 Uppsala, Sweden

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ABSTRACT

The domestic pig originates from the Eurasian wild boar (Sus scrofa). We have sequenced mitochondrial DNA and nuclear genes from wild and domestic pigs from Asia and Europe. Clear evidence was obtained for domestication to have occurred independently from wild boar subspecies in Europe and Asia. The time since divergence of the ancestral forms was estimated at \( \sim 500,000 \) years, well before domestication \( \sim 9,000 \) years ago. Historical records indicate that Asian pigs were introduced into Europe during the 18th and early 19th centuries. We found molecular evidence for this introgression and the data indicated a hybrid origin of some major “European”pig breeds. The study is an advance in pig genetics and has important implications for the maintenance and utilization of genetic diversity in this livestock species.

THE wild boar is widespread in Eurasia and occurs in Northwest Africa; the existence of at least 16 different subspecies has been proposed (Ruvinsky and Rothschild 1998). Domestication of the pig is likely to have occurred first in the Near East \( \sim 9000 \) YBP and may have occurred repeatedly from local populations of wild boars (Bökönyi 1974). However, it is not yet established whether modern domestic pigs showing marked morphological differences compared with their wild ancestor have a single or multiple origin. Darwin (1868) recognized two major forms of domestic pigs, a European (Sus scrofa) and an Asian form (Sus indicus). The former was assumed to originate from the European wild boar, while the wild ancestor of the latter was unknown. Darwin considered the two forms as distinct species on the basis of profound phenotypic differences. It is well documented that Asian pigs were used to improve European pig breeds during the 18th and early 19th centuries (Darwin 1868; Jones 1998) but to what extent Asian pigs have contributed genetically to different European pig breeds is unknown. In a recent study the divergence between major European pig breeds and the Chinese Meishan breed was estimated at \( \sim 2000 \) years using microsatellite markers (Paszek et al. 1998). Limited studies of mitochondrial DNA (mtDNA) have indicated genetic differences between European and Asian pigs but no estimate of the time since divergence has been provided (Watanabe et al. 1986; Okumura et al. 1996).

The aim of this investigation was to provide a more comprehensive molecular analysis of the origin of domestic pigs by analyzing wild and domestic pigs from both Asia and Europe. The molecular analysis included the entire coding sequence of the mtDNA cytochrome B (cytB) gene and 440 bp of the hypervariable mtDNA control region. In addition, we have analyzed three nuclear genes: melanocortin receptor 1 (MC1R), tyrosinase (TYR), and a glucosephosphate isomerase pseudogene (GPIP). We have reported previously that MC1R mutations cause coat color variation in pigs (Kijas et al. 1998). An interesting finding was that the allele for black color in Asian Meishan and British Large Black pigs differed by as many as four nucleotide substitutions from the consensus of MC1R alleles in European domestic and wild pigs. The observation was interpreted to reflect the introgression of an MC1R allele of Asian origin to the Large Black population. TYR encodes the tyrosinase enzyme, which has a key role in pigment synthesis. Loss-of-function mutations in this gene cause albinism in many species. We investigated this gene previously in a wild boar/Large White intercross but the observed sequence polymorphism did not correlate with any coat color variation. GPIP is clearly a pseudogene as it contains many potentially inactivating mutations (Haritz et al. 1993). The gene was included in this study because we assume that the selection pressure on this sequence should be minimal.

MATERIALS AND METHODS

Animals: Hair or blood samples were available from the domestic and wild boar populations listed in Table 1. The Large White, Landrace, Hampshire, and Duroc domestic pigs all originated from Swedish populations. The Meishan domestic pigs were from the PiGMaP reference pedigrees for gene.
map (Archibald et al. 1995). Genomic DNA was extracted from blood by standard methods or from hair by chelex extraction.

**Analysis of mitochondrial DNA:** The primers LmPro/ L51997 and TDKT/H16498 (Ward et al. 1991) were used to amplify and sequence a 440-bp fragment that included ~20 bp of the tRNA^{Met} and 420 bp of the hypervariable (5') portion of the control region. The complete (1140-bp) cytochrome B sequence was amplified by PCR and was sequenced by using combinations of the primers L14724, L14841, L15408, H15149, H15915 (Irwin et al. 1991) and the pig-specific primers L0616 (5'-TATCCTGCAGCAACGGAGAT) and H1106 (5'-AGGTGTGTTTGGTATGCTAG). PCR products were sequenced directly using the Big Dye terminator chemistry and an ABI377 Prism DNA sequencer (Perkin Elmer, Norwalk, CT). Sequences described in this work are AF136555-AF136568, Genetic distances between mitochondrial sequences were calculated using the MEGA software (Kumar et al. 1993). Bootstrap analyses (using 1000 replications) were used to assess the confidence in branching order. Maximum parsimony trees were constructed using PAUP 4.0 and the branch-and-bound method. The average pairwise distance between mtDNA sequences from the European and Asian clades was calculated according to Nei (1987).

