# Mapping of QTL on chromosome X for fat deposition, muscling and growth traits in a wild boar $\times$ Meishan F<sub>2</sub> family using a high-density gene map

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#### Summary

Quantitative trait loci (QTL) for fat deposition, growth and muscling traits have been previously mapped on the basis of low-density linkage maps in a wild boar × Meishan  $F_2$  family to the chromosome X region flanked by *SW2456* and *SW1943*. Improved QTL resolution was possible using data for  $F_2$  animals with a marker density of 2.7 cM distance in the *SW2456* to *SW1943* region, including *AR*, *SERPINA7* and *ACSL4* as candidate genes. The resolution of the QTL scan was increased substantially, as evidenced by the higher *F*-ratio values for all QTL. Maxima of *F*-ratio values for fat deposition, muscling and growth traits were 28.6, 18.2 and 16.5 respectively, and those QTL positions accounted for 7.9%, 5.0% and 4.5% of the  $F_2$  phenotypic variance (VF<sub>2</sub>) respectively. QTL for fatness and growth and for most muscling traits mapped near *ACSL4*, with the exception of the QTL for ham traits that mapped proximally, in the vicinity of *AR*. An analysis performed separately for  $F_2$  male animals showed the predominant QTL affecting fat deposition traits (up to 13.6% VF<sub>2</sub>) near *AR* and two QTL for muscling traits (up to 9.9% VF<sub>2</sub>) mapped close to *ACSL4*. In the  $F_2$ female animals, QTL affecting muscling (up to 12.1% VF<sub>2</sub>) mapped at *ACSL4* and *SW2456*, and QTL for fat deposition (10% VF<sub>2</sub>) and growth (up to 10.5% VF<sub>2</sub>) mapped at *ACSL4*.

Keywords chromosome X, fatness, growth, mapping, muscling, pig, quantitative trait loci.

#### Introduction

In Meishan × Western breed pedigrees, quantitative trait loci (QTL) for fat deposition, growth, carcass composition (Knott *et al.* 1998; Rohrer & Keele 1998; Harlizius *et al.* 2000; Rohrer 2000; Bidanel *et al.* 2001; De Koning *et al.* 2001; Milan *et al.* 2002; Sato *et al.* 2003), testis size and FSH (Ford *et al.* 2001; Rohrer *et al.* 2003), testis size and FSH (Ford *et al.* 2001; Rohrer *et al.* 2001; Sato *et al.* 2003) mapped to the centromeric region of chromosome X (SSCX). Analyses of QTL on SSCX encompassing six breeds (wild boar, Large White, Landrace, Meishan, Iberian and Piétrain) and five different crosses (Bidanel *et al.* 2001; Milan *et al.* 2002; Pérez-Enciso *et al.* 2002; Geldermann *et al.* 2003) with almost 3000 genotyped individuals showed the most prominent QTL for fatness, which is of Asiatic origin. Furthermore, a distinct QTL for ham weight segregating

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between Large White and the rest of the breeds, and a locus segregating between Iberian and Landrace affecting live weight were found (Pérez-Enciso *et al.* 2005). QTL for fat deposition, growth and muscling traits also have been detected in a wild boar × Meishan (W × M)  $F_2$  family (Čepica *et al.* 2003) on the SSCX chromosome segment flanked by microsatellites *SW2456* and *SW1943*. This QTL region encompasses a chromosome block that displays a low genetic recombination rate (Rohrer *et al.* 2001; McCoard *et al.* 2002). Recently, a high-density gene-based linkage map of the chromosome X QTL region has been published (Čepica *et al.* 2006).

The goal of this work was to develop a high-density linkage map of the QTL region on porcine chromosome X encompassing microsatellites and gene-based markers including candidate genes, and to use this map for analyses of fat deposition, growth and muscling traits in a  $W \times M$  family.

#### Materials and methods

The structure of the three-generation  $F_2$  reference family, its housing and description of quantitative traits were presented

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related to fat deposition, growth and muscling. Marker density of the previously utilized W × M linkage map (Čepica *et al.* 2003) was increased by adding microsatellite *SW2476* (Alexander *et al.* 1996), the *AR* gene using the *SY11* microsatellite (Seifert *et al.* 1999), and eight orthologs of human genes chosen from the corresponding human Xq13.1 to Xq24 region (Čepica *et al.* 2001, 2006) namely: *RPS4X* (AJ429141:g.138T>C), *XIST* (AJ429140:g. 769T>G), *POU3F4* (AJ429271:g.248G>A), *SERPINA7* (AJ293944:g.495A>T), *ACSL4* (AJ785784:g.388G>C), *CAPN6* (AJ429142:g.267A>C), *PAK3* (AJ429269:g. 440T>C) and *SLC25A5* (AM746979:g.451-466del16). Details of the markers and linkage map are given in Table S1.

