A QTL on pig chromosome 4 affects fatty acid metabolism: Evidence from an Iberian by Landrace intercross[1]

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ABSTRACT: Three Iberian boars were bred to 31 Landrace sows to produce 79 F_1 pigs. Six F_1 boars were mated to 73 F_1 sows. The F_2 progeny from 33 full-sib families (250 individuals) were genotyped for seven microsatellites spanning the length of chromosome 4. Least squares procedures for interval mapping were used to detect quantitative trait loci (QTL). A permutation test was used to establish nominal significance levels associated with QTL effects, and resulting probability levels were corrected to a genomewide basis. Observed QTL effects were (genomewide significance, position of maximum significance in centimorgans): percentage of linoleic acid in subcutaneous adipose tissue (< 0.01, 81); backfat thickness (< 0.01, 83); backfat weight (< 0.01, 80); longissimus muscle area (0.02, 83); live weight (0.19, 88); and percentage of oleic acid in subcutaneous adipose tissue (0.25, 81). Gene action was primarily additive. The Iberian genotypes were fatter, slower growing, and had lower linoleic and higher oleic acid contents than Landrace genotypes. The interval from 80 to 83 cM contains the FAT1 and A-FABP loci that have been shown previously to affect fat deposition in pigs. This is the first report of a QTL affecting fatty acid composition of subcutaneous adipose tissue in pigs and provides a guide for the metabolic pathways affected by candidate genes described in this region of chromosome 4.

Key Words: Fat, Fatty Acids, Landrace, Pig Breeds, Quantitative Trait Loci

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Introduction

There is ample evidence for a quantitative trait locus (**QTL**) affecting fat deposition and growth located on porcine chromosome 4. Such a QTL has been found in experiments with F_2 crosses involving wild boar (Andersson et al., 1994; Knott et al., 1998) and Meishan (Bidanel et al., 1998; Walling et al., 1998; Paszek et al., 1999). This locus has been named FAT1 after Marklund et al. (1999).

We developed an F_2 cross between Iberian × Landrance pigs (the IBMAP cross) to study the differential genetic basis of growth, carcass, meat quality, and histochemical traits in the Iberian and the Landrace breeds (IBMAP Consortium, 1998). The Iberian breed is the most important Mediterranean type, and one of the few "unimproved" breeds that survive in modern pig breeding schemes. It is also a very interesting genetic material for the study of meat quality (Serra et al., 1998). Iberian pigs are characterized by early maturity, dark coat, high subcutaneous and intramuscular fat

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content, and appetite. At present, almost all meat from Iberian pigs is consumed as cured products, which are highly appreciated and priced (López-Bote, 1998). The objective of this research was to confirm the effects of the FAT1 locus in the IBMAP genetic material and characterize the effects of this region of chromosome 4 on metabolism of fatty acids.

Materials and Methods

Experimental Design and Traits Analyzed. The Iberian line used, Guadyerbas, is a unique black hairless line that has been genetically isolated since 1945. It has an average inbreeding coefficient above 0.3 (Rodrigáñez et al., 1997) and extremely low prolificacy. The Landrace line used is a non-inbred lean maternal line from the experimental farm Nova Genètica S.A. (Lleida, Spain). This line is currently selected for an index combining litter size, backfat, and growth performance. Thus, the two lines used in this experiment are highly divergent for the traits studied (Serra et al., 1998).

The population studied consisted of three Iberian boars, 31 Landrace sows, 79 F_1 individuals (6 male and 73 female), and 577 F_2 pigs. Here we report results based on 250 F_2 pigs from 33 full-sib families. The parental Landrace sows were homozygous for the Hal^N allele, and the Iberian breed is free from the Ryr1 mutation. The F_2 pigs were raised under normal intensive conditions in the experimental farm of Nova Genètica. Feeding was ad libitum, and males were not castrated. The pigs were slaughtered in four contemporary groups between December 1997 and March 1998 following a commercial protocol. The average age at slaughter was 175.5 ± 0.3 d.