## RESULTS

**Sequence analyses reveal three distinct pig mtDNA clades:** We sequenced the entire coding sequence (1140 bp) and amplified a 308-bp fragment (spanning polymorphic positions 316, 388, 389, and 415) that was used to specifically amplify 784 bp of GITP. The primers included eight and seven mismatched positions, respectively, compared with the functional GITP gene (Harbitz et al. 1993). Internal primers GITP2 (5'-CTTGCCTGC TGGCTTGGC-3') and GITP3 (5'-ATCCATCCTTACCAAGT GC-3') amplified a 308-bp fragment (spanning polymorphic positions 316, 388, 389, and 415; see Figure 3) that was used for SSCP analysis as described above. The GenBank accession numbers for the nuclear sequences described in this work are AF181958-AF181961 (GITP); AF181962, AF181963 (TYR); AF181964 (MC1R).

### Detection of sequence polymorphism in three nuclear genes:

The primers and reaction conditions used to amplify and sequence MC1R have been described (Kijas et al. 1998). A 727-bp region (including primers) of TYR exon 1 was amplified with the primers TYRP1 (5'-AGGGTGAGCTGGAAGAA GAA-3') and TYRP2 (5'-GAATCCAGCAAGAGAGTGC-3') using standard conditions but with the addition of 5% DMSO. SSCP analysis of TYR was carried out with the internal primers TYrex1K1 (5'-ACTACCGAGCCAAGACTTG-3') and TYrex1K2 (5'-AGGCAATAATGCCTCTCCGAGC-3'), which were used to amplify a 173-bp product spanning polymorphic positions 544 and 628 (see Figure 3). Denatured PCR product (1 μl) solution was loaded on gels and was electrophoresed for 17 hr at 1.0 W in a 10% native polyacrylamide gel (130 × 130 × 0.5 mm) before visualization using standard silver staining.

**Table 1:** Distribution of mitochondrial cytochrome B variants among domestic pig and wild boar populations

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The different variants were distinguished by SSCP. The corresponding sequences are defined in Figure 1B.

a Hampshire and Duroc are European-type domestic pigs but were developed mainly in the United States.

**Table 1**

<table>
<thead>
<tr>
<th>Population</th>
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<th>A1</th>
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The different variants were distinguished by SSCP. The corresponding sequences are defined in Figure 1B.

a Hampshire and Duroc are European-type domestic pigs but were developed mainly in the United States.
The Origin of the Domestic Pig

The European clade 2 included only three wild boars from Southern Europe (Italy). All mtDNA haplotypes having a presumed European origin and found in domestic pigs belonged to European clade 1. The phylogenetic analysis of the cytochrome B sequences (Figures 1B and 2B) displayed again a statistically supported Asian clade but the presence of two distinct European clades was not statistically significant. European and Asian haplotypes could be distinguished easily by SSCP analysis of a 377-bp PCR product from the cytB gene. SSCP screening confirmed the conclusions from the tree analysis and showed that Asian mtDNA haplotypes are present in European Large White, Landrace, and Duroc domestic pigs (Table 1). Very similar tree topo-
average pairwise nucleotide distance between European and Asian mtDNA cytB sequences belonging to clade E1 and A was $17 \pm 1.4$ substitutions ($1.45 \pm 0.12\%$). A lower estimate of $1.0\%$ was obtained by calculating the interpopulation distance, which attempts to take into account the genetic diversity existing in the common ancestor of the two populations (Nei 1987). This more conservative estimate indicates that the time since divergence of the two populations is of the order of 500,000 YBP, evidently well before domestication 9000 YBP. The most likely explanation for the fairly high frequency of Asian mtDNA haplotypes in some European domestic breeds is that this is due to the documented introgression of Asian pigs during the 18th and early 19th centuries. The maternal inheritance of mtDNA implies that Asian sows were used for introgression and this is consistent with both written records and contemporary art.

