ANNEXES

ANNEX 1

A QTL on pig chromosome 4 affects fatty acid metabolism: Evidence from an Iberian By Landrace Intercross

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Els estudis de detecció de QTLs en porcí han estat l'objectiu de diversos grups de recerca durant el darrers anys. El 1994, Andersson *et al.* publicaren el primer treball desenvolupat en aquest camp. Aquest treball descrivia l'existència d'un QTL al cromosoma 4 amb efecte sobre la deposició de greix dorsal, la longitud de la canal i la longitud de l'intestí prim. Aquest QTL fou confirmat en anàlisis posteriors en el mateix material animal, atribuint-li fins i tot altres efectes sobre caràcters de qualitat de la canal i de la carn (Andersson-Eklund *et al.*, 1996; Knott *et al.*, 1998; Marklund *et al.*, 1999; etc...) i en altres pedigrees (Walling *et al.*, 1998; 2000; Wang *et al.*,. 1998; Rohrer *et al.*, 1998a; 1998b; Bidanel *et al.*, 2001; etc...). Marklund *et al.* (1999) anomenaren aquest QTL FAT1.

Fins a la data de publicació d'aquest article no hi havia descrit cap treball de detecció de QTLs per a caràcters de qualitat del greix en animals domèstics.

L'objectiu del present treball consisteix en presentar els primers efectes d'un QTL sobre la composició en àcids greixosos del teixit adipós subcutani dorsal. Aquest QTL coincideix per la seva posició i per efectes paral·lels sobre altres caràcters amb el FAT1. Aquests resultats es varen obtenir en l'anàlisi preliminar de 250 animals F_2, agrupats en 33 famílies de germans complets, d'una població experimental creada expressament per a l'estudi de regions genètiques amb efecte sobre caràcters d'interès econòmic-productiu. Aquesta població es va formar mitjançant l'encreuament de 3 mascles de la línia consanguínia de porc Ibèric coneguda com a Guadyerbas amb 31 femelles de la raça Landrace. Després d'haver desenvolupat un mapa de lligament amb 7 microsatèl·lits distribuïts per tot el cromosoma 4, es va estimar el genotip d'un possible QTL en una posició concreta del genoma, condicionat al genotip dels dos marcadors polimòrfics que flanquejaven aquella posició. El genotip teòric del QTL en cada individu F_2, es va comparar amb el seu fenotip per als caràcters analitzats mitjançant el mètode de regressió descrit per Haley *et al.* (1994) i utilitzant com a covariable bé el pes de la canal o bé el gruix del greix dorsal.

L'interès pràctic d'aquest resultat es deu a la creixent importància que tenen els caràcters de qualitat del greix pels seus efectes en la salut i en l'aptitud tecnològica de les peces càrniques.

En concret, aquest QTL va presentar efectes importants sobre el gruix del greix dorsal, l'àrea del múscul *Longissimus* i el percentatge d'àcid linoleic en el panicle adipós dorsal. Els resultats intuï en la presència d'un efecte sobre el percentatge d'àcid oleic i sobre l'índex de dobles enllaços (DBI) del conjunt d'àcids grassos del teixit analitzat, motivada probablement per la influència del QTL sobre el percentatge d'àcid linoleic. L'al· lel Ibèric reduï a el percentatge de linoleic mentre augmentava el d'oleic i, conseqüentment, disminuï a DBI. Aquestes dades concorden amb els resultats obtinguts per Serra *et al*. (1998) en comparar fenotípicament individus de la població del porc Guadyerbas amb animals de la mateixa línia Landrace utilitzada per crear el pedigree analitzat en l'article.

L'efecte del QTL sobre el percentatge de linoleic, obtingut quan la covariable era el pes de la canal, no coincidia amb l'obtingut quan s'utilitzava com a covariable el gruix del greix dorsal. En aquest segon cas, tots els efectes es reduï en fins a nivells suggestius, la qual cosa suggerí que l'efecte del QTL sobre el percentatge de linoleic estava lligat a l'efecte sobre l'espessor del greix dorsal i que per tant, es tractava, en definitiva, de dues mesures diferents del mateix caràcter.

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_y^2) explained by a QTL was computed assuming that alternative alleles were fixed in each breed; i.e., $h_Q^2 = a^2/2\ \sigma_y^2$.

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

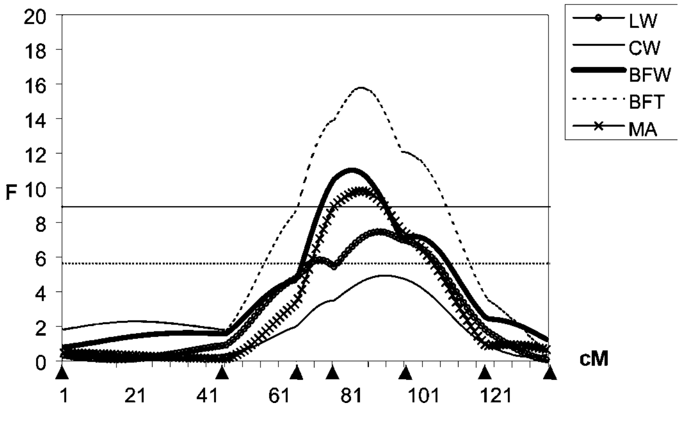

Figure 1. *F*-profile of the QTL scan: Growth and carcass traits. The horizontal solid line is the approximate 5% genomewide significance threshold; dashed line is the 5% chromosomewise significance threshold. Arrows indicate microsatellite positions. LW, liveweight; CW, carcass weight; BFW, backfat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

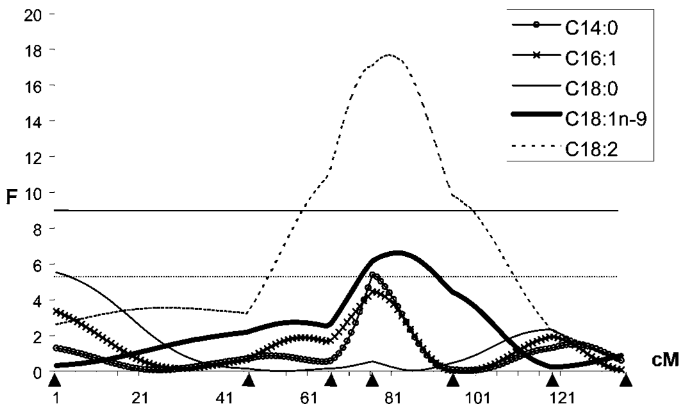

Figure 2. *F*-profile of the QTL scan: Fatty acid composition corrected for carcass weight (only the most significant profiles are shown). The horizontal solid line is the approximate 5% genomewide significance threshold; dashed line is the 5% chromosomewise significance threshold. Arrows indicate microsatellite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

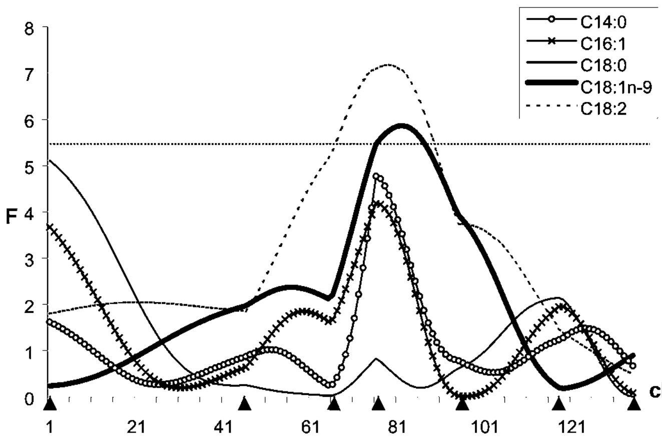

Figure 3. *F*-profile of the QTL scan: Fatty acid composition corrected for backfat thickness (only the most significant profiles are shown). The horizontal solid line is the approximate 5% genomewide significance threshold; dashed line is the 5% chromosomewise significance threshold. Arrows indicate 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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ANNEX 2

QTL mapping in an Iberian X Landrace F_2 pig intercross: composition and metabolic ratios of fatty acids.