The traits analyzed are liveweight, carcass weight, backfat thickness, backfat weight, longissimus muscle area, and fatty acid composition of subcutaneous backfat. Liveweight was recorded 1 or 3 d before slaughter and carcass weight was obtained 30 min postmortem. Backfat from the left half-carcass was weighed after a commercial cutting procedure 24 h postmortem. A sample from the loin starting from the last rib and spanning four ribs was removed for various meat quality and laboratory analyses. Subcutaneous fat thickness between the 3rd and 4th last ribs and longissimus muscle area were measured on the transverse cut of the longissimus thoracis between the 3rd and 4th last rib at 24 h postmortem.

Fatty acid composition was analyzed from a sample of backfat by gas chromatography. The average chain length of fatty acid composition was calculated as **ACL** = $\Sigma(F_{ni} \times ni)/100$, where F_{ni} is the percentage of fatty acids with a chain length of ni number of carbon atoms. The double bond index was calculated as **DBI** = $\Sigma(UF_{bi} \times bi)/100$, where UF_{bi} is the percentage of unsaturated fatty acids with bi number of double bonds. The unsaturated index is **UI** = DBI/percentage of saturated fatty acids. These metabolic ratios provide indirect evidence about physiological mechanisms involved in fatty acid differences; changes in UI or DBI suggest different desaturase activities, whereas ACL is related to chain elongation reactions (Pamplona et al., 1998).

Genotyping. DNA from the parental individuals was extracted from blood using a saline precipitation protocol, and DNA from F_1 and F_2 pigs was extracted using a commercial saline precipitation-based protocol (Boehringer Mannheim). Animals were genotyped for seven microsatellites (SW2404, S0301, S0001, SW839, S0214, SW445, S0097). These were chosen because they had been found to be highly informative based on the index of Ron et al. (1995) and because they provided complete and uniform coverage of the chromosome. An automatic PCR ABI PRISM 877 integrated thermal cycler (Perkin Elmer) was used for PCR. The PCR products were analyzed with Genescan software on capillary electrophoresis equipment with fluorescent detection (ABI PRISM 310 genetic analyzer). Genotypes were stored in the Gemma database (Iannuccelli et al., 1996).

Statistical Analyses. Linkage analysis was carried out with the CRI-MAP program, option "build" (Green et al., 1990). Marker information contents were obtained as in Knott et al. (1998). We employed a regression method for QTL detection (Haley et al., 1994). The method assumes that the putative QTL is diallelic with alternative alleles fixed in each parental breed, here QQ for the Iberian genotype (with effect a) and qq for the Landrace genotype (with effect –a). The statistical model used was

$$y = \text{sex} + \text{family} + \text{covariate} + c_a\, a + c_d\, d + e \quad [1]$$

where y is the phenotype, family is the full-sib family (here 33 levels), the covariate was the age at weight for liveweight, age at slaughter for carcass weight, and carcass weight for backfat thickness, backfat weight, and longissimus muscle area. Fatty acid percentage was corrected either for carcass weight or backfat thickness. The coefficient c_a is the probability P(QQ) – P(qq), and c_d is P(Qq), at the chromosome position of interest. The dominance deviation (d) and additive effect (a) are the parameters to be estimated. The residuals are represented by e. Model [1] was fitted every centimorgan using the average sex distances. The regression *F*-statistics that resulted from testing model [1] vs a model without fitting a and d was computed at each position. A two-QTL model was also explored but in no case was a second QTL significant and the results are not presented. The additive fraction of F_2 phenotypic variance (σ^2_y) explained by a QTL was computed assuming that alternative alleles were fixed in each breed; i.e., $h^2_Q = a^2/2\ \sigma^2_y$.

