A further look of the genetic origin and singularity of the 
Torbiscal Iberian pig line

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Abstract
Although the Torbiscal line of Iberian pigs has been largely studied, some aspects of its history are not well known. In this paper, we used pedigree-based methods on a complete genealogy of 4,077 entries in order to get a comprehensive analysis of its four founder strains and to evaluate the expected genetic contribution of each ancestral strain to the successive generations of the composite Torbiscal line. Between-strain differences and specific heterotic effects on piglet weight at 50 days of age were estimated from records of 9,052 piglets born in 1,571 litters of a complete diallel cross among the four strains. Moreover, we assessed the genetic singularity of the current Torbiscal pigs by other three studies, based on whole genome SNP genotypes, focused on the measure of its genetic diversity and differentiation with respect to other domestic and wild pig populations. The STRUCTURE algorithm detected two uppermost levels of the whole population structure, corresponding to European and Asian ancestries. These results confirmed the exclusive European origin of the Torbiscal and other Iberian pigs and the admixed origin of the Duroc breed. Finally, the comparison of Torbiscal with a representative pool of Iberian pigs showed a maximum genetic differentiation in regions of chromosomes three and seven, including some genes related to the regulation of muscle development.

Additional keywords: pedigree analysis; piglet weight; diallel-cross; Fst index; genetic diversity; genetic differentiation.

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Introduction
From a publication on the seasonal influence on fecundity and litter performance in Iberian pigs (Dobao et al., 1983) until a recent study on the effects of breed, feeding status, and diet on adipogenic, lipogenic, and lipolytic gene expression in growing Iberian and Duroc pigs (Benítez et al., 2018), the research activity performed on the Torbiscal line has substantially contributed to increase the scientific knowledge of Iberian pigs. A remarkable number of papers, using this line as material, have been published in international journals concerning very different topics, including animal behaviour (Dobao et al., 1984), quantitative genetics (Toro et al., 1988, 2006; Pérez-Enciso & Gianola, 1992; Rodríguez et al., 1994; Fernández et al., 2002a, 2008a; Silió et al., 2013, 2016; Muñoz et al., 2017), nutrition and feeding systems (Rey et al., 2006; Daza et al., 2007; López-Bote et al., 2008; Ayuso et al., 2015), quality of meat and cured products (Hernández et al., 2004; Muriel et al., 2004; Carrapico & García, 2008), genetic diversity and population structure (Toro et al., 1998, 2002; Alves et al., 2003, 2006; Fabuel et al., 2004; Rodrígáñez et al., 2008); association between genetic markers and productive traits (Muñoz et al., 2004; Fernández et al., 2008b), functional and structural genomics (Esteve-Codina et al., 2013; Óvilo et al., 2014a; Gómez-Raya et al., 2015) and nutrigenomics (Óvilo et al., 2014b; Benítez et al., 2015).

Moreover, the supply of Torbiscal breeding animals to Iberian pig farmers, decisively supported the partial recovery of breed census along the last three decades of the past century, after its greater crisis caused by the market rejection of fat carcasses and the eradication...
of first African swine fever epidemics. The notable diffusion of the line led to the official acknowledgement of Torbiscal pigs as a new Iberian variety. More recently, the Torbiscal line has been studied in new private breeding programs for improving productive traits of Iberian pigs (Ibáñez-Escriche et al., 2014, 2016).

Although the composite origin of the Torbiscal line has been concisely described in some of the quoted papers, the relevance of this population justifies a more comprehensive genealogical and productive characterization of its founder strains, its relatedness with these ones and its genetic singularity with respect to other pig populations, particularly with the remaining Iberian pigs. These are the objectives of the present study.

Material and methods

Animals

The Torbiscal line was obtained in 1963 by blending four ancient Iberian pig strains preserved by private breeders, and since 1944-45 maintained with pedigree and data recording in the experimental herd of “El Dehesón del Encinar” (Oropesa, Toledo, Spain). Two of these strains were reddish and came from the Portuguese herds of the Count of Ervideira (Ervora) and Mr. Picao Caldeira (Elvas). The others, both hairless and black coated, came from the herds of the Donoso brothers (Campanario), and Mr. Fabián Lozano (Puebla de la Calzada) in Odrozola (1976). The last strain (named today Guadyerbas) and the Torbiscal line are still kept in a conservation programme. The complete pedigree of Torbiscal from 1944 to 2013 was analysed in this study. It consists of 4,077 entries (individual-sire-dam) including 1,411 ancestor reproducers: 312 Ervideira (RE), 321 Campanario (BHC), 37 Caldeira (RC), 404 Puebla (BHP) and 198 admixed ones.

A complete diallel cross was performed among the four quoted strains in order to test their reproductive and productive performance and the possible heterotic effects among them (Garcia-Casco et al., 2012). Here we analysed the piglet weight at 50 days of age using the available records from 9,052 piglets born in 1,571 litters representing the 16 genetic types resulting from the 4 × 4 possible crosses. The distribution of these piglets per cross and the number of sires and dams of each strain are shown in Table 1.

### Table 1. Number of animals with weight records and number of sires and dams per strain (between brackets) used in a diallel crossing scheme among four Iberian strains (Ervideira, RE; Caldeira, RC; Campanario, BHC; Puebla, BHP) founders of the Torbiscal composite line.

| Sire line (No. of sires) | Dam line (No. of dams) |
|--------------------------|------------------------|
| RE (40)                  | RC (134)               |
|                         | BHC (145)              |
|                         | BHP (169)              |
|                         | Total (583)            |
| RE (135)                 | 1413                   |
|                         | 156                    |
|                         | 138                    |
|                         | 569                    |
|                         | 2276                   |
| RC (28)                  | 124                    |
|                         | 1319                   |
|                         | 378                    |
|                         | 172                    |
|                         | 1993                   |
| BHC (37)                 | 133                    |
|                         | 497                    |
|                         | 1293                   |
|                         | 168                    |
|                         | 2091                   |
| BHP (34)                 | 404                    |
|                         | 84                     |
|                         | 110                    |
|                         | 2094                   |
|                         | 2692                   |
| Total (139)              | 2074                   |
|                         | 2056                   |
|                         | 1919                   |
|                         | 3003                   |
|                         | 9052                   |