Manuscrit en preparació

En aquest treball es descriu l'estudi de detecció de QTLs amb efecte sobre la composició en àcids grassos del greix dorsal, en tot el genoma i en 321 animals F_2 agrupats en 58 famílies de germans complets.

Els microsatèl·lits analitzats al cromosoma 4 foren els mateixos que els descrits en l'annex 1 i el mapa de lligament obtingut també coincidí amb l'anterior. A més, s'hi va incloure un polimorfisme de restricció del gen *DECR* (annex 3). Els mètodes estadístics emprats foren els mateixos que els descrits en l'annex 1.

Aquest treball confirma l'efecte sobre el percentatge d'àcid linoleic en el cromosoma 4 i presenta nous QTLs amb efecte sobre altres àcids grassos. Al cromosoma 6 es detectà un clar efecte sobre l'índex de dobles enllaços (DBI) i l'índex d'insaturació (UI) dels àcids grassos del teixit analitzat, recolzat per efectes de significació suggestiva sobre el percentatge d'àcid linoleic (LIN), àcid palmític (PA), palmitoleic (PAL) i esteàric (STE), així com sobre la longitud mitjana de la cadena de carbonis (ACL) i l'índex de peroxidabilitat (PI) dels àcids grassos. L'al·lel Ibèric redueix DBI, UI, PI, ACL, LIN i PAL, mentre que augmenta PA i STE. Al cromosoma 8 s'observen efectes clarament significatius sobre PA i PAL, així com per a ACL. L'al·lel Ibèric augmenta el percentatge d'ambdós i com a conseqüència, disminueix ACL. El cromosoma 10 mostra un efecte significatiu sobre el percentatge de mirístic (MYR). El cromosoma 12 presenta un clar efecte sobre el percentatge d'àcid linolènic (LINL), un efecte que s'apropa al llindar de significació genòmic del 95% sobre el percentatge d'àcid gadoleic (GAD) i un efecte suggestiu sobre el percentatge d'àcid vaccènic, ACL i PI. En general, aquests valors coincideixen amb els resultats obtinguts per Serra *et al.* (1998), que arribava a la conclusió que l'estirp Guadyerbas presentava, en general, major proporció d'àcids grassos monoinsaturats i menor de poliinsaturats que els animals Landrace.

En corregir aquests valors pel gruix del greix dorsal enlloc del pes de la canal, els resultats varien considerablement. Així, els QTLs detectats sobre LIN i DBI al cromosoma 4 disminueixen fins a valors inferiors al llindar de significació cromosòmic del 95%, i només l'efecte sobre el percentatge d'àcid oleic (OLE) manté la seva significació per damunt d'aquest llindar. Al cromosoma 6, l'efecte per DBI, així com els efectes per a PI i LIN disminueixen fins a una valor inferior al llindar de significació cromosòmic del 95%, en canvi els efectes sobre UI i PA disminueixen, però mantenen una significació superior al llindar cromosòmic del 95%. Els efectes sobre PAL, STE i ACL es mantenen a nivells similars. Els valors observats al cromosoma 8 es mantenen o fins i tot augmenten lleugerament. El QTL per a MYR del cromosoma 10 manté un valor de significació molt similar i lleugerament inferior al llindar de significació genòmic del 95%. Quelcom semblant succeeix amb els QTLs detectats al cromosoma 12, que mantenen les seves significacions molt similars. D'altra banda, al cromosoma 11 apareix un efecte sobre MYR amb una significació propera al llindar genòmic del 95%, mentre que quan la covariable era el pes de la canal, no s'observà cap indici d'aquest QTL.

Així, es pot concloure que els efectes detectats en els cromosomes 4 i 6 estan molt lligats a l'espessor del greix dorsal, mentre que els QTLs dels cromosomes 8, 10 i 12 no es veuen influenciats pel gruix del panicle adipós. El QTL del cromosoma 11 podria estar ponderat per algun caràcter que afectés també el pes de la canal.

Aquest treball es complementa amb dos manuscrits que descriuen els efectes detectats en tot el genoma sobre caràcters de qualitat de la canal (Varona *et al*., manuscrit en preparació) i de la carn (Ovilo *et al*.; sotmès a publicació).

QTL MAPPING IN AN IBERIAN X LANDRACE F_2 PIG INTERCROSS: COMPOSITION AND METABOLIC RATIOS OF FATTY ACIDS.

SUMMARY

Detection of QTLs affecting fatty acid content and related metabolic ratios in backfat in 321 animals of an F_2 Iberian X Landrace pigs intercross has been obtained. The Iberian and Landrace pigs show strong phenotypic differences in fatty acid traits as well as in other productive characteristics. We confirmed a previously detected QTL on chromosome 4 affecting linoleic and oleic fatty acids percentage. This QTL also affects double bound index (DBI) and peroxidizability index (PI) of fatty acids. On Chromosome 6 different associations with palmitic, palmitoleic, stearic and linoleic fatty acids content as well as average chain length of fatty acids (ACL), DBI and the unsaturated index of fatty acids (UI) have been detected in different positions of the chromosome. In chromosome 8, the effect is related to the palmitic and palmitoleic percentages as well as for ACL. Chromosome 10 has shown a suggestive QTL for the myristic percentage. Finally, we have detected associations in chromosome 12 with vaccenic, linolenic and gadoleic fatty acids percentages and with ACL and PI.