Genomewide and chromosomewise significance levels were obtained. Chromosomewise significance thresholds were calculated by permuting 20,000 times the records within family and sex, in order to maintain the data structure. A preliminary study showed critical values of the distributions of *F*-statistics were similar for all traits so that we used backfat thickness data

permutations to obtain significance levels for all traits. Approximate genomewide thresholds were obtained applying the Bonferroni correction as described in Knott et al. (1998). Suppose that a given value F corresponds to a chromosome significance level P_c, the genome significance level associated is given by $P_G = 1 - (1 - P_c)^{19}$; 19 is the haploid number of pig chromosomes. This formula assumes lengths and marker spacing in all chromosomes are identical so that results are to be taken only as approximate. The 5 and 1% significance thresholds were $F = 5.26$ and 7.11, respectively, for the chromosomewise test. The corresponding 5 and 1% genomewide statistics were F = 8.82 and 10.71, respectively. These statistics are very similar to those reported in the literature (e.g., Knott et al., 1998). Confidence intervals (**CI**) for QTL location were obtained using the chi-square drop approximation (equivalent to the LOD score drop approximation). An F-statistic is equal to χ^2_P/p, approximately, where p is the number of parameters estimated, here two, the additive and dominance effects. The 95% threshold is $\chi^2_{2,\,95} = 3.85$. Thus, the 95% confidence interval limits were obtained at the chromosome locations where the F-statistics decreased 3.85/2 = 1.92 units starting in both directions from the position corresponding to the maximum F. This method performs reasonably well for large effect QTL but is not valid for small effect QTL (Mangin et al., 1994).

Results

Table 1 shows summary statistics for the traits analyzed. Linkage analysis found a marker order identical to that reported in the literature and distances were similar to those in Rohrer et al. (1994) and in Gerbens et al. (2000). There were minor differences in map length between sexes, with the female map being 13% longer on average (Table 2). Differences in allelic frequencies between breeds were very high, with the sole exception of marker SW2404, in agreement with the supposition that the two lines are genetically distant.

Table 1. Main statistics in the F_2 population genotyped

Trait	N[a]	Mean	σ_y	Diet
Growth and carcass traits				
Liveweight, kg	245	94.58	9.67	—
Carcass weight, kg	250	67.20	7.73	—
Backfat weight, kg	249	2.08	0.46	—
Backfat thickness, mm	247	24.06	6.27	—
Longissimus muscle area, cm^2	235	33.31	4.08	—
Fatty acid composition, %				
Myristic, 14:0	247	1.32	0.14	1.19
Palmitic, 16:0	247	18.86	1.12	28.63
Palmitoleic, 16:1	247	2.45	0.29	1.56
Stearic, 18:0	247	9.87	0.83	10.16
Oleic, 18:1	247	43.98	1.39	33.09
7-Octadecenoic, 18:1n-7	247	2.94	0.28	1.92
Linoleic, 18:2	247	15.37	1.09	30.12
Linolenic, 18:3	247	1.31	0.19	2.3
Eicosenoic, 20:1	247	0.95	0.22	0.36
Eicosadienoic, 20:2	247	0.65	0.03	0.20
Metabolic ratios				
Average chain length	247	17.55	0.03	—
Double bond index	247	0.91	0.02	—
Unsaturated index	247	2.95	0.19	—

[a]N is the number of individuals with record and genotype; Mean is the mean corrected for sex effect (referred to males), σ_y is the residual standard deviation after fitting the fixed effects and covariates, except the QTL. Diet is the percentage of fatty acids in the food (average of three samples).

Table 2. Marker positions and statistics

Marker	Position (sex average)	Position (female)	Position (male)	le[a]	IC
SW2404	0.0	0.0	0.0	0.57	0.510
S0301	45.1	46.9	43.5	0.84	0.805
S0001	64.6	62.1	67.4	0.89	0.844
SW839	75.1	69.3	81.7	0.96	0.992
S0214	93.7	92.3	95.7	0.96	0.998
SW445	117.5	130.1	107.3	1.00	0.948
S0097	134.2	144.1	127.7	0.86	0.773

[a]le, Ron et al. (1995) index; IC, information content at marker positions.