The method of QTL detection for crosses between outbred lines (Haley et al. 1994) was used for the  $W \times M$  family in steps of 1 cM (reduced <1 cM when markers were closer than 1 cM) by calculating additive components for F2 males and both sexes or additive and dominance components for F2 females. These components were included in a linear model together with continuous (age at slaughter) and discrete (2-month classes as a seasonal factor, litter number, sex) independent variables to calculate the additive effect and, in the model for females, the dominance effect. Critical chromosome X threshold values of the test statistics specific for three different models (a model with the additive component for female and male  $F_2$  animals, a model with the additive component for male F2 animals and a model with the additive and dominant component for female F<sub>2</sub> animals) were derived by a permutation test (Churchill & Doerge 1994) with 1000 permutations for each model. Genome-wide thresholds were calculated from chromosome-wide probabilities applying a Bonferroni correction (Miller 1981).

### **Results and discussion**

The  $W \times M$  female linkage map (Table S1) that includes 19 markers is 151.6 cM long. The order of the framework

microsatellite loci was SW949, SW980, AR (SY11), SW259, SW1943 and SW2588, identical with the current USDA-MARC map (http://www.marc.usda.gov/genome/ htmls/LinkageMap.jsp?Species=sus&Chromosome=X). Locus SW2476 was mapped on the USDA-MARC 2 map (Rohrer *et al.* 1996) distal to SW259 while this microsatellite was placed proximal to SW259 on our  $W \times M$  map, similar to the T43RH map (McCoard *et al.* 2002). The order of gene markers (RPS4X, XIST, POU3F4, SERPINA7, ACSL4, CAPN6, PAK3 and SLC25A5) that mapped between SW259 and SW1943 was identical with the human chromosome X map (Build 36.2: http://www.ncbi.nlm.nih.gov/ mapview/maps.cgi?taxid=9606&chr=X).

Chromosome X threshold F-values for the three statistical models are given in Table 1. Results of analyses including all F<sub>2</sub> animals for OTL affecting fatness, muscling and growth traits are summarized in Table 2 (part a). Only QTL with F-values, corresponding to significance at genomewide threshold were considered. Maxima of F-ratio values for ten fat deposition traits, three muscling traits and three growth traits were 28.6, 18.2 and 16.5 respectively, which explained 7.9%, 5.0% and 4.6% respectively of the  $F_2$  phenotypic variance (VF<sub>2</sub>). The additional markers substantially increased the F-ratio values in comparison with the previous analysis (Čepica et al. 2003). For example, the F-ratio value of the shoulder fat depth QTL increased from 16.8 to 28.6. All QTL for fatness and growth and most muscling traits mapped at map position 90 cM (Table S1) to the ACSL4 gene (Fig. 1) corresponding to 80 cM on the current USDA-MARC linkage map (Čepica et al. 2006). QTL for ham weight and ham meat weight mapped at position 85.7 cM, in the vicinity of AR at 85.3 cM on the W×M map and 73 cM on the USDA-MARC map. In agreement with Pérez-Enciso et al. (2005), animals carrying OTL alleles from Meishan had higher values for fat deposition, growth and muscling traits not related to carcass weight. However, OTL alleles with higher values for muscling traits related to carcass weight were inherited from the wild boar.

The reciprocal crosses that produce the  $F_1$  male(s) influence the behaviour of the X chromosomes and, therefore, effects estimated on this chromosome in  $F_2$  animals (Broman *et al.* 2006). The male grandparent in our study was wild boar and all female grandparents were Meishan pigs; therefore, only two genotypes were present in each sex

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Model		Significance threshold			
		Chromosome-wide	Genome-wide		
	Number of animals	P = 0.05	P = 0.05	<i>P</i> = 0.01	
Male and female F <sub>2</sub> animals (additive component)	335	7.9	13.4	16.9	
Male F <sub>2</sub> animals (additive component)	169	7.6	13.2	16.6	
Female $F_2$ animals (additive and dominance components)	166	5.5	8.7	10.6	

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**Table 2** Genome-wide significant QTL effects for fat deposition, muscling and growth traits on chromosome X in a European wild boar × Meishan  $F_2$  family.