Pedigree analysis

A founder is defined, for pedigree analysis purpose, as an animal with no relationship to any member of the pedigree except its offspring. The number of discrete equivalent generations traced (EqG), which is the expected number of generations from the base population if generation proceeded discretely, and the coefficients of inbreeding (F) and coancestry (fjk) were computed for each ith individual and for their parents j and k tracing the pedigree back to the founder animals (Woolliams & Mäntysaari, 1995; Caballero, 1995; Caballero & Toro, 2000). These parameters are closely linked to the classical concept of genetic contributions (James & MacBride, 1958), which also sustains other genealogical parameters calculated in this study, such as the effective number of founders (Nef) and non-founders (Nge) and the founder genome equivalents (Ngf), related among them by the expression 1/ Nge = 1/ Nef + 1/ Nenf (Toro et al., 2000). For some specific calculations, the entire number of traced generations (t) was determined for each individual as the rounded number of discrete equivalent generations. The realized effective population size was estimated from the increase coancestry over generations by measuring IBΔ (identical by descent) probabilities, through the well-known formula: Ne = 1/2ΔIBD, where ΔIBD is the rate of IBΔ. ΔIBD values were calculated from individual coancestry rates by the expression Δfjk = 1 - (fa)1/2 - (fa)1/2 - (fa)1/2 - (fa)1/2 (Cervantes et al., 2011) and averaged each generation as (1/2Δfjk), being the effective census Neff = 1/2 Δfjk. To take into account the possible bottlenecks, the effective number of ancestors (fa) or minimum number of ancestors necessary to explain the genetic diversity of a population was also calculated by each generation according to Boichard et al. (1997).

In order to examine the relationship between the Torbiscal composite line and their founder strains, the expected genetic contribution of each founder to any Torbiscal reproductor was measured by means of coancestry coefficients between animals and founders (James, 1972). The proportional genetic contribution of each founder to a specific generation is $p_j = \sum_{k=1}^{N} \frac{f_{jk}}{N}$. 

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where $a_{jk}$ is the additive relationship coefficient between founder $j$ and animal $k$, being $N$ the number of reproducers in the generation. The extension to the calculus of contributions of each one of the founder strains ($S$) is immediate by means of $\sum_{j \in S} p_j$ referred to the founders belonging to each one.

Moreover, to inspect whether the alleles contributing to inbreeding of Torbiscal animals came from specific founders, the inbreeding coefficient ($F_i$) can be partitioned into components due to each one of the 116 founders animals: $F_i = \sum_{j=1}^{116} F_{ij}$, that measures, for any individual, the probability of being homozygous for a gene coming from each founder. These coefficients, calculated by using a modification of the additive matrix method for calculating inbreeding coefficients (Lacy et al., 1996; Rodríguez et al., 1998), have been grouped into four components ascribable to each one of the founder strain $F_S = \sum_{j \in S} F_{ij}$, sums of coefficients with respect to founder individuals belonging to each founder population. The sum of these four partial coefficients is equal to the overall inbreeding.

**Analysis of piglet weight at 50 days of age**

The animal model used in the analysis of weight records can be represented in matrix notation as

$$y = X\beta + Z_1u + Z_2m + Z_3c + e$$

where $y$ is an $n \times 1$ vector of observations ($n=9,052$); $X$, $Z_1$, $Z_2$, and $Z_3$ are known incidence matrices of order $n \times 37$, $n \times 9052$, $n \times 583$ and $n \times 1571$ relating location parameters $\beta$, $u$, $m$, and $c$, respectively, to $y$; $\beta$ is a $37 \times 1$ vector of systematic effects, including the effect of sex (2 levels: male and female), parity order (6 levels: 1st to 5th and $\geq 6$), number of weaned piglets per litter (11 levels), crossbreeding parameters (16 levels: mean; three individuals and three maternal effects of Caldeira; Campanario and Puebla strains; six specific heterosis between strains and three reciprocal effects) according to the model of Dickerson (1969), and one regression coefficient ($b_{eq}$) corresponding to the inbreeding effect of the dam; $u$, $m$, and $c$ are the random vectors of additive genetic effects, maternal genetic effects and common litter environmental effects and $e$ is the vector of random residual effects. Inferences about these parameters were obtained by a Bayesian procedure using the Gibbs sampling algorithm implemented in the TM software (Lagarra et al., 2011). The usual dispersion and location parameters were calculated using the BOA software (http://cph.uiowa.edu/boa) from saved samples of the marginal posterior distributions of the parameters of interest.

**Genotypes**

A total number of 61 Torbiscal pigs, 75 Iberian pigs of diverse Portuguese and Spanish origins, 52 Duroc from Spain, USA and several European countries, 65 European Wild boars from Spain, Tunisia, Poland and other countries, and 52 pigs of different Asian breeds (Meishan, Jiangquai, Jinhuaxiang) were genotyped using the Porcine SNP60 BeadChip (Illumina) according to the manufacturer’s recommendations. Data quality control was performed according to the following filtering criteria: $i)$ call rate of the sample $> 0.96$, $ii)$ single nucleotide polymorphisms (SNPs) with a call rate $> 0.99$, $iii)$ GenTrain score $> 0.70$, $iv)$ mean of the normalized $r$-values for the AB genotypes $> 0.35$. A SNP was removed if: $v)$ number of inheritance errors $> 5$, $vi)$ unknown position on the genome or mapped on chromosomes X or Y, $vii)$ minor allele frequency MAF = 0. After all these editing steps only 43,693 SNPs were retained in the data set used for checking the possible admixture of Iberian with other porcine populations and for assessing their genetic diversity and differentiation.

**Analysis of genetic diversity and differentiation**

A Bayesian clustering method in STRUCTURE software (Pritchard et al., 2000) was employed, using the quoted genotypes, to assign individuals to one of the K-clusters representing ancestral populations, or jointly to two or more populations if their genotypes indicated that they were admixed. The number K was previously determined by the method of Evanno et al. (2005) using a partial SNP datatile (8,738 genotypes) and a range of possible values from two to five. A warm-up of 20,000 iterations followed by 30,000 preserved samples was obtained in all the performed calculations.

We measured the genetic diversity according to Nei (1973) as the heterozygosity expected under the Hardy-Weinberg equilibrium conditions. Caballero & Toro (2002) showed as, in a metapopulation with $n$ breeds, the total genetic diversity or expected heterozygosity ($GD_r = H_r$), may be partitioned into a within breeds component ($GD_{ws} = H_s$) and another between breeds ($GD_{ws} = H_s - H_l$):

$$H_S = 1 - \frac{1}{n} \sum_{i=1}^{n} (\sum_{k=1}^{m} p_{ik})$$

$$H_T = 1 - \sum_{k=1}^{m} (\sum_{i=1}^{n} p_{ik})^2$$

where $p_{ik}$ is the frequency of allele $k$ in the breed or line $i$. In the present study $n = 5$ and $m = 2$ alleles $\times 43,693$ SNPs. An additional partition of $GD_{ws}$ may be performed in genetic diversity within individuals ($GD_{wi}$) and between individuals ($GD_{w}$) calculated in terms of average molecular coancestry ($f$) and self-coancestry.
(s) according to Fabuel et al. (2004). Wright’s (1969) fixation index is the proportion of diversity between breeds relative to the total diversity: $F_{ST} = GD_{BS} / GD_{T} = (H_I - H_S) / H_T$. Hedrick (2005) has proposed to standardise it by the maximum level that can be obtained, $F_{ST(max)} = (1-H_S) / (1+H_S)$, given the heterozygosity within breeds. Thus, $F_{ST}^* = F_{ST} / F_{ST(max)}$ is a measure of population differentiation relative to the maximum possible, which allows the comparison with different levels of variation. Bootstrap confidence intervals of heterozygosity and differentiation metrics were calculated using 10,000 bootstrap samples created by repeated random sampling with replacement of the $m$ loci.