Results from the QTL analyses are presented in Table 3. Confidence intervals for QTL location are shown only for the QTL significant at a genomewide level. The F profiles are shown in Figures 1 and 2 for the carcass traits and fatty acid composition, respectively. A highly significant QTL for fat and longissimus muscle area maps to position 80 cM (CI bounds = 71 to 93 cM). A lower second peak with effect on growth traits is located 8 cM telomeric. The F-statistics for growth traits do not reach the genomewide 5% significance level, and only live weight reaches the 5% chromosomewise level. The effects were in the expected direction (i.e., the Iberian alleles increased fatness and decreased growth rate and muscle area).

The most significant QTL found was that affecting percentage of linoleic acid (Figure 2). It maps to the same position as the fatness QTL with CI bounds (71 to 86 cM) nested within the fatness QTL CI limits. Individuals homozygous for the Iberian allele are expected to have 1.5% less linoleic acid than those homozygous for the Landrace allele. In a previous study (Serra et al., 1998), we found that the difference in linoleic acid content between both breeds was 4%, which means that this QTL may explain almost 40% of phenotypic breed differences. This QTL explained 25% of all the F_2 phenotypic variance for content linoleic acid adjusted to a constant carcass weight (Table 3). The QTL also affected oleic content, although in the opposite direction, and the P-value was much smaller than for linoelic acid percentage. We did not find any other relevant association with fatty acid composition. Results for metabolic ratios are caused primarily by the effect on linoleic acid content. Consequently, their significance levels were much smaller than for linoleic acid percentage. The correction for backfat thickness instead of carcass weight had a dramatic effect on linoleic acid content, but it was not as important for the remaining fatty

Table 3. QTL analysis: live weight was corrected for age, carcass weight for age at slaughter, and the remaining traits were corrected for carcass weight

Trait[a]	Position (CI)[b]	a ± S.E.	d ± S.E.	h^2_Q	F_{Max}	P_c	P_G
LW	88	–3.34 ± 1.04	2.07 ± 1.59	0.06	7.02	1.1×10^{-2}	0.19
CW	89	–2.29 ± .83	1.18 ± 1.23	0.04	4.94	6.7×10^{-2}	0.73
BFW	80 (71–90)	0.22 ± .05	–0.03 ± .07	0.11	11.08	4.5×10^{-4}	<0.01
BFT	83 (73–91)	3.65 ± .67	–0.45 ± 1.02	0.17	15.85	$<10^{-5}$	<0.01
MA	83 (72–93)	–2.02 ± .46	0.24 ± .70	0.12	9.87	9.0×10^{-4}	0.02
Fatty acid							
14:0	75	0.02 ± .01	0.06 ± .02	0.01	5.40	4.5×10^{-2}	0.58
16:0	83	0.30 ± .13	0.38 ± .20	0.04	3.71	0.182	0.98
16:1	75	0.04 ± .03	0.11 ± .04	0.01	4.42	0.101	0.87
18:0	0	0.23 ± .11	0.50 ± .19	0.04	5.63	3.6×10^{-2}	0.51
18:1n-9	81	0.49 ± .15	–0.29 ± .23	0.06	6.68	1.5×10^{-2}	0.25
18:1n-7	0	–0.06 ± .04	–0.12 ± .06	0.02	3.02	0.309	0.99
18:2	79 (71–86)	–0.77 ± .13	–0.12 ± .19	0.25	17.36	$<10^{-5}$	<0.01
18:3	29	–0.03 ± .03	–0.11 ± .05	0.01	2.53	0.438	0.99
20:1	75	–0.05 ± .02	–0.04 ± .03	0.02	2.86	0.347	0.99
20:2	0	0.03 ± .02	0.05 ± .04	0.50	1.48	0.796	0.99
ACL	75	–0.94 ± .34	–1.10 ± .47	0.04	6.04	2.6×10^{-2}	0.39
DBI	80	–1.21 ± .29	–0.44 ± .44	0.12	8.65	3.0×10^{-3}	0.06
UI	84	–0.06 ± .02	–0.05 ± .03	0.05	4.20	0.121	0.91

[a]Traits: LW, live weight; CW, carcass weight; BFW, backfat weight; BFT, backfat thickness; MA, longissimus muscle area; ACL, average chain length; DBI, double bond index; UI, unsaturated index; h^2_Q is the fraction of the phenotypic variance in the F_2 explained by the QTL.