INTRODUCTION

The fatty acid composition is highly relevant for the technological properties and quality of meat, plays an important role in human health and it is an important factor in the maturation of traditional pork products. In human health, ingested fatty acids influence the blood lipids and the risk of suffering cardiovascular diseases. The linoleic acid (C18:2 n-6), is the precursor of the prostaglandines and tromboxanes, which are related to the cardiovascular equilibrium *(Yu-Poth et al., 1999).* The linolenic acid, affects specific functions in vision and in brain (Connor *et al*., 1992) Stearic, oleic, linoleic and linolenic fatty acids have an hypocholesterolemic function (*Grundy and Vega, 1988; Gardner and Kraemer, 1995*). Linolenic fatty acid is an essential fatty acid from the series ω-3 which are under special attention in human nutrition and health. Furthermore, fatty acid composition is important for meat technology. The leaner carcasses have a higher percentage of linoleic fatty acid (Lauritzen *et al*., 2000). The fat cuts with high percentage of linoleic fatty acid are too soft to be processed and they have a tendency towards oxidative rancidity. Moreover, high linoleic fat composition in meat is also associated with low juiciness and low consumer acceptability *(Lawrence and Fowler, 1997)*. Fatty acid composition is also very important in Iberian Pig cured products since it is the official criterion to qualify them. Lipid degradation mainly through oxidation of free unsaturated fatty acids produce off-flavours and rancidity in meat, but it is an important part of traditional pork products maturation. A fundamental aspect of the lipid-based flavour volatiles in meat products as dry-salted hams is that their origin is primarily from unsaturated fatty acids (Chizzolini et al., 1998), mainly oleic (Martin et al. 2000). Higher levels of oleic acid and lower levels of linoleic acid increases the quality value of these products *(De Pedro et al., 1998)*. There are some fatty acids like the linoleic and linolenic-α acids that can not be synthesized in the animal body, the so-called essential fatty acids. In consequence, all the carcass linoleic and linolenic-α composition is exogenous (from the diet). In contrast, the oleic acid, like many others, can be synthesized *de novo* in the adipose tissue.

There exist many projects focused in the detection of QTLs for carcass and meat quality traits in pig. These are mostly based in the genome scanning with microsatellite markers in a pedigree constructed by crossing two divergent populations. Using this approach, several studies confirmed the existence of a QTL in chromosome 4 affecting some production traits as growth, fat deposition and small intestine length *(Andersson et al, 1994; Walling et al. 1998; Knott et al. 1998 and Wang et al. 1998, Bidanel et al., 2001)*. Other groups have described QTLs in different chromosomes affecting fat related traits, as in chromosome 1 *(Rohrer and Keele, 1998a; Rohrer, 2000, Bidanel et al., 2001)*, chromosome 2 *(De Koning et al., 1999; Rattink et al., 2000, Rohrer 2000),* chromosome 6 *(De Koning et al. 1999; Gerbens et al., 2000; Ovilo et al. 2000; Grindflek et al 2001)* and chromosome 7 *(Rothschild et al. 1995, 1998, Wang et al. 1998; Rohrer and Keele, 1998a; De Koning et al., 1999; Wada et al., 2000; Rohrer , 2000; Rattink et al., 2000, Bidanel et al., 2001)*. Suggestive QTLs have also been found in chromosomes 10 by Rohrer and Keele, (1998a) and Bidanel et al. (2001) and 12 by Rohrer and Keele (1998a) affecting backfat. None of these studies analysed the fatty acid composition and the only QTLs described in swine for this trait has been recently reported by Perez-Enciso et al. (2000) and Grindflek et al. (2001) in chromosome 4.

The Iberian pig can be considered the most important Mediterranean rustic breed by the number of animals and by its economic impact. This breed is characterized for its dark coat, fat carcass, high intramuscular fat content, reduced lean deposition and high appetite. The genetic basis of these particular phenotypes makes the Iberian an interesting breed for pig genomic studies *(López-Bote, 1998).*

An experimental cross between the Iberian (IB) and Landrace (LD) pig strains was performed to map quantitative trait loci for diverse productive traits *(Ibmap Consortium, 1998)*. We present here the results corresponding to the analysis of characteristics related to fatty acid composition and its metabolic ratios.

MATERIAL AND METHODS

Animal material

The Guadyerbas strain is a highly inbred experimental line of the Iberian pig (inbreeding coefficient above 0.3). (*Toro et al., 2000*). The Guadyerbas and the Landrace breeds are highly divergent for the production traits studied here (*Serra et al., 1998*).

3 Iberian boars from the Guadyerbas line (IB) were mated to 31 Landrace sows from the selected line from the experimental farm Nova Genètica S. A (LD). The characteristics of the pedigree, the management of the animals and the characteristics of slaughtering are described in Pérez-Enciso *et al.*, 2000 and in Ovilo *et al.*, 2000.

In this work we report the results from the analysis of 321 F_2 animals pertaining to 58 full-sib families.

The DNA extraction was made from blood samples by conventional saline precipitation based protocol (*Miller et al., 1988*).

Traits analysed

Fatty acid composition was measured by capillary gas chromatography (Díaz and García-Regueiro, 1987) in samples from backfat taken between the third and fourth ribs. The following metabolic ratios were calculated: average chain length of fatty acids (ACL), double bond index of fatty acids (DBI), unsaturated index of fatty acids (UI) and peroxidizability index (PI). (Pamplona et al., 1998).

Genotyping

To cover the 18 autosomes we used 90 fluorescent microsatellites distributed uniformly along the chromosomes and previously chosen for their position and informativity, estimated from the F_0 by the index that calculates the frequencies in the LD sows of the alleles that are present in the IB boars, similar to the Ron informativity Index (Ron et al.; 1995) and 2 RFLPs. The PCR products were analysed by capillary electrophoresis and fluorescent detection (ABI PRISM 310 Genetic Analyser, Applied Biosystems). Genotypes were analysed and stored in the GEMMA database (*Iannucelli et al.; 1996*). The RFLPs were located in the exon 2 of the *DECR* gene (2,4-Dienoyl-CoA Reductase), which maps in chromosome 4 Clop et al. (submitted) and in the second exon of the GH gene in chromosome 12 (*Larssen and Nielssen, 1993*).

Statistical analysis

The linkage map was constructed using the option “build” of the CRI-MAP version 2.4 program (*Green et al., 1990*). Marker information content in the F_2 were obtained as in Knott et al. (1998). The QTL analysis was carried out as described in Haley et al. (1994). The linear model was:

$$Y = \text{sex} + \text{family} + \text{cov} + c_a a + c_d d + e \qquad [1]$$

where Y is the phenotype, sex and family are the fixed effects, c_a (P(QQ) – P(qq)) and c_d (P(Qq)), are the coefficients for the additive and the dominant effects, respectively. The genotype of the putative QTL is calculated conditional upon the marker genotypes at each cM. **a** is the additive effect and **d** is the dominance deviation. The covariate was either the carcass weight or the backfat thickness. The residual error is expressed in **e**. The model was fitted at every cM according to the average sex distances map. The model was tested versus a model without fitting **a** and **d** at each position to obtain the regression F – statistics. The contribution of the QTL on the additive fraction of the phenotypic variance (σ^2) in the F_2 was computed assuming alternative fixed alleles in each breed, i. e. $h^2_Q = 2\ \sigma^2_y$.

Genome-wise and chromosome-wise significance threshold were calculated by permuting the measures 20,000 times within the sex and the along the 18 autosomes (Churchill and Doerge, 1994). The 5%, 1% and 0.1% genome-wise threshold values were 8.53, 10.39 and 13.07, respectively.

The 95% confidence intervals for the location of the QTL were obtained by the chi-drop approximation (*Mangin et al., 1994*) as described in Pérez-Enciso et al., (2000).

RESULTS

The phenotypic records of the traits analysed are shown in table 1. The oleic acid is the most abundant fatty acid in backfat, followed by palmitic, linoleic and stearic acids. In contrast, the eicosadienoic and the gadoleic acids are present in the lowest amounts. The position and distances of the microsatellites are in general agreement with other mapping projects and with the USDA genome database www.genome.iastate.edu/maps/marcmap.html.