As proposed by Akey et al. (2010), the locus specific differentiation of each group was measured by unbiased estimates of pairwise $F_{ST}$. For each SNP and $i$ population may be calculated the statistics:

$$d_i = \frac{\sum_{j \neq i} F_{ij} - E[F_{ij}]}{SD[F_{ij}]}$$

where $E[F_{ij}]$ and $SD[F_{ij}]$ are the mean and standard deviation of the $F_{ij}$ between $i$ and $j$ breeds calculated from the 43,693 SNPs. For each group, $d_i$ values were averaged for sliding overlapping windows of ten successive SNPs. Most differentiated regions were identified as the 99.5th percentile of the genome-wide distribution of the averaged $d_i$ values. In this study we only present the results relative to the pair Torbiscal ($i$) and Other Iberian pigs ($j$). Gene content across candidate regions was determined using the Sus scrofa genome (assembly Sscrofa11.1; https://www.ncbi.nlm.nih.gov/genome?term=sus%20scrofa).

**Results**

**The founder strains**

We computed the contribution of founder and non-founder reproducers to the pairwise coancestry between individuals of each generation $t$ (rounded value of $EqG$) of Ervideira, Caldeira, Campanario and Puebla besides of the coefficients of coancestry ($f$) and inbreeding ($F$). The respective averaged coancestry coefficients increased from 0.055, 0.062, 0.054 and 0.047 in the first generation of the respective strain up to 0.199, 0.222, 0.164 and 0.186 in the last generation. The respective contributions to these values of founders and non-founders were 0.032 and 0.167 (RE), 0.061 and 0.161 (RC), 0.050 and 0.114 (BHC), and 0.048 and 0.138 (BHP). Note that the Campanario complete pedigree only consists of five equivalent generations instead of seven in the other strains.

The parameters $N_{ef}$, $N_{enf}$, and $N_{ge}$ constitute an alternative to represent the information concerning genetic contributions to coancestry. The change of these parameters over successive generations of each founder strain is shown in Figs. 1a, b, c, d. The first parameter is related to the genetic contributions of founder reproducers to each generation which stabilize
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One particular aspect of the productive differences among strains was examined by the genetic analysis of piglet weight at 50 days using the data file described in Table 1. Mean and standard deviation of this trait were 11.31 ± 2.54 kg. The main results obtained from the analysis are summarized in Fig. 2 and Table 2. The relationship between the number of piglets weaned per litter, including cross-fostered, and piglet weight at 50 days is represented in Fig. 2, as deviations from litters of one weaned piglet, showing a pattern with an optimum number of weaned piglets from three to seven and negative deviations for the greatest litters. Given the late weaning of litters at 50 days of age, maternal effects. The proportion of phenotypic variance (\(c^2\)) explained by the common litter environmental effect was also important. Parity effects expressed as deviations from the first parity showed a remarkable value up to the fifth parity. Significant weight differences between males and females were also inferred. Individual and maternal strain effects were inferred as differences respect to Ervideira, although other contrasts have been carried out from the respective marginal posterior distributions. The only relevant strain difference among individual effects was found between Puebla and Caldeira. The other differences were lower, including the zero value their respective 95% highest posterior density intervals (95% HPD). Neither effects different from zero were found among the four maternal strains. However, the available samples of marginal posterior distributions of all the parameters of interest allow calculating additional contrasts, as between the sum of maternal and individual strain effects \([l_j + m_j]\) and \([l_j + m_j]\). Measured by this procedure, the mean differences of piglet weight between Puebla and the other strains were 1.25 (Ervideira), 1.87 (Caldeira) and 1.21 (Campanario), with values of the posterior probability to be greater than zero \(P_{Prob} > 0\) equal to 0.980, 0.999 and 0.973, respectively. Four out of the six specific heterotic effects on piglet weight showed significant values ranged from 0.31 to 0.86 kg, equivalent to percentages of the mean trait from 2.7 to 7.8%. However, null heterotic effects were detected between pairs Ervideira/Campanario \((PM = 0.054, P_{Prob} > 0 = 0.583)\) and Caldeira/Puebla \((PM = 0.034, P_{Prob} > 0 = 0.552)\). Inferred reciprocal strain effects were not different from zero.

The composition of Torbiscal line

Crosses between strains for founding the Torbiscal line were carried out from generation seven to nine. The following seven types of crosses were initially implemented: two between two strains \([RE \times BHP\) and \(BHC \times BHP]\), and five between three strains \([RE \times (RE \times BHP), RC \times (RE \times BHP), BHP \times (RE \times BHP), RE \times (BHC \times BHP)\) and \(BHP \times (BHC \times BHP)\)]. Other intercrosses were performed later to obtain red hairy coated pigs with contributions of the four ancestral strains, which were identified as the first individuals of the new composite line. Only 71 out of the 116 founders actually contributed to the build-up of Torbiscal.