**Sequence polymorphism in three nuclear genes is consistent with a European and Asian origin of domestic pigs:** The genetic diversities of three nuclear genes, MC1R, TYR, and GPIP, were also investigated. Our previous MC1R study (Kijas et al. 1998) showed that the MC1R*$2$/dominant black allele present in Chinese Meishan and British Large Black pigs shares two synonymous and two nonsynonymous substitutions absent from MC1R alleles in other European domestic breeds and in European wild boars (MC1R*$1$-$4$; Figure 3A). The observation that the MC1R sequence from Japanese wild boars (MC1R*$5$; Figure 3A) shares one of the synonymous substitutions found in MC1R*$2$ indicates that the latter originates from an Asian rather than a European ancestor. MC1R is essentially monomorphic within domestic breeds due to strong selection for coat color homogeneity and we have not observed any heterogeneity among wild boars. We did not attempt to use MC1R for calculating time since divergences because the observed rate of nucleotide substitutions may be affected by the strong phenotypic selection at this locus.

We sequenced the major part of TYR exon 1 (727 bp) from two animals each of European and Japanese wild boars and several domestic breeds. Two alleles differing by four synonymous substitutions were found (Figure 3B). There were no fixed differences between continents but TYR*$1$ occurred predominantly in Japanese wild boars and Meishan domestic pigs, while TYR*$2$ was most common in European wild boars and domestic pigs (Table 2).

Since both MC1R and TYR are coding sequences, the GPIP pseudogene was included as a noncoding nuclear sequence. Sequence analysis of 784 bp of this pseudogene from 14 animals representing domestic and wild pigs from both continents revealed four alleles differing by multiple nucleotide substitutions (Figure 3C). Once again, there was a clear tendency for more pronounced allele frequency differences between continents than between wild and domestic pigs within continents.
The Origin of the Domestic Pig

Figure 3.—Sequence polymorphism in three nuclear genes in the pig: (A) MC1R, (B) TYR exon 1, and (C) GPIP. Nonsynonymous substitutions are indicated in boldface letters.

Table 2

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DISCUSSION

This study has important implications for pig genetics and the history of domestication. We report clear evidence for independent domestication of both European and Asian subspecies of the wild boar. We estimated the time since divergence of the ancestors for European and Chinese Meishan domestic pigs at ~500,000 YBP on the basis of interpopulational distances for mtDNA cytB sequences, which we think is the most reliable and conservative estimate we have obtained. It is clear that this is still a very rough estimate for several reasons. First, there is a fairly large sampling error since we have studied only ~10% of the total mtDNA genome and a few nuclear genes. However, since the submission of this article, we have sequenced the entire mtDNA and can confirm the existence of the three major clades E1, EII, and A (Figure 2) and the large distance between European clade E1 and Asian clade A (K = 1.2 ± 0.09%; J. H. M. Kijas and L. Andersson, unpublished results). Second, the molecular clock rate shows a considerable variation among lineages, possibly due to differences in efficiency in DNA repair, generation time, and/or metabolic rate (Li 1997). However, we can safely conclu-
clude that the time since divergence must predate the domestication of pigs \( \sim 9000 \) YBP. Our results agree with Darwin’s view (Darwin 1868) that there is a considerable genetic distance between European and Asian domestic pigs but they disagree with the hypothesis that Asian pigs originate from a wild boar species (S. indus) unknown from the wild. Our data show that European domestic pigs and Chinese Meishan pigs are closely related to existing subspecies of the Eurasian wild boar (S. scrofa). The marked morphological divergence between Asian and European domestic pigs noted by Darwin may be due to the long history of selective breeding. Our results are in sharp contrast to the estimate of \(~ 2000\) years of divergence between Chinese Meishan pigs and European domestic pigs based on allele frequencies at six linked microsatellite loci (Paszek et al. 1998). However, this latter approach is invalid if introgression between the two forms has occurred.