The most relevant results from the QTL analyses when the carcass weight is used as a covariate are reported in table 2, which shows the maximum F-values, its position and the additive and dominant effects. There are 5 chromosomes with clear significant QTLs.

Chromosome 4 In this chromosome (Figure 1), between markers S0001 and S0214, we found a strong effect on the percentage of linoleic acid (LIN), as well as a suggestive effect on the percentage of oleic acid (OLE) and clear effects on DBI and on PI. The effects on LIN and PI are the most significant QTLs of this work and they mapped at position 75 (67-87) cM as they were reported in a previous analysis with fewer animals (*Pérez-Enciso et al. 2000*). The phenotypic variance explained by both QTLs correspond to 12.73% and 12.08%, respectively.

Chromosome 6 This chromosome showed a significant QTL centred at 105 (99-117) cM from the first marker, affecting DBI and, at suggestive level, an effect on LIN at 107 (99-120) cM. Other significant QTL was detected at 34 (21-54) cM affecting the UI. Other suggestive effects were found on this chromosome at different positions affecting the percentages of palmitic (PA), palmitoleic (PAL), and stearic (STE) fatty acids, as well as ACL (Figures 2 and 3).

Chromosome 8 A highly significant QTL was detected at 86 cM on chromosome 8 with effect on PAL, PA and ACL (Figure 4). This QTL explains 6.51% an 9.7% of the phenotypic variance of PA and PAL, respectively. Besides, a suggestive effect (F = 5.83) on OLE was found in another position of this chromosome (47 cM).

Chromosome 10 In the position 82 cM of chromosome 10 we detected a QTL affecting the percentage of myristic acid (MYR), which F-value is about the 5% genome-wise threshold (Figure 5) and which is the responsible of the 9.86% of the phenotypic variance of the trait.

Chromosome 12 In this chromosome (Figures 6 and 7), we found a significant effect on the percentage of linolenic fatty acid (LINL) and other suggestive effects on the percentages of vaccenic (VAC) and gadoleic (GAD) fatty acids, as well as on ACL and PI. These effects corresponds probably to a single QTL since their confidence intervals are overlapped.

We detected suggestive effects on fatty acids in other genomic regions that should be confirmed in future analysis. On chromosome 2 (49 cM) we found an effect (F = 5.9) on PAL. On chromosome 5 (126 cM) we detected a QTL (F = 5) affecting the PAL. A region on chromosome 7 (40 cM) was affecting the percentage of STE (F = 5.67). OLE was influenced (F = 5.94) by a region on chromosome 9 (7 cM). Finally, on chromosome 15 (45 cM), we detected an effect on PAL (F = 6.66).

As table 2 shows, when the covariate is the backfat thickness, we observe significant QTLs affecting PA (F = 11.38), PAL (F = 13.36) and ACL (F = 16.57) on chromosome 8 (85 cM). Another significant QTL affecting LINL (F = 9.72) is detected in the position 31 cM and ACL (F = 8.50) at 14 cM of chromosome 12. Other effects with an F-value slightly below the genome-wise significance level can be observed in chromosome 12, affecting GAD (F = 8.46) and PI (F = 8.38), as well as in chromosome 10 (80 cM) and 11 (15 cM), which affects MYR (F = 8.18 and 8.12, respectively). Suggestive effects are observed in chromosome 2 for PAL and STE, chromosome 4 on OLE, chromosome 5 for PAL, chromosome 6 on PA, PAL, STE, and UI, chromosome 8 and 9 on OLE, chromosome 12 on LIN, VAC, and finally, in chromosome 15, for PA. the F-value for the QTLs on chromosome 4 decreases to non-significant values, and only the effect of this chromosome on OLE shows a suggestive F-value.

DISCUSSION

As the high number of significant QTLs detected in this work shows, the Iberian Guadyerbas line and the Landrace strain are two outbreed populations with a very divergent characteristics, including fatty acid composition and metabolic ratios. Thus, an experimental crossbreed between both lines is a powerful tool to detect loci affecting quantitative traits.

The region between markers S0001 and S0214 in chromosome 4 has a large effect on LIN in backfat. Its F value is similar to that described in Pérez-Enciso et al. (2000) in a previous analysis with fewer animals, but the percentage of the phenotypic variance explained now by the QTL is half the described previously. The Iberian alleles increase backfat deposition whereas LIN, as well as the carcass length, the loin eye area and meat darkness are decreased when the Iberian QTL is present. Thus, it seems that both traits are highly correlated. Since linoleic is an essential fatty acid, it can not be synthesized by animals, and the increase in fat deposition is implemented with synthesized fatty acids. This indicates that differences on LIN are due to the difference in fat deposition, rather than in “de novo” synthesis differences. The effect of this region on DBI and PI could be indirect consequences in linoleic content. All these traits showed a clear additive effect. Even though in Perez-Enciso *et al.* (2000), the QTL for LIN raises a suggestive F-value when correcting by backfat thickness, in the present work, this value is below the 95% chromosome-wise significance level. Even more, none of the effects detected in this chromosome when the covariate is the carcass weight, raises the 95% genome-wise significance threshold when the effects are corrected by backfat thickness. It is noticeable that this region shows a strong effect on backfat depth (*Varona, personal communication*). That indicates that these effects are either influenced by the backfat thickness or that the effects are different expressions of the same trait. The QTL fits in the same position as the QTL detected by Andersson et al. (1994) and confirmed by Marklund et al. (1999) in a wild boar X Large White intercross, where the wild boar allele increases fat depth and decreases growth and small intestine length. A QTL in the same position with effect on fat deposition was also detected by Walling et al. (1998), Wang et al. (1998), Bink et al. (2000) and Bidanel et al. (2001). Altogether, it seems that there is a single QTL with pleiotropic effects in this region. Recently, Grindflek et al. (2001) have detected a putative QTL affecting C17:0 fatty acid in a similar position (between markers S0214 and SW445), which is a fatty acid that has not been recorded in our analysis.

QTLs detected in chromosome 6 have many different effects spanning from 0 cM (PAL) to 107 cM (LIN). Only DBI exceeds the 5 % genome-wise threshold, whereas UI significance is above this level. The rest of fatty acid QTLs (PA, PAL, STE, LIN and ACL) show a suggestive significance. However, the QTL on DBI suggest that, in fact, any of the fatty acid QTLs are real effects, and the low significance level should improve when more animals were typed or more detailed maps were constructed. These associations show clear overdominance effects. The fact that the two significant QTLs are in different regions (Figure 2) suggest that at least, two QTLs could be segregating in chromosome 6. However, we can not exclude that a single QTL is the responsible of all the effects since all the traits are under overdominance. Nevertheless, when the covariate is the backfat thickness, all the effects decreases to non-significant F-values, which indicates that these effects could be a consequence of the differences on fat deposition. It must be taken into account that the same region shows a strong effect on backfat depth (*Ovilo personal communication*). Chromosome 6 was also associated with, intramuscular fat and loin eye area at position 100-116 cM (*Ovilo et al., 2000*). De Koning et al. (1999) suggested a QTL in the same position with dominant effect on backfat and a suggestive QTL affecting intramuscular fat and Wilkie et al. (1996) found, in different regions of chromosome 6, associations with carcass length, loin eye area and growth. Rohrer (2000) found an effect on backfat deposition at position 83 cM in this chromosome and Bidanel et al. (2001) found the same effect in a similar region.