The proportional genetic contribution of each strain to the successive generations of the Torbiscal line is represented in the Fig. 3. Note that this figure starts

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**Figure 2.** Effect on the piglet weight at 50 days (kg) of the number of weaned littermates, represented as deviations respect to the effect of one weaned piglet per litter.
Table 2. Main statistics of marginal posterior distributions of direct ($h^2_d$) and maternal ($h^2_m$) heritabilities, genetic correlation between direct and maternal effect ($\rho$), coefficient of common litter environmental effect ($c^2$), and most relevant effects of crossbreeding parameters, gender and parity order for weight at 50 days (kg).

|                 | PM↑ | PSD | 95% HPD          | PProb > 0 |
|-----------------|-----|-----|------------------|-----------|
| **Variance ratios** |     |     |                  |           |
| $h^2_d$         | 0.130 | 0.032 | 0.070 / 0.195   | 1.000     |
| $h^2_m$         | 0.190 | 0.049 | 0.095 / 0.286   | 1.000     |
| $\rho$          | -0.412 | 0.168 | -0.086 / -0.720 | 0.020     |
| $c^2$           | 0.207 | 0.015 | 0.179 / 0.237   | 1.000     |
| **Gender effect** |     |     |                  |           |
| Male - Female   | 0.605 | 0.043 | 0.522 / 0.693   | 1.000     |
| **Parity order** |     |     |                  |           |
| 2nd – 1st       | 1.204 | 0.102 | 1.013 / 1.409   | 1.000     |
| 3rd – 1st       | 1.262 | 0.114 | 1.024 / 1.473   | 1.000     |
| 4th – 1st       | 1.316 | 0.138 | 1.054 / 1.592   | 1.000     |
| 5th – 1st       | 1.315 | 0.164 | 0.989 / 1.626   | 1.000     |
| ≥6th – 1st      | 0.584 | 0.147 | 0.301 / 0.880   | 1.000     |
| **Strain effects** |     |     |                  |           |
| $l_{ERP} - l_{RC}$ | 1.509 | 0.846 | -0.192 / 3.145  | 0.960     |
| **Specific heterosis** |     |     |                  |           |
| $h_{RERC}$      | 0.860 | 0.239 | 0.391 / 1.326   | 0.999     |
| $h_{REBHP}$     | 0.306 | 0.151 | 0.001 / 0.588   | 0.979     |
| $h_{RCBHC}$     | 0.384 | 0.155 | 0.072 / 0.680   | 0.992     |
| $h_{BHCBP}$     | 0.713 | 0.245 | 0.253 / 1.207   | 0.998     |

§ Posterior mean (PM), Posterior standard deviation (PSD), 95% highest posterior density interval (95% HPD) and Bayesian posterior probability to be greater than zero (PProb > 0).

Figure 3. Expected genetic contributions to the Torbiscal line of the Ervideira, Caldeira, Campanario and Puebla founder strains over successive rounded numbers ($t$) of equivalent discrete generations ($Eq_G$).

Figure 4. Genetic relationships between Torbiscal and relevant pig populations.

The application of Evanno et al. (2005) method to a preliminary clustering analysis of 305 individuals representing five pig populations, determined $K = 2$ as the number of ancestral groups on the superior hierarchical level of the data structure. This number coincides with the two well-known main focus of pig domestication that took place ten thousand years ago.
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in East Europe and Asia from different wild ancestors diverged 1 M years ago (Larson et al., 2007). For this reason, clusters were named as European and Asian. The final results of the application of the STRUCTURE algorithm using the whole number of SNP genotypes are presented in Fig. 5. Torbiscal, other Iberian pigs and European Wild pigs were ascribed to a common ancestral group (European) with inferred mean proportions 1.000, 0.979 and 0.945, respectively. A similar proportion of the genome of Asian pigs (0.985) was ascribed to the other ancestral group (Asian), while the Duroc pigs showed remarkable admixing of both ancestors, with respective mean proportions of 0.671 and 0.329.

The mean expected heterozygosities (and 95% CI) of Torbiscal, other Iberian, European Wild pigs, Duroc and Asian pigs were 0.194 (0.193/0.196), 0.248 (0.246/0.250), 0.270 (0.268/0.272), 0.319 (0.317/0.320) and 0.218 (0.216/0.219), respectively. A more detailed partition of the genetic diversity for each i population is stated in Table 3. The values of individual and population self-coancestry \((s_i, f_i)\), average distance between individuals \((D_i)\), inbreeding \((F)\), H-W deviations \((\alpha)\) and proportion of diversity between individuals \((G)\) for each population i.

| Population | \(f_i\) | \(s_i\) | \(D_i\) | \(F\) | \(\alpha\) | \(G\) |
|------------|--------|--------|--------|------|--------|------|
| Torbiscal  | 0.806  | 0.899  | 0.093  | 0.798| -0.040 | 0.480|
| Other Iberians | 0.752  | 0.890  | 0.138  | 0.780| 0.116  | 0.558|
| European   | 0.708  | 0.882  | 0.175  | 0.765| 0.196  | 0.598|
| Duroc      | 0.681  | 0.859  | 0.178  | 0.718| 0.116  | 0.558|
| Asian      | 0.786  | 0.918  | 0.131  | 0.835| 0.229  | 0.614|

\(\text{WB}^1\) WB: wild boar.

A more detailed picture of the divergence between the genomes of Torbiscal and the analysed pool of Iberian pigs of other origins is presented in the Manhattan plot of Fig. 6. The numbers on Y-axis correspond to \(d_i\) values between Torbiscal and other Iberian pigs averaged for sliding overlapping windows of ten successive SNPs. Differentiated 10 SNP windows are identified as exceeding the 99.5th percentile their whole distribution, represented as an horizontal line. Only four chromosomes (SSC 9, 10, 11 and 16) do not show significant differentiation. A total of 33 divergent regions are identified in the remaining

**Table 3.** SNPs based metrics of coancestries \((s_i, f_i)\), average distance between individuals \((D_i)\), inbreeding \((F)\), H-W deviations \((\alpha)\) and proportion of diversity between individuals \((G)\) for each population i.

**Figure 4.** Partial components of Torbiscal inbreeding ascribable to the founder strains over successive rounded numbers \((t)\) of equivalent discrete generations \((E_{eq})\).

**Figure 5.** Bayesian probabilistic individual assignments to clusters representing European (light color) and Asian (dark color) ancestral origins. Figure built by STRUCTURE.
14 chromosomes, being SSC6 the chromosome with a greater number (seven) of differentiated regions with a total length of 4.3 Mb. The maximum differentiation is found on SSC3 (95.45–96.50 Mb) and SSC7 (101.96–102.54 Mb). The examination of gene content using the more recent assembly of pig genome (Sscrofa11.1) allowed the detection of 94 protein-coding genes inside 33 divergent regions. Seven of these genes code proteins related to muscle growth, eight genes to lipid metabolism and only one (JAG1) involved in hair differentiation. Their symbols and chromosome positions are detailed in Table 5.

**Discussion**

Miguel Odriozola, who was the founder of Torbiscal line, and devoted much of his brilliant career to the study of Iberian pigs, classified livestock populations in two classes according to their degree of artificialness. First degree populations of farm animals are those controlled by a large number of farmers, being genetically developed by adaptation to their particular environment and production system, without any standard racial or herd-book. Otherwise, second degree populations, with a lower environmental influence, undergo genetic changes mainly determined by a small group of breeders and resulting in modern breeds with standard racial, herd-book and data recording. In the middle of the past century, the Iberian pigs, with more than 600,000 sows, were an example of a first degree population extended over the South-West of the Iberian Peninsula. The quoted four founder strains were chosen as representative of the main varieties existing at this time: the golden type from the Alentejo (Ervideira), the chestnut type (Caldeira) and the two hairless types: the bony Campanario and the early fat Puebla. It may be stated that the history of the Iberian breed pig began with the systematic recording of pedigree and data of these four founders and the subsequent establishing of the Torbiscal line. The above results fulfil this particular history, highlighting genealogical and productive aspects not reported in previous studies.