[b]Position in centimorgans corresponding to F_{Max}, confidence interval (CI) bounds are shown only for $P_G < 0.05$; a, additive effect; d, dominance effect; fraction of phenotypic variance explained by the QTL; P_c, *P*-value for the chromosomewise test; P_G, approximate *P*-value for the genomewide test.

acids (Table 4, Figure 3). Gene action was additive for traits showing the most significant QTL effects. This agrees with results from other experiments (e.g., Knott et al., 1998; Walling et al., 1998).

Discussion

The most significant effect found in this work corresponded to the percentage of linoleic acid content. Effects on backfat thickness, backfat weight, and longissimus muscle area were also highly significant and mapped to the same position as the linoleic acid content QTL. The evidence with respect to growth is much weaker. Linoleic acid is an essential fatty acid for mammals because they lack desaturase capacity beyond the 9th carbon atom (Vance and Vance, 1996). It is a key component for cellular membranes and a precursor of prostanglandins and thromboxanes. It is also stored in adipose tissue or β-oxidized for energy production. In fact, it is

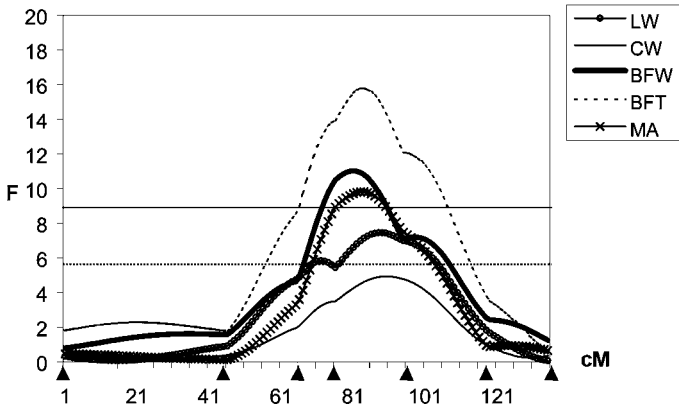

Figure 1. *F*-profile of the QTL scan: Growth and carcass traits. The horizontal solid line is the approximate 5% genomewide significance threshold; dashed line is the 5% chromosomewise significance threshold. Arrows indicate microsatellite positions. LW, liveweight; CW, carcass weight; BFW, backfat weight; BFT, backfat thickness; MA, longissimus muscle area.

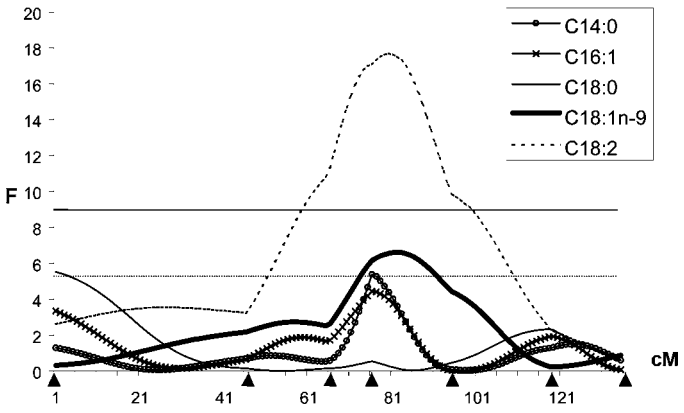

Figure 2. *F*-profile of the QTL scan: Fatty acid composition corrected for carcass weight (only the most significant profiles are shown). The horizontal solid line is the approximate 5% genomewide significance threshold; dashed line is the 5% chromosomewise significance threshold. Arrows indicate microsatellite positions.