Chromosome 8 has a QTL in which the Iberian allele increases PA and PAL, which are 16 carbon chain fatty acids, and thus, a clear effect on ACL is observed. The effects for PAL and ACL are dominant. It is noticeable that these effects persist when correcting by backfat thickness, which indicates that these QTLs are not directly related to or influenced by fatness. Andersson-Eklund et al. (1998) detected a QTL with effect on carcass length but in the opposite region of the chromosome when is compared with the QTL described here. Rohrer and Keele (1998a; 1998b) found a suggestive association with leaf fat and loin eye area in an equivalent position of the QTL found in our animals, and the backfat QTL was confirmed by Rohrer (2000). Bidanel et al. (2001) also found a QTL for this trait but in another confidence interval.

The QTL detected in chromosome 10, with effects on MYR fatty acid is above the 5 % genome-wise threshold and has a dominant effect. The effect has a similar F-value when correcting for backfat thickness. Knott et al. (1998) found a QTL affecting growth on a different region of chromosome 10 and Rohrer and Keele (1998a) detected association with a suggestive F-value in a close position, associated with backfat depth over the midline at the first rib. Recently, Bidanel *et al.* (2001) found an association of the same region with backfat depth.

The results on chromosome 12 are as expected since the percentage of the polyunsaturated linolenic fatty acid decreases in the Iberian animals, whereas the content of monounsaturated fatty acid vaccenic increases when the Iberian allele is present. The percentage of the gadoleic fatty acid also decreases when the Iberian allele is present. According to these results, ACL and PI show the expected tendency. When the regression approach is corrected by backfat depth, the same effects can be observed with a similar F-value. This may indicates that there is in that region, at least, one gene influencing fatty acid composition on backfat independently but with none effects on fatness. It is noticeable that the linolenic acid is an essential fatty acid under special attention in human nutrition and health. Most of the associations reported in the literature for this chromosome are related to the GH gene (*Nielssen et al., 1995; Knorr et al., 1997*), which position maps close to the QTL described in this work, and the only QTL that has been described in this chromosome was affecting early growth (Rohrer, 2000).

It is interesting to notice that in chromosome 11, we detected an effect on MYR only when correcting by backfat thickness, but not when the covariate is the carcass weight. That indicates that in any way, this QTL is influenced by either birth weight or growth.

The region in chromosome 4 shows evident effect on backfat deposition traits, length of carcass, weight of shoulders, weight of left loin without backfat and weight of belly. Another region in chromosome 4 affects meat colour and haem content. The fatty acid QTL region in chromosome 6 shows influences in backfat deposition, intramuscular fat percentage, loin depth and loin eye area, and weight of shoulders, weight of left loin without backfat and weight of belly (Varona, unpublished).

The list of positional candidate genes for the detected QTLs can be huge, but taking into account their physiological role in fatty acids metabolism we can remark some genes that appear as possible candidates to be related to the described effects.

The 2,4-dienoyl-CoA-reductase (*DECR*) gene encodes an enzyme that participates in the β-oxidation pathway of the linoleic fatty acid by catalysing the reduction of trans-2-cis-4-dienoyl-CoA to 3-enoyl-CoA (Kunau and Dommes, 1978). This gene maps to chromosome 4 in the same region of the QTL described in this chromosome (Clop et al., submitted).

The fatty acid binding proteins plays an important role on uptaking and transportation of fatty acids. *a-FABP* gene (*FABP4*), which is only expressed in adipocytes, is located on pig chromosome 4 and resides between S0001 and S0217 (*Gerbens et al. 2000*), where the QTL described in this work is located. This locus is associated with intramuscular fat content in Duroc according to Gerbens et al. (1998) but could not be related to the same trait and backfat deposition in a F_2 intercross Meishan-Large White (*Gerbens et al*., 2000).

The *h-FABP* gene maps into the QTL region in chromosome 6 described in this article and an association to intramuscular fat content and backfat thickness has been found by Gerbens et al. (2000). The medium chain of Acyl-Coenzyme A dehydrogenase maps to the 6q32-33 region, close to the QTL for the percentage of linoleic acid and DBI, and it is involved in the β-oxidation of fatty acids. The leptine receptor gene (*LEPR*), maps to 6q32-35, and the cholecystokinin type-A receptor locus (*CCKAR*), located in chromosome 8 and linked to S0017 (*Clutter et al. 1998*), are both implicated in feeding modulation and map nearby to the QTL. Finally, the Acetyl Coenzyme A Carboxylase Alpha, which is involved in the synthesis of fatty acids maps in a close region where we found association to fatty acid traits in chromosome 12. Association analysis for allelic variant of these genes should be performed in order to ascertain their influence in the described QTLs.

In summary, this work provides evidence of the existence of QTLs for fatty acid composition in pigs, a character of critical importance in meat quality and of great economical impact for the industry, only afforded by nutritional basis up to day. The existence in pigs of genetical influence in fat composition opens the possibility in the future, to implement selection for this trait in breeding programs.

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Table 1 Phenotypic records of fatty acids related traits in the F_2 animals.

Trait	*Abbreviation*	*N*	*Mean*	*s. d.*
% Myristic (C14:0)	MYR	321	1.5	0.17
% Palmitic (C16:0)	PA	321	21.8	1.46
% Palmitoleic (C16:1)	PAL	321	2.47	0.37
% Stearic (C18:0)	STE	321	10.88	0.91
% Oleic (C18:1n-9)	OLE	321	44.12	1.67
% Vaccenic (C18:1n-7)	VAC	321	2.94	0.28
% Linoleic (C18:2)	LIN	321	14.43	1.45
% Linolenic (C18:3)	LINL	321	1.08	0.18
% Gadoleic (C20:1)	GAD	321	0.86	0.21
% Eicosadienoic (C20:2)	EIC	321	0.63	0.17
Average Chain Length	ACL	321	17.5	0.04
Double Bond Index	DBI	321	0.84	0.03
Unsaturated Index	UI	321	2.52	0.23
Peroxidizability Index	PI	321	18.49	1.6

Table 2. Results of QTL analysis when corrected either for carcass weight (CW) or backfat thickness (BF).