The performed pedigree analyses of founder strains illustrate the way they were maintained as closed lines during five or seven generations with small effective population sizes of about $N_e \approx 20$. The respective evolution of coancestries and inbreeding coefficients along generations reflect systematic departures of random mating. The $\alpha$ coefficient, related to these coefficients by the expression $(1-F) = (1-f) (1-\alpha)$, indicates the degree of deviation from Hardy-Weinberg proportions in a population, and their negative values -generally observed in all the cases- point to a regular use of mating tactics for avoiding inbreeding.

The conservation of the four strains was combined with the simultaneous obtaining of growth and litter size data from a complete diallel cross. In the present study we accomplished the analysis of records of piglet weight at 50 days which confirm the positive effect of the Puebla strain on the early growth, previously reported for piglets at 21 days of age (Silio et al., 1994) and growing pigs at 120 days (Fernández et al., 2002b). However, the relative growth performance of these strains was very different in the fattening period, Ervideira being reported as the heaviest one at 365 days and with the same weight differences at 465 days, before the slaughter (García-Casco et al., 2012). Substantial heterotic effects on weight between-

**Table 4.** Mean and 95% confidence interval of pairwise values\(^3\) of the standardized differentiation coefficient ($F_{ST}$) among the five analyzed pig populations.

|                  | Other Iberians | European WB | Duroc   | Asian pigs |
|------------------|----------------|-------------|---------|------------|
| Torbiscal        | 0.102 (0.101/0.104) | 0.189 (0.187/0.192) | 0.329 (0.325/0.332) | 0.647 (0.643/0.651) |
| Other Iberians   | 0.131 (0.129/0.133) | 0.251 (0.248/0.254) | 0.588 (0.584/0.592) |
| European WB      | 0.258 (0.255/0.261) | 0.550 (0.547/0.555) |
| Duroc            |                | 0.492 (0.488/0.496) |

\(^3\)Calculated from 43,693 SNPs and 10,000 Bootstrap samples. WB: wild boar.

**Figure 6.** Genome-wide empirical distribution of $d_i$ values for the Torbiscal line and the pool of other Iberian pigs. Horizontal line denotes the 99.5th percentile.
strains have been estimated at different ages. Besides the values of specific heterosis here estimated, similar results have been obtained analysing diallel-cross weight records at 21, 120, 365 and 465 days (Silío et al., 1994; Fernández et al., 2002b; García-Casco et al., 2012). Note that heterotic effects on growth up to 100 kg were greater in pigs with restricted feeding than in the pigs hand-fed to appetite according to the expected greatest heterosis in poorer environments (Fernández et al., 2002). Minor between-strain differences for litter size were estimated in previous studies, being most notable the differences at the two first parities with a lower prolificacy of about -0.5 alive born piglets of the Ervideira sows. Specific heterotic effects on litter size were also conditional to parity order, with greater values for the third and later parities ranging from +0.6 to +1.0 piglets alive born per litter (García-Casco et al., 2012).

Miguel Odriozola was very conscious of the positive effects of the crossbreeding between the founder strains based on non-additive effects of dominance and epistasis, but he could not carry out a deep analysis of the complete diallel-cross data. Hence the Torbiscal line was synthesized with contributions from the four strains without exhausting the potential future changes by selection. According to the values represented in Fig. 3, the expected proportions of these contributions were unequal, although the sums of the respective proportions of the black and of the red strains were almost equal. The new composite line took advantage of some retained heterosis effects on growth and litter size (Pérez-Enciso & Gianola, 1992). As soon as the desired contributions were achieved, an empirical selection for pig growth was performed along the first fifteen years since the start of the Torbiscal line, based on weight records at weaning and at 240 days. The intensity of this selection was limited by the focus on the preservation of genetic variability and the simultaneous attention to other traits, such as carcass composition whose records were systematically obtained in the farm’s slaughterhouse. Positive realized selection differentials and genetic responses for these traits have been estimated in the studies of Béjar et al. (1993) and García-Casco (1993), with rates of genetic change of 59 and 943 g/year for weight at weaning and at 240 days, respectively. The success of this selective breeding was verified, three decades after, by independent comparative trials of the Torbiscal line with other Iberian strains from prestigious stockbreeders. The Torbiscal line showed greater growth in the fattening period, leaner body composition and greater percentages on carcasses of premium-cuts (Forero, 1999; Benito et al., 2000).

Our further look to the Torbiscal line was also directed to the last phase of its history. We showed the main results of three studies, based on SNP genotypes, focusing on the characterization of the genetic singularity of the current animals with respect to other domestic and wild pig populations. Among these populations, the choice of other Iberian and European Wild pigs was mandatory by their respective close or remote relatedness. Two arguments justified the comparison with Duroc genotypes: Red Iberian pigs imported from Portugal and Spain in the XIX century contributed to the origin of the Duroc-Jersey breed in the United States (Vaughan, 1950), and nowadays the current Duroc breed is the only breed authorized for crossbreeding with Iberian pigs and besides of a probable source of introgression into the Iberian genetic pool. Finally, the inclusion of genotypes from Asian pig breeds seems also necessary according to the well-known Asian influence in the genetics of most of the cosmopolitan European and American breeds. Previous studies based on mtDNA complete sequences or SNPs massive genotyping of a low number of sampled pigs (Alves et al., 2009; Burgos-Paz et al., 2013) have not found presence of Asian haplotypes in Iberian pigs. We performed a new whole-genome study for checking the potential admixture with Asian pigs based on an exhaustive sampling of Iberian pigs of diverse varieties and lines. The results provide a stronger support for the absence of introgression of Asian alleles in Iberian pigs, including Torbiscal, and European Wild boars and to their exclusive origin from European ancestors. By contrast, there is evidence of the widespread Asian influence in the other European pig breeds, although this introgression is lower in local breeds as Cinta Senese, Nera Siciliana or Mangalica.