Table 4. QTL analysis for the most significant fatty acid percentages; traits corrected for backfat thickness

Fatty acid	Position[a]	a ± S.E.	d ± S.E.	h^2_Q	F_{Max}	P_c	P_G
14:0	75	0.01 ± .01	0.06 ± .02	0.00	4.76	7.7×10^{-2}	0.78
16:1	0	–0.08 ± .04	–0.12 ± .07	0.04	4.04	0.137	0.94
18:0	0	0.20 ± .11	0.50 ± .19	0.03	5.17	5.4×10^{-2}	0.65
18:1n-9	81	0.46 ± .15	–0.28 ± .23	0.06	5.85	3.0×10^{-2}	0.44
18:2	78	–0.43 ± .12	–0.11 ± .17	0.08	6.97	1.2×10^{-2}	0.20

[a]Position in centimorgans corresponding to F_{Max}; a, additive effect; d, dominance effect; fraction of phenotypic variance explained by the QTL (h^2_Q); P_c, *P*-value for the chromosomewise test; P_G, approximate *P*-value for the genomewide test.

highly digestible and is preferentially deposited compared with other fatty acids (Lawrence and Fowler, 1997). The linoelic acid QTL alone explains 25% of phenotypic variance in the F_2, a much larger fraction than is usually reported for QTL in porcine F_2 crosses. The estimated positions of the linoleic acid percentage and backfat thickness QTL coincide (79 to 83 cM), making it most likely that backfat thickness and linoleic acid differences result from pleiotropic effects of the same QTL. The dramatic drop in significance of the linoleic acid content QTL when correcting for backfat thickness (Table 4, Figure 3) is thus only a consequence that they are, to a large extent, the same trait. We have also studied backfat thickness corrected for linoleic content, and the QTL was clearly not significant (F_{Max} = 1.11). That is, there is no effect of the QTL on fatness at equal linoleic levels, as would occur if its primary effect were on linoleic acid content rather than on backfat thickness. A fat animal is expected to have low linoleic acid content (because it cannot be synthesized de novo) and high oleic acid content, because this fatty acid is the main storage component in pigs. Thus, a negative correlation between linoleic acid percentage and fat deposition across breeds is usually observed (Sellier and Monin, 1994; Nürnberg et al., 1998). However, we have reported a QTL on chromosome 6 that influences intramuscular fat and backfat thickness (Ovilo et al., 2000) and that does not show any significant correlative effect on fatty acid composition (F_{Max} = 4.41 for linoleic acid content; unpublished results). Altogether, it seems that the effect of the QTL on linoleic acid content is not an artifact caused by an increased fatness. Thus, we conclude that the metabolism and(or) deposition rate of linoleic acid is under (partial) control of a QTL on chromosome 4.

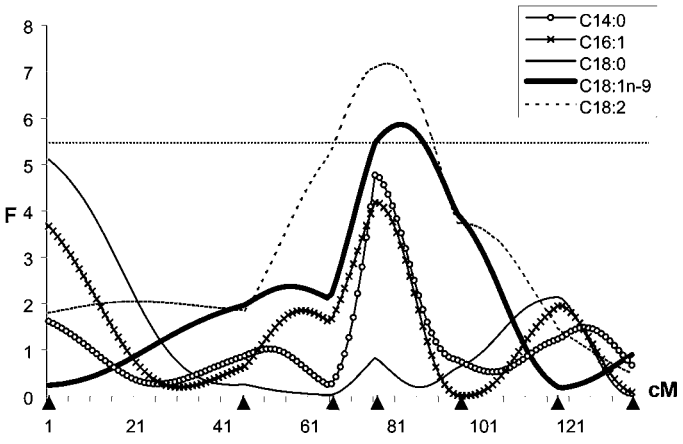

Figure 3. *F*-profile of the QTL scan: Fatty acid composition corrected for backfat thickness (only the most significant profiles are shown). The horizontal solid line is the approximate 5% genomewide significance threshold; dashed line is the 5% chromosomewise significance threshold. Arrows indicate microsatellite positions.