Cr.	***Trait***	***Pos(CW)***	***F(CW)***	***a***	***s.e.***	***d***	***s.e.***	h^2_{QTL}	***Pos(BF)***	***F(BF)***
1	PA	0	3.99	-	-	-	-	-	0	4.76
2	PAL	49 (29,61)	5.90	0.11	0.034	-0.07	0.05	-	49	5.81
2	STE	36	4.69	-	-	-	-	-	36	6.11
4	LIN	75 (67,87)	17.13	-0.65	0.11	-0.00	0.16	0.13	67	4.20
4	OLE	76 (66,92)	7,14	0.47	0.13	-0.17	0.19	0.06	76	5.92
4	DBI	73 (62,87)	9.89	-1.01	0.23	-0.26	0.33	0.07	73	1.51
4	PI	75 (66,86)	16.10	-0.74	0.13	-0.05	0.19	0.12	75	3.72
5	MYR	131	4.79	-	-	-	-	-	89	5.21
5	PAL	126 (111,-)	5.00	-	-	-	-	-	126	5.30
6	PA	44 (31,49)	7.86	0.28	0.09	0.35	0.13	0.06	44	5.51
6	PAL	0 (-,12)	6.78	-0.08	0.03	-0.15	0.05	0.08	0	6.41
6	STE	13 (-,23)	7.094	0.27	0.12	0.72	0.23	0.16	10	7.33
6	LIN	107 (99,120)	6.60	-0.28	0.13	0.48	0.18	0.05	102	2.45
6	ACL	44 (32,49)	7.00	-0.75	0.28	-1.01	0.38	-	-	-
6	DBI	105 (99,117)	9.12	-0.83	0.26	0.99	0.38	0.08	29	4.48
6	PI	107 (100,122)	5.89	-0.35	0.15	0.47	0.21	-	102	1.62
6	UI	34 (21,54)	8.71	-0.06	0.02	-0.11	0.04	0.12	27	6.97
7	STE	40 (25,55)	5.67	0.02	0.09	0.46	0.14	-	40	4.82
8	PA	86 (78,93)	8.63	0.41	0.10	-0.07	0.14	0.06	85	11.38
8	PAL	86 (77,94)	12.97	0.14	0.03	-0.07	0.04	0.10	85	13.36

8	OLE	47 (31,57)	5.83	-0.36	0.13	-0.35	0.19	0.05	47	6.01
8	ACL	86 (80,91)	12.66	-1.41	0.28	0.42	0.42	0.09	86	16.57
9	OLE	7 (-,24)	5.94	-0.47	0.14	0.16	0.23	-	7	5.57
10	MYR	82 (59,-)	8.61	0.07	0.02	0.02	0.04	0.10	80	8.18
11	MYR	31	0.84	-	-	-	-	-	15	8.12
12	LIN	23 (7,39)	4.84	-	-	-	-	-	23	6.47
12	GAD	25 (12,38)	8.42	-0.08	0.02	-0.067	0.036	0.0919	25	8.46
12	VAC	21 (4,38)	6.75	0.10	0.03	-0.138	0.06	0.1041	16	7.24
12	LINL	31 (18,40)	8.84	0.03	0.02	0.091	0.024	0.0985	31	9.72
12	ACL	16 (-,40)	7.80	-1.44	0.37	0.194	0.659	0.0955	14	8.50
12	PI	23 (11,37)	6.40	-0.38	0.17	0.807	0.281	0.0943	24	8.38
15	PAL	45 (36,53)	6.66	0.06	0.03	0.152	0.049	-	45	6.73

Cr., Chromosome; Pos(CW), Position of the maximum F-value when corrected for CW; F(CW), confidence interval bounds are shown, in brackets, only for the 95% genome-wise significance level. F-value at the position Pos(CW); a, additive effect of the QTL on pos(CW); d, dominant effect of the QTL on Pos(CW); Pos(BF) Position of the maximum F-value when corrected for BF; F(BF) F-value at the position Pos(BF).

Figure 1. F-value curve of fatty acid related traits across chr 4. The horizontal solid and the dashed lines indicates the 95 % genome-wise and the 95 % chromosome-wise thresholds, respectively.

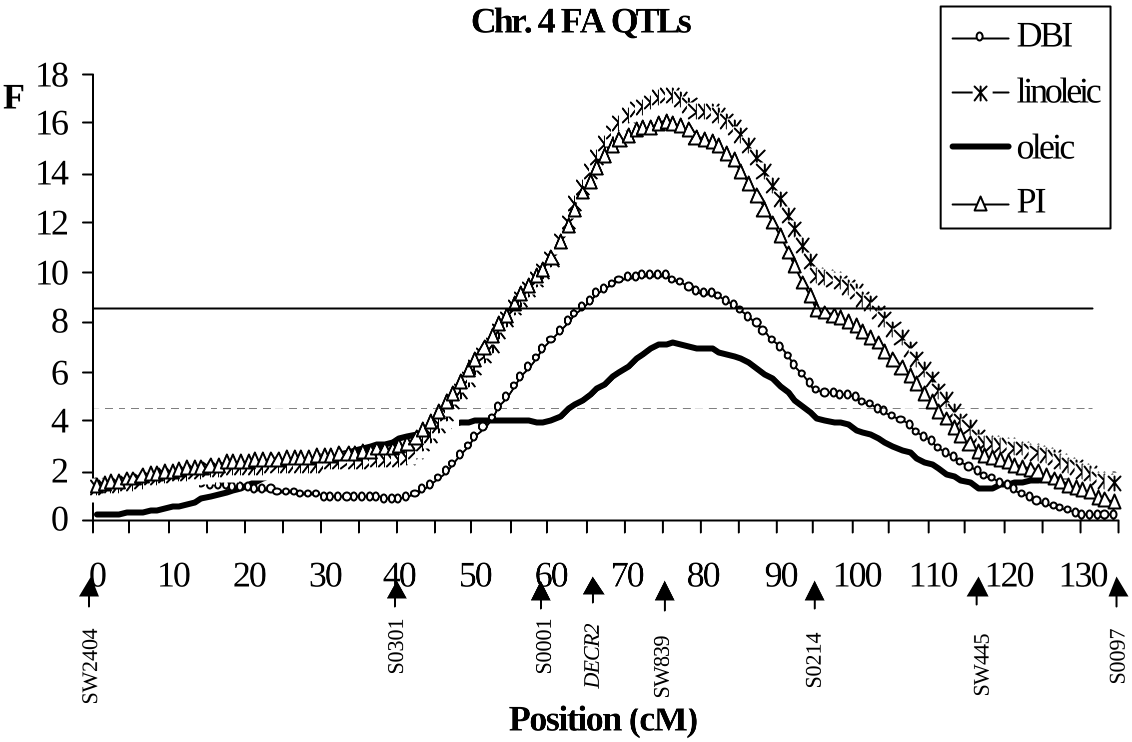

Figure 2. F-value curve of fatty acid metabolic ratios across chr 6. The horizontal solid and the dashed lines indicates the 95 % genome-wise and the 95 % chromosome-wise thresholds, respectively.