| Chromosome | Region (Mb) | No of genes | Most relevant genes |
|------------|-------------|-------------|---------------------|
| 1          | 99.20–99.34 | 7           | ACA2, MYOSB         |
| 3          | 95.45–96.50 | 10          | PPM1B, LRPPRC, PLEKHH2, ZFP36L2 |
| 4          | 32.30–32.51 | 2           | LRP12               |
| 6          | 97.46–97.91 | 6           | APCDD1              |
| 6          | 101.67–104.97 | 10       | MYOM1               |
| 17         | 19.60–20.01 | 1           | JAG1                |

Table 5. Chromosome regions differentiated between Torbiscal and Other Iberian pigs with relevant gene content.
(Yang et al., 2017). In comparison with the other analysed Western pig populations, Torbiscal pigs – maintained around 20 generations as a closed line of moderate effective size – present greater values of self-coancestries and inbreeding with lower average distance between individuals (Table 3). Permanent tactics implemented in this line avoiding mating between relatives result in an excess of observed versus expected heterozygosity \( (\alpha<0) \) or more variability stocked within than between individuals \( (G_i<0.50) \). According to the genetic isolation of the four breeds (Meishan, Jiangquai, Jinhua and Xiang) included in the analysed Asian group, the partition of the genetic diversity of this group is extremely different, with the highest values of self-coancestry, inbreeding, more variability gathered between individuals, and the lowest rate between observed and expected heterozygosities. Taken the above paragraphs into account, the great genetic differentiation, measured by the \( F_{ST} \) values, among the Asian group of breeds and the other populations is not surprising (Table 4). Moreover, the corresponding \( F_{ST} \) values indicate that the two Iberian groups are more genetically differentiated with respect to the Duroc breed that respect to the European Wild boars, being always more differentiated the Torbiscal closed line than the group of other Iberian. Note that we used here the standardized \( F_{ST} \) coefficients to allow these comparisons, based on markers with different informativeness in each group because of Iberian pigs were not considered among the breeds included in the design of the Porcine SNP60 BeadChip.

Our aim was also to investigate more precisely the genetic differentiation between Torbiscal and the analysed pool of other Iberian pigs. We have taken advantage of genome-wide SNP datasets for identifying footprints of the history of farm populations assignable to selection, adaptation or random genetic drift. We used a \( F_{ST} \) outliers approach (Akey et al., 2010) to detect the most differentiated genome regions and then to annotate their gene content. Each point of the Manhattan plot (Fig. 6) represents the average divergence of frequencies of sliding windows of ten successive SNPs, and the most interesting outlier windows are those adjacent shaping 33 divergent chromosome regions. The longer one of these divergent regions includes 28 windows located on SSC6 (101.77–104.97 Mb) and encloses ten genes (Table 5). But only one of these genes, the Myomesin 1 (MYOM1), may be considered relevant by its implication in the myofibrillar network organisation affecting loin texture parameters in pigs (Piórkowska et al., 2018). One of the regions maximally differentiated (SSC3: 95.45 - 96.50) also contains ten genes, four of them \( (PPM1B, LRPPRC, PLEKH1H2, ZFP36L2) \) related to the regulation of the muscle development in mammals, pigs included. These genes are outlined because a greater loin development is a well-known productive advantage of the Torbiscal pigs respect to the other Iberians. We report these and other genes identified in the divergent regions and related to other relevant traits (Table 5), although we understand the limitations of this study and are not able to provide a sound interpretation of its results. A deeper research combining diverse statistical approaches and more complete and accurate annotations of the pig genome will be necessary for achieving a better explanation of the genome singularity of the Torbiscal line. It will be the task of other geneticists involve in the conservation of the Torbiscal line and interested on the history of the Iberian pigs.

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**References**

Akey JM, Ruhe AI, Akey DT, Wong AK, Connelly CF, Madeoy J, Nicholas TJ, Neff MW, 2010. Tracking footprints of artificial selection in the dog genome. Proc Natl Acad Sci USA 107: 1160-1165. https://doi.org/10.1073/pnas.0909918107

Alves E, Óvilo C, Rodríguez MC, Silió L, 2003. Mitochondrial DNA sequence variation and phylogenetic relationships among Iberian pigs and other domestic and pig populations. Anim Genet 34: 319-324. https://doi.org/10.1046/j.1365-2052.2003.01010.x

Alves E, Fernández AI, Barragán C, Óvilo C, Rodríguez C, Silió L, 2006. Inference of hidden population substructure of the Iberian pig breed using multilocus microsatellite data. Span J Agric Res 4: 37-46. https://doi.org/10.5424/sjar/2006041-176

Alves E, Fernández AI, Fernández-Rodríguez A, Pérez D, Benitez R, Óvilo C, Rodríguez MC, Silió L, 2009. Identification of mitochondrial markers for genetic traceability of European wild boar and Iberian and Duroc pigs. Animal 3: 1216-1223. https://doi.org/10.1017/S1751731109004819
Ayuso M, Óvilo C, Rodríguez-Bertos A, Rey AI, Daza A, Fernández A, González-Bulnes A, López-Bote CJ, Isabel B, 2015. Dietary vitamin A restriction affects adipocyte differentiation and fatty acid composition of intramuscular fat in Iberian pigs. Meat Sci 108: 9-16. https://doi.org/10.1016/j.meatsci.2015.04.017

Béjar F, Rodríguez MC, Toro MA, 1993. Estimation of genetic trends for weaning weight and test number in Iberian pigs using mixed model methodology. Livest Prod Sci 33: 239-251. https://doi.org/10.1016/0301-6226(93)90005-3

Benítez R, Núñez Y, Fernández A, Isabel B, Fernández AI, Rodríguez C, Barragán C, Martín- Palomino P, López-Bote C, Silio L, Óvilo C, 2015. Effects of dietary fat saturation on fatty acid saturation and gene transcription in different tissues of Iberian pigs. Meat Sci 102: 59-68. https://doi.org/10.1016/j.meatsci.2014.12.005

Benítez R, Fernández A, Isabel B, Núñez Y, De Mercado E, Gómez-Izquierdo E, García-Casco J, López-Bote C, Óvilo C, 2018. Modulatory effects of breed, feeding status, and diet on adipogenic, lipogenic, and lipolytic gene expression in growing Iberian and Duroc pigs. Inter J Molec Sci 19: 22. https://doi.org/10.3390/ijms19010022

Benito J, Vázquez C, Menaya C, Ferrera JL, García-Casco JM, Silio L, Rodríguez J, Rodríguez MC, 2000. Evaluation of the productive parameters in different strains of Iberian pigs. Opt Mediterr 41: 113-121.