The molecular data presented here, clearly indicating an introgression of Asian domestic pigs into European breeds, are consistent with historical written records (Darwin 1868; Jones 1998). A hybrid origin of the European Large White breed was suggested previously on the basis of restriction site mapping of mtDNA (Watanabe et al. 1986). Our results indicate a surprisingly high proportion of Asian mtDNA in this breed. However, this may not truly reflect the degree of introgression because the frequency of mtDNA types may have changed by genetic drift and/or selection during the \(~ 200\) years that have passed since the major introgression occurred. The hybrid origin of some major breeds may in fact be a unique advantage for the genetic dissection of complex traits of agricultural significance. More or less intense pig breeding has been practiced for thousands of years in both Asia and Europe. Introgression of Asian pigs into certain European breeds occurred \(~ 200\) years ago and was followed by intense phenotypic selection. Thus, we expect Asian alleles with favorable phenotypic effects to be fixed or to occur at a high frequency in European pig breeds with a hybrid origin. This is well illustrated by the M CIR allele for dominant black color (with a presumed Asian origin) fixed in the European Large Black breed (Kijas et al. 1998). The large number of generations that has passed since major crossbreeding occurred (\( +100\) generations) implies that linkage disequilibrium occurs only within very narrow regions of genomic DNA. Thus, these breeds with a hybrid origin may be considered as very advanced intercross lines suitable for high-resolution quantitative trait loci mapping (Darvasi and Soller 1995; Darvasi 1998). The possibility of using large numbers of single nucleotide polymorphisms provides the tool for detecting islands of linkage disequilibrium created by introgression and phenotypic selection. The hybrid origin of the Large White breed must also be taken into account when evaluating the results of pig gene mapping experiments involving crosses between this breed and European wild boars (Andersson et al. 1994) or Chinese Meishan pigs (Rohrer and Keeler 1998).

The data presented on the domestic pig add to an emerging picture of independent domestication of distinct populations of the wild ancestors of major domestic species. In cattle, a considerable genetic divergence between European/African (Bos taurus taurus) and Asian (Bos taurus indicus) cattle has been documented on the basis of both mtDNA and nuclear DNA sequences (Lofus et al. 1994; MacHugh et al. 1997). The presence of distinct European and Asian mtDNA clades in domestic sheep has also been reported (Hienleder et al. 1998). The considerable genetic diversity detected in these species has been interpreted to largely reflect genetic divergence prior to domestication. In contrast, ancient domestication (> \(100,000\) YBP) was invoked to explain the pattern of genetic diversity in the control region of mtDNA among dogs (Vila et al. 1997). The average genetic distance between the European and Asian clades of mtDNA cytB sequences was estimated at \(1.5\%\), which is about three times higher than the \(0.5\%\) observed between the most divergent human mtDNA haplotypes (Hori et al. 1995). The sequence divergence between the alleles at the three nuclear genes included in this study is also several times higher than that generally observed in humans (Chakravarti 1999). These differences in pattern of genetic diversity are consistent with a strikingly different population history of humans and domestic animals. Humans appear to have expanded enormously from a rather small population present \(100,000\) YBP (Harpending et al. 1998). At that time, the wild boar was abundant and widespread in Eurasia. The independent domestication of European and Asian wild boars followed by introgression provided a broad genetic basis for the domestic pig.

The molecular markers described here give an opportunity to further explore the origin of domestic pigs. It is clear that a more thorough sampling of domestic breeds, particularly from Asia, and of wild boar populations is needed to provide a more comprehensive picture of the domestication of pigs. It would be of particular interest to include wild boar populations with a karyotype of \(2n = 36\) in contrast to \(2n = 38\) in other wild boar populations as well as in all domestic pigs. It will now be possible to trace the origin of different breeds of pigs as well as feral pigs present in North and South America, Australia, and on Pacific islands. This study gives a first glimpse of what this type of study may reveal. The single pig tested from Cook Island in Polynesia appears to belong to a hybrid population since the mtDNA and TYR sequence was identical to those predominantly found in European pigs whereas the G PIP allele was almost identical to the allele found in Chinese Meishan pigs. The result is not unexpected as the ancestral Polynesians brought domestic pigs with them (Diamond 1997, p. 60), presumably of Asian ori-
gin, and European seafarers used domestic pigs as on-
voyage food supply during expeditions around the
world. Such pigs sometimes escaped or were released
and founded feral populations. Moreover, it may be
possible to investigate the early history of the domestic
pig by analyzing mtDNA from the rich collections
of pig bones from Neolithic to medieval times. This
may also shed light on the early migration of agricultural
tribes in Eurasia.

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cellent technical assistance, and R. Eiger, E. Geffen, T. Hori, R. Gianna-
telli, J. Kuryl, E. Randi, L. Varga, and the PiGMaP consortium for
providing tissue or DNA samples. The Swedish Research Council for
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