The QTL locations corresponding to maximum *F* for fatness and growth were separated by 8 cM or less in this work and have overlapping CI. Similarly, in the wild boar cross, the QTL locations do not coincide, being separated by approximately 20 cM with the growth QTL telomeric to the fatness QTL (Andersson et al., 1994). However, in most experiments involving Meishan, only one QTL affecting growth has been detected on chromosome 4 (Bidanel et al., 1998; Wang et al., 1998; Paszek et al., 1999). Additionally, De Koning et al. (1999) did not detect a QTL affecting backfat thickness, nor did Gerbens et al. (2000) detect a QTL affecting adipocyte fatty acid-binding protein on chromosome 4 using crosses involving the Meishan breed. In contrast, Walling et al. (1998) detected both a QTL for growth and a relatively smaller QTL for fat thickness on chromosome 4 in Meishan crosses. Again, the growth and fatness QTL did not coincide. Thus, it is possible there are two QTL in this region of chromosome 4, one affecting fat deposition and the second affecting growth. This hypothesis can be supported by studies of the FAT1 locus (Marklund et al., 1999), which has been mapped to this region of chromosome 4. The FAT1 locus effects on growth were diminished in wild boar × Large White backcrosses when boars with different FAT1 genotypes were progeny tested. However, the effect of FAT1 on fatness remained constant. We conclude that the Iberian crosses used in the present research were more similar to wild boar crosses than to Meishan crosses in that the primary QTL effect observed on chromosome 4 affected fatness rather than growth. This is consistent with the well-known fact that the pig was domesticated

independently in Asia and in Europe, from local wild pig populations (Clutton-Brock, 1981).

A question posed by these results is whether the observed QTL affecting fatness and linoleic content is the same as the FAT1 locus (Andersson et al., 1994; Marklund et al., 1999). The evidence supports an affirmative response. First, the marker interval containing the QTL SW839 - S0214 in this work overlaps with the FAT1 interval (Marklund et al., 1999). Exact coincidence is not possible because the markers genotyped are different in each work. Second, both QTL affect fat deposition and explain about the same percentage of F_2 variation for fat thickness, 17% here and 15% in Knott et al. (1998). In contrast to previous results with chromosome 4, the effect on growth was much smaller than that on fatness and we did not find a genomewide significant association with growth. A possible reason is that the reported QTL on chromosome 4 seems to predominantly affect early growth (Knott et al., 1998). Unfortunately, we did not record weight at early stages in these F_2 animals. An alternative explanation is that alleles are not fixed within the parental breeds, which causes a loss of power with regression methods (Alfonso and Haley, 1998; Pérez-Enciso and Varona, 2000), or fixed for the same allele in both breeds.

Irrespective of whether the QTL is the FAT1 locus, the QTL reported here has a large potential impact in the industry because of its influence on fatty acid composition. First, the fatty acids ingested show some effects on human blood lipids and on cardiovascular health (Yu-Poth et al., 1999). Second, there are increasing problems with extremely lean carcasses that have high linoelic acid content fat; they are difficult to process because of its softness and are very prone to oxidative rancidity. Linoleic acid has a strong influence on oxidative stability of fat and muscle tissues, and it needs to be modulated by formulating appropriate animal diets to avoid excessive oxidation. High linoleic acid contents are also associated with low tenderness and consumer acceptability (Whittinghton et al., 1986; Cameron and Enser, 1991; Lawrence and Fowler, 1997). Finally, fatty acid content is the official criterion to qualify Iberian cured products. Minimum oleic and maximum linoleic acid concentrations are required, the exact level determining the quality category in which the product is classified (De Pedro, 1998).

Implications

This experiment illustrates the usefulness of autochthonous breeds in the study of physiological and genetic consequences of selection for current commercial objectives (i.e., lean content or growth). We have found a QTL on chromosome 4 with a large effect on the linoleic acid content of subcutaneous fat. Eventual identification of the gene may have an important economic impact on pig breeding.

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