Boichard D Maingé L, Verrier E, 1997. The value of using probabilities of gene origin to measure genetic variability in a population. Genet Sel Evol 29: 5-23. https://doi.org/10.1186/1297-9686-29-1-5

Burgos-Paz W, Souza CA, Megens HJ, Ramayo-Caldas Y, Melo M, Lemás-Flores C, Caal E, Soto HW, Martínez R, Álvarez LA et al., 2013. Porcine colonization of the Americas: a 60k SNP story. Heredity 110: 321-330. https://doi.org/10.1038/hdy.2012.109

Caballero A, 1995. On the effective size of populations with separate sexes with particular reference to sex-linked genes. Genetics 139: 1007-1011.

Caballero A, Toro M, 2000. Interrelations between effective population size and other pedigree tools for the management of conserved populations. Genet Res 75: 331–343. https://doi.org/10.1017/S0016672399004449

Caballero A, Toro M, 2002. Analysis of genetic diversity for the management of conserved subdivided populations. Conserv Genet 3: 289-299. https://doi.org/10.1023/A:1019956205473

Carrapizo AI, García C, 2008. Effect of the Iberian pig line on dry-cured ham characteristics. Meat Sci 80: 529-534. https://doi.org/10.1016/j.meatsci.2008.02.004

Cervantes I, Pastor JM, Gutiérrez JP, Goyache F, Molina A, 2011. Computing effective population size from molecular data: The case of three rare Spanish ruminant populations. Livest Sci 138: 202-206. https://doi.org/10.1016/j.livsci.2010.12.027

Daza A, Menoyo D, Olivares A, Cordero G, López-Bote CJ, 2007 Effect of Iberian pig feeding system on tissue fatty-acid composition and backfat rheological properties. J Anim Feed Sci 16: 408-419. https://doi.org/10.2235/jafs.66797/2007

Dickerson GE, 1969. Experimental approaches in utilizing breed resources. Anim Breed Abstr 37: 191-202.

Dobao MT, Rodrígáñez J, Silío L, 1983. Seasonal influence on fecundity and litter performance characteristics in Iberian pigs. Livest Prod Sci 10: 601-610. https://doi.org/10.1016/0301-6226(83)90052-0

Dobao MT, Rodrígáñez J, Silío L, 1984. Choice of companions in social play in piglets. App Anim Behav Aci 13: 359-366.

Esteve-Codina A, Paudel Y, Ferretti L, Raineri E, Jan Megens H, Silío L, Rodríguez MC, Groenen M, Ramos-Onsins S, Pérez-Enciso M, 2013. Dissecting structural and nucleotide genomewide variation in inbred Iberian pigs. BMC Genomics 14: 148. https://doi.org/10.1186/1471-2164-14-148

Evanno S, Regnaut S, Goudet J, 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Mol Ecol 14: 2611-2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Fabuel E, Barragán C, Silío L, Rodríguez MC, Toro MA, 2004. Analysis of genetic diversity and conservation priorities in Iberian pigs based on microsatellite markers. Heredity 93: 104-113. https://doi.org/10.1038/sj.hdy.6800488

Fernández A, Rodríguez MC, Rodrígáñez J, Silío L, Toro MA, 2002a. Use of Bayesian analysis of growth functions to estimate crossbreeding parameters in Iberian pigs. Livest Prod Sci 73: 213-223. https://doi.org/10.1016/S0301-6226(01)00249-4

Fernández A, Rodrígáñez J, Toro MA, Rodríguez C, Silío L, 2002b. Inbreeding effects on the parameters of the growth function in three strains of Iberian pigs. J Anim Sci 80: 2267-2275. https://doi.org/10.2527/2002.8092267x

Fernández A, Rodrígáñez J, Zuzuáregui J, Rodríguez MC, Silío L, 2008a. Genetic parameters for litter size and weight at different parities in Iberian pigs. Span J Agric Res 6 (Special issue): 98-106. https://doi.org/10.5424/sjar/200806S1-378

Fernández A, Alves E, Fernández A, De Pedro E, López-García MA, Óvilo C, Rodríguez MC, Silío L, 2008b. Mitochondrial genome polymorphisms associated with longissimus muscle composition in Iberian pigs. J Anim Sci 86: 1283-1290. https://doi.org/10.2527/jas.2007-0568

Forero, 1999. Estudio comparativo de cinco estirpes de cerdo ibérico. Diputación Provincial de Huelva, Spain. Servicio de Publicaciones, 254 pp.

García Casco JM, 1993. Aspectos genéticos de la mejora de caracteres de crecimiento en cerdos ibéricos. Doctoral thesis, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid.
García-Casco J, Fernandez A, Rodriguez MC, Silió L, 2012. Heterosis for litter size and growth in crosses of four strains of Iberian pig. Livest Sci 147:1-8. https://doi.org/10.1016/j.livsci.2012.03.005

Gómez-Raya L, Rodriguez MC, Barragán C, Silió L, 2015. Genomic inbreeding coefficients based on the distribution of the length of runs of homozygosity in a closed line of Iberian pigs. Genet Sel Evol 47: 81. https://doi.org/10.1186/s12711-015-0153-1

Hedrick PW, 2005. A standardized genetic differentiation measure. Evolution 59: 1633-1638. https://doi.org/10.1111/j.0012-7203.2005.tb03609.x

Hernández P, Zomeño B, Ariño B, Blasco A, 2004. Antioxidant, lipolytic and proteolytic enzyme activities in pork meat from different genotypes. Meat Sci 66: 525-529. https://doi.org/10.1016/S0309-1740(03)00155-4

Ibáñez-Escriche N, Varona L, Magallón E, Noguera J, 2014. Crossbreeding effects on pig growth and carcass traits from two Iberian strains. Animal 8: 1569-1576. https://doi.org/10.1017/S1751731114001712

Ibáñez-Escriche N, Magallón E, González E, Tejeda JF, Noguera J, 2016. Genetic parameter and crossbreeding effects of fat deposition and fatty acid profiles in Iberian pig lines. J Anim Sci 94: 28-37. https://doi.org/10.2527/jas.2015-9433

James JW, 1972. Computation of genetic contributions from pedigrees. Theor Appl Genet 42: 272-273. https://doi.org/10.1007/BF00277555

James JW, McBride G, 1958. The spread of genes by natural and artificial selection in a closed poultry flock. J Genet 56: 55-62. https://doi.org/10.1017/FJ02984720

Lacy RC, Alaks G, Walsh A, 1996. Hierarchical analysis of inbreeding depression in Poromycus polonion. Evolution 50: 2187-2200. https://doi.org/10.1111/j.1558-5646.1996.tb03609.x

Larson G, Albarella U, Dobney K, Rowley-Conwy P, Schibler J, Tresset A, Vigné JD, Edwards CJ, Schlumbaum A, Dinu A et al., 2007. Proc Nat Acad Sci 104: 15276-15281.