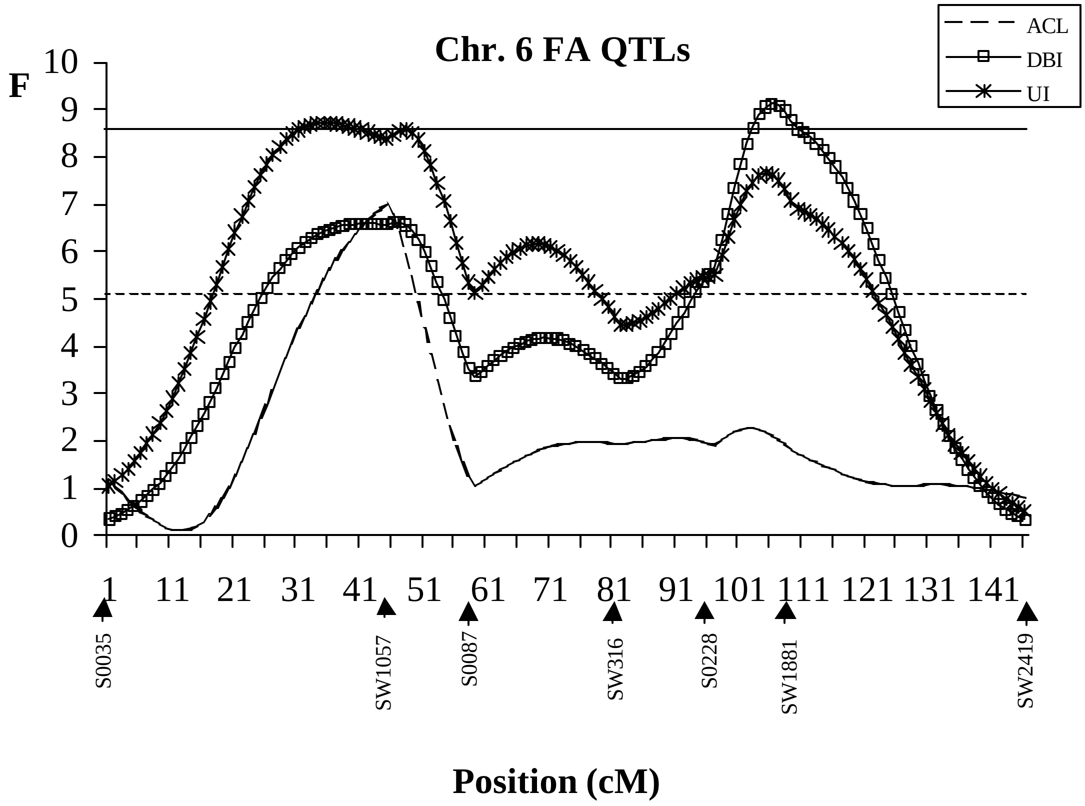

Figure 3. F-value curve of fatty acid composition on backfat across chr 6. The horizontal solid and the dashed lines indicates the 95 % genome-wise and the 95 % chromosome-wise thresholds, respectively.

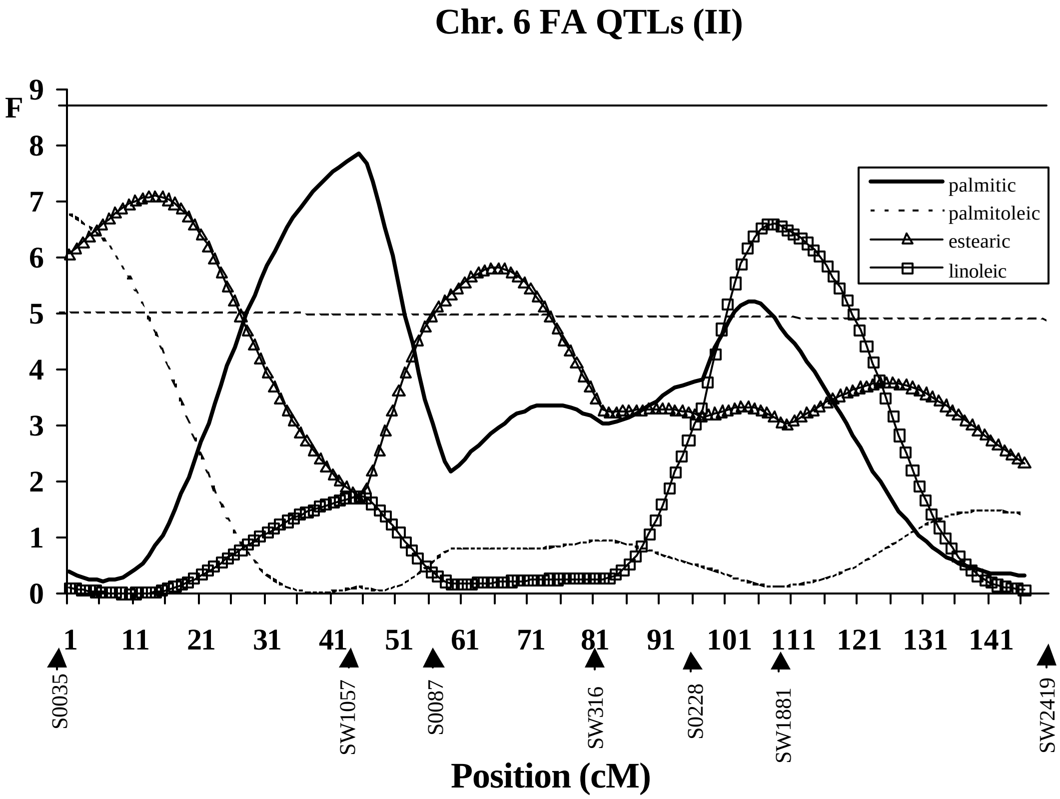

Figure 4. F-value curve of fatty acid related traits across chr 8. The horizontal solid and the dashed lines indicates the 95 % genome-wise and the 95 % chromosome-wise thresholds, respectively.

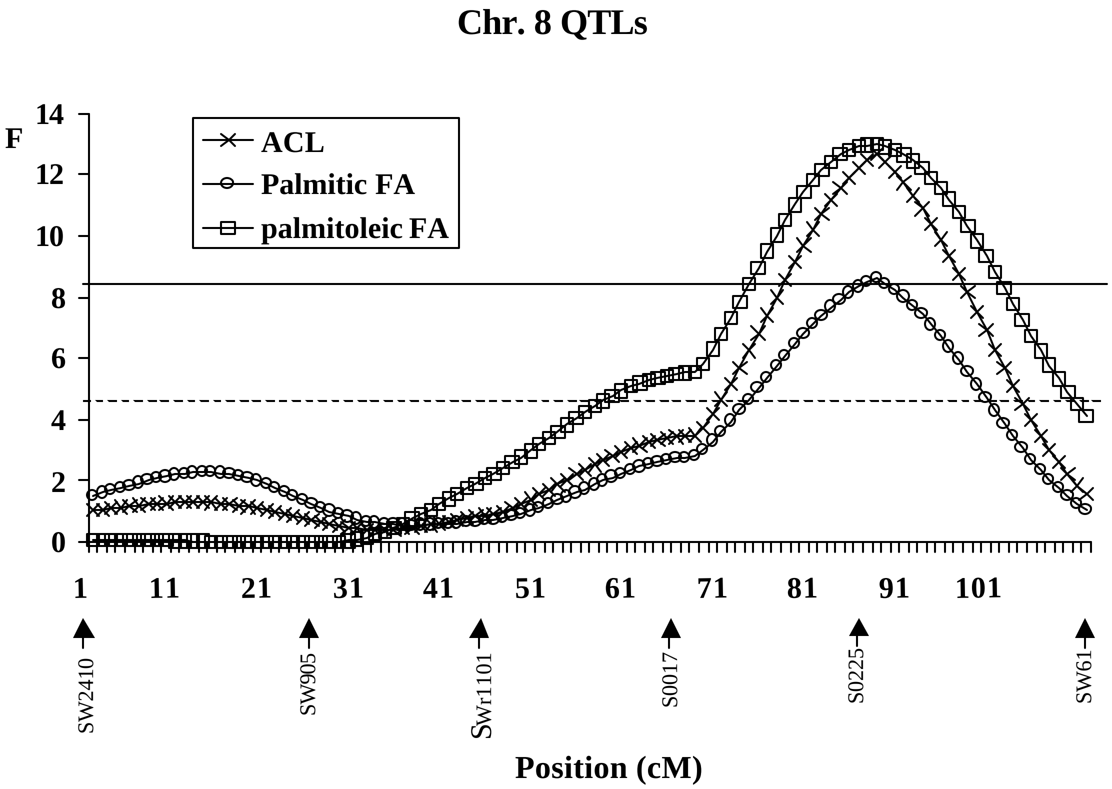

Figure 5. F-value curve of myristic fatty acid across chr 10. The horizontal solid and the dashed lines indicates the 95 % genome-wise and the 95 % chromosome-wise thresholds, respectively.

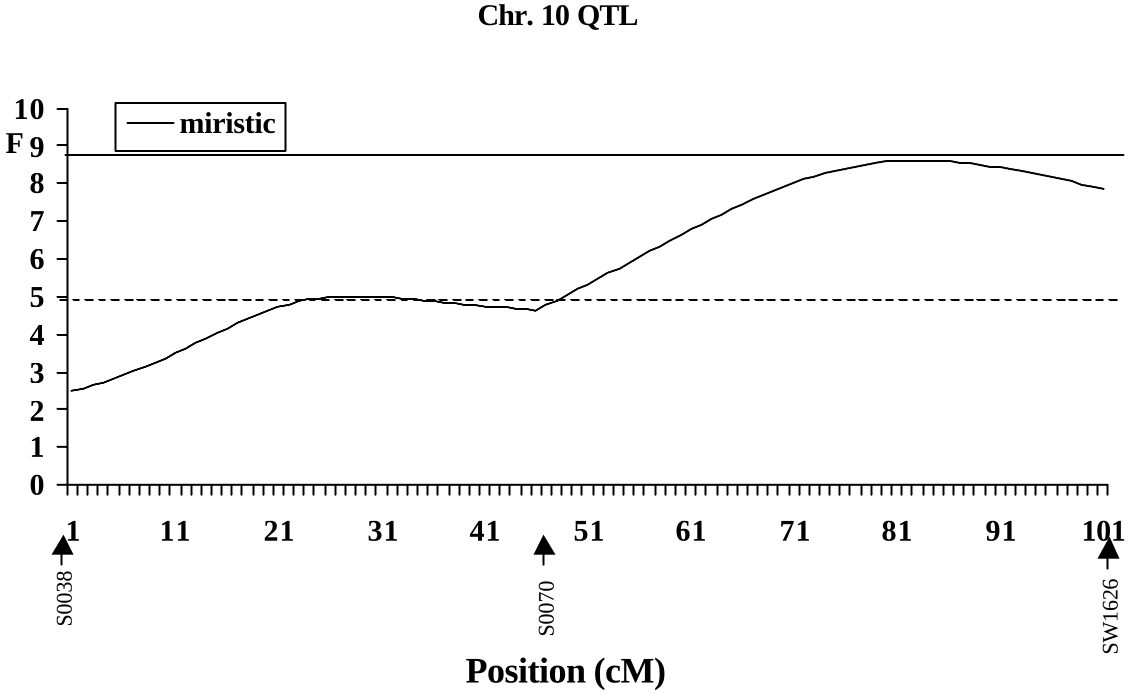

Figure 6. F-value curve of fatty acid related traits across chr 12. The horizontal solid and the dashed lines indicates the 95 % genome-wise and the 95 % chromosome-wise thresholds, respectively.

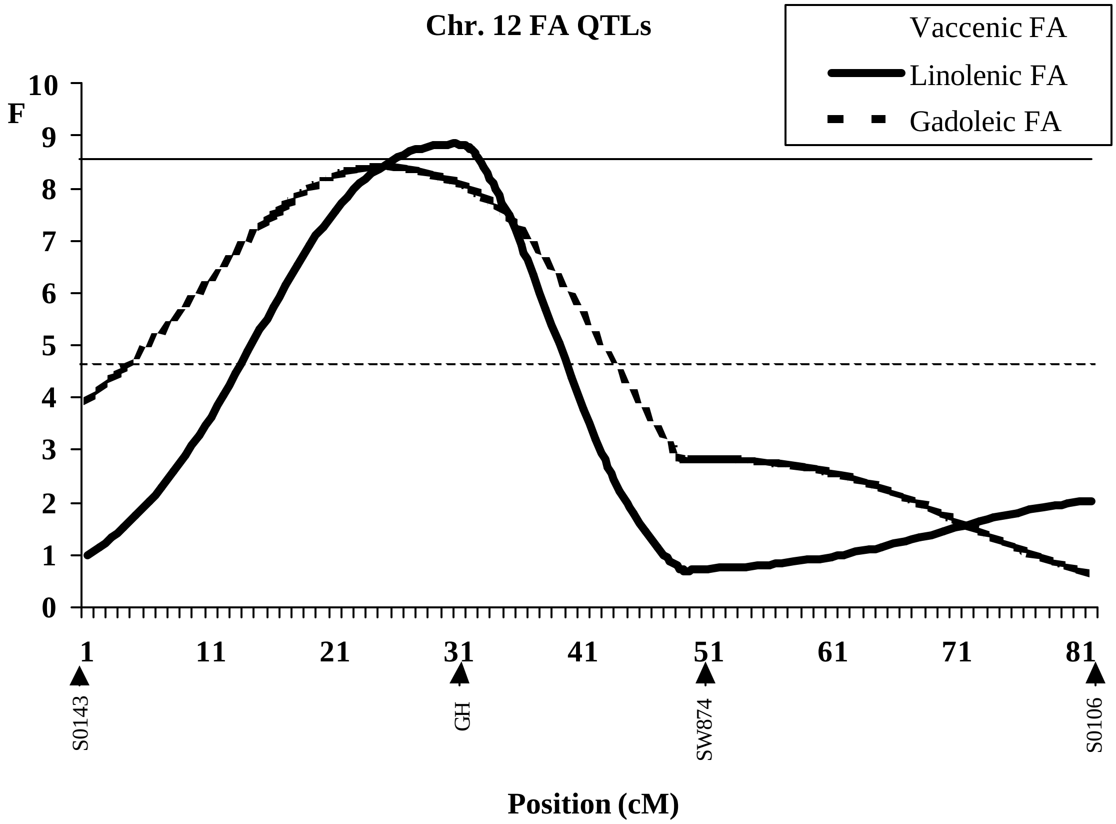

Figure 7. F-value curve of fatty acid related traits across chr 12. The horizontal solid and the dashed lines indicates the 95 % genome-wise and the 95 % chromosome-wise thresholds, respectively.