Legarra A, Varona L, López de Maturana E, 2011. TM Threshold Model. http://snp.toulouse.inra.fr/~alegarra/formulas/index.php?fr=/~alegarra/manualtm.pdf. [Last accessed March 2013].

López-Bote CJ, Toldrá F, Daza A, Ferrer JM, Menoyo D, Silió L, Rodriguez MC, 2008. Effect of exercise on skeletal muscle proteolytic enzyme activity and meat quality characteristics in Iberian pigs. Meat Sci 79: 71-76. https://doi.org/10.1016/j.meatsci.2007.08.002

Muñoz G, Óvilo C, Sánchez A, Rodriguez MC, 2004. Mapping of the porcine estrogen receptor β gene (ESR-β) and association study with litter size in Iberian pigs. Anim Genet 35: 242-244. https://doi.org/10.1111/j.1365-2052.2004.01141.x

Muñoz M, Rodríguez MC, García-Cortés LA, Gonzalez A, García-Casco JM, Silió L, 2017. Direct and maternal additive effects are not the main determinants of Iberian piglet perinatal mortality. J Anim Breed Genet 134: 512-519. https://doi.org/10.1111/jbg.12298

Muriel E, Ruiz J, Ventanas J, Pérez-Enciso M, 2006. Meat quality characteristics in different lines of Iberian pigs. Meat Sci 70: 299-307. https://doi.org/10.1016/j.meatsci.2005.10.018

Nei M, 1973. Analysis of gene diversity in subdivided populations. Proc Nat Acad Sci 70 (12): 3321-3323. https://doi.org/10.1073/pnas.70.12.3321

Odriozola M, 1976. Investigación sobre los datos acumulados en dos piastras experimentales. IRYDA, Madrid.

Óvilo C, Benítez R, Fernández A, Núñez Y, Ayuso M, Fernández AI, Rodríguez C, Isabel B, Rey AI, López-Bote C, Silió L, 2014a. Longissimus dorsi transcriptome analysis of purebred and crossbred Iberian pigs differing in muscle characteristics. BMC Genomics 15: 413. https://doi.org/10.1186/1471-2164-15-413

Óvilo C, Benítez R, Fernández A, Isabel B, Núñez Y, Fernández AI, Rodríguez C, Daza A, Silió L, López-Bote C, 2014b. Dietary energy source largely affects tissue fatty acid composition but has minor influence on gene transcription in Iberian pigs. J Anim Sci 92: 939-954. https://doi.org/10.2527/jas.2013-6988

Pérez-Enciso M, Gianola D, 1992. Estimates of genetic parameters for litter size in six strains of Iberian pigs. Livest Prod Sci 32: 283-293. https://doi.org/10.1016/S0301-6226(92)80007-8

Piórkowska K, Żukowski K, Ropka-Molik K, Tyra M., 2018. Detection of genetic variants between different Polish Landrace and Pulawska pigs by means of RNA-seq analysis. Anim Genet 49 (3): 215-225. https://doi.org/10.1111/age.12654

Pritchard JK, Stephens M, Donnelly T, 2000. Inference of population structure using multilocus genotype data. Genetics 155: 945-959.

Rey A, Daza A, López-Carrasco, López-Bote C, 2006. Feeding Iberian pigs with acorns and grass in either free-range or confinement affects the carcass characteristics and fatty acids and tocopherols accumulation in Longissimus dorsi muscle and backfat. Meat Sci 73: 66-74. https://doi.org/10.1016/j.meatsci.2005.10.018

Rodríguez MC, Rodrígñez J, Silió L, 1994. Genetic analysis of maternal ability in Iberian pigs. J Anim Breed Genet 111: 220-227. https://doi.org/10.1111/j.1439-0388.1994.tb00461.x

Rodrígñez J, Toro MA, Rodríguez MC, Silió L, 1998. Effect of founder allele survival and inbreeding depression on litter size in a closed line of Large White pigs. Anim Sci 67: 573-582. https://doi.org/10.1073/s1357729800033014
Spanish wild and domestic pig populations estimated from microsatellite markers. Span J Agric Res 6 (Special issue): 107-115. https://doi.org/10.5424/sjar/200806S1-379

Silió L, Rodríguez MC, Toro MA, Rodrígáñez J, 1994. Maternal and individual genetic effects on piglet weight. Proc 5th World Congress Genetics Applied Livestock Production, Guelph, Ontario, (Canada), August 7-12.

Silió L, Rodríguez MC, Fernández A, Barragán C, Benítez R, Óvilo C, Fernández AI, 2013. Measuring inbreeding and inbreeding depression on pig growth from pedigree and SNP-derived metrics. J Anim Breed Genet 130: 349-360. https://doi.org/10.1111/jbg.12031

Silió L, Barragán C, Fernández AI, García-Casco J, Rodríguez MC, 2016. Assessing effective population size, coancestry and inbreeding effects on litter size using the pedigree and SNP data in closed lines of the Iberian pig breed. J Anim Breed Genet 133: 145-154. https://doi.org/10.1111/jbg.12168

Toro MA, Silió L, Rodrígáñez J, Dobao MT, 1988. In-breeding and family index selection for prolificacy in pigs. Anim Prod 46: 79-85. https://doi.org/10.1017/S0003356100003135

Toro MA, Rodrígáñez J, Silió L, Rodríguez MC, 2000. Genealogical analysis of a closed herd of black hairless Iberian pigs. Conserv Biol 14: 1843-1851. https://doi.org/10.1046/j.1523-1739.2000.99322.x

Toro MA, Barragán C, Rodrígáñez J, Rodríguez MC, Silió L, 2002. Estimation of coancestry in Iberian pigs using molecular markers. Conserv Genet 3: 309-320. https://doi.org/10.1023/A:1019921131171

Toro MA, Fernández A, García-Cortés LA, Rodrígáñez J, Silió L, 2006. Sex ratio variation in Iberian pigs. Genetics 173: 911-917. https://doi.org/10.1534/genetics.106.055939

Vaughan HW, 1950. Breeds of live stock in America. Long’s College Book Co., Columbus, OH, USA.

Woolliams JA, Mäntysaari EA, 1995. Genetic contributions of Finnish Ayrshire bulls over four generations. Anim Sci 61: 177-187. https://doi.org/10.1017/S1357729800013709

Yang B, Cui L, Pérez-Enciso M, Traspov A, Crooijmans RPMA, Zinovieva N, Schook L, Archibald A, Gatphyayk K, Knorr C et al., 2017. Genome-wide SNP data unveils the globalization of domesticated pigs. Genet Sel Evol 49: 71. https://doi.org/10.1186/s12711-017-0345-y