Trait	F-ratio <sup>1</sup>	Position (cM) <sup>2</sup>	Additive effect ± SE	Dominance effect ± SE	VF2 <sup>4</sup> (%)
(a) Female and male $F_2$ animals					
Fat deposition					
, Shoulder fat depth (mm)	28.6***	90	$-4.00 \pm 0.74$		7.9
Average backfat depth (mm)	27.3***	90	-3.38 ± 0.65		7.5
Backfat depth on M. long. dorsi at 13th/14th rib (mm)	26.0***	90	$-4.28 \pm 0.84$		7.2
Fat cuts (%)	25.0***	90	-1-71 ± 0.34		6.9
Ham external fat weight (kg)	23.7***	90	$-0.32 \pm 0.07$		6.5
Fat area on M. long. dorsi at 13th/14th rib (cm <sup>2</sup> )	22.9***	90	$-3.04 \pm 0.63$		6.3
Backfat weight (kg)	22.8***	90	$-0.37 \pm 0.08$		6.3
Loin fat depth (mm)	20.7***	90	-3.19 ± 0.70		5.7
Fat depth at 10th rib (mm)	20.7***	90	-2.98 ± 0.66		5.7
Shoulder external fat weight (kg)	15.3**	90	-0.11 ± 0.03		4.2
Muscling					
Dressing A (%) <sup>3</sup>	18.2***	90	0.71 ± 0.17		5.0
Ham weight (kg)	16.0**	84	$-0.57 \pm 0.14$		4.4
Lean cuts (%)	13.6**	90	1.36 ± 0.37		3.7
Loin and neck meat weight (kg)	13.4**	90	$-0.26 \pm 0.07$		3.7
Growth					
Half carcass weight (kg)	16.5**	90	$-2.35 \pm 0.58$		4.6
Carcass weight (kg)	15.5**	90	-4.60 ± 1.17		4.3
Live weight at slaughter (kg)	13.7**	90	-5.13 ± 1.39		3.8
(b) Male F <sub>2</sub> animals					
Fat deposition					
Fat cuts (%)	25.9***	84	-2.51 ± 0.49		13.6
Backfat depth on M. long. dorsi at 13th/14th rib (mm)	24.4***	83	-6.04 ± 1.22		12.8
Average backfat depth (mm)	22.3***	84	$-4.38 \pm 0.93$		11.8
Fat depth at 10th rib (mm)	20.3***	85	$-4.20 \pm 0.93$		10.8
Shoulder fat depth (mm)	19.9***	83	-4.85 ± 1.09		10.7
Loin fat depth (mm)	16.8***	83	$-4.09 \pm 1.00$		9.0
Fat area on M. long. dorsi at 13th/14th rib (cm <sup>2</sup> )	15.3**	84	$-3.68 \pm 0.94$		8.2
Backfat weight (kg)	14.9**	84	$-0.45 \pm 0.12$		8.0
Muscling					
Lean cuts (%)	18.5***	88	2.31 ± 0.54		9.9
Dressing A (%) <sup>2</sup>	18.0***	89	1.06 ± 0.25		9.7
(c) Female F <sub>2</sub> animals					
Fat deposition					
Ham external fat weight (kg)	9.6**	90	$-0.58 \pm 0.16$	0.30 ± 0.18	10.0
Muscling					
Loin and neck meat weight (kg)	11.7***	90	$-0.72 \pm 0.17$	0.42 ± 0.19	12.1
Ham meat weight (kg)	11.2***	74	$-0.83 \pm 0.19$	$0.55 \pm 0.21$	11.6
Ham weight (kg)	10.6***	76	-1.56 ± 0.38	0.99 ± 0.42	11.0
Shoulder meat weight (kg)	9.5**	90	$-0.45 \pm 0.12$	0.26 ± 0.13	9.8
Growth					
Half carcass weight (kg)	10.2**	90	-5.82 ± 1.42	3.66 ± 1.58	10.5
Carcass weight (kg)	10.2**	90	-11.7 ± 2.9	7.28 ± 3.20	10.5

\*\*Significant at genome-wide threshold P < 0.05; \*\*\*significant at genome-wide threshold P < 0.01.

<sup>1</sup>Thresholds for particular models were applied.

 $^{2}$ QTL positions are taken from the female linkage map of a European wild boar  $\times$  Meishan family.

<sup>3</sup>Weight of ham meat relative to half carcass weight.

 $^{4}$ Explained phenotypic variance across  $F_{2}$  animals.

of the  $F_2$  generation. For females, one X chromosome originated from a Meishan pig, and alleles on the second X chromosome could be from either breed. For males, alleles on the X chromosome could come from either breed. For each sex, therefore, only the differences between the two possible genotypes could be analysed. As these effects are



**Figure 1** Profiles of *F*-ratio values on SSCX for QTL of fat deposition (shoulder fat depth), muscling (weight of ham meat relative to half carcass weight) and growth (half carcass weight) traits using female and male  $F_2$  animals. Genome-wide thresholds were P = 0.01 and P = 0.05 whereas the chromosome-wide threshold was P = 0.05.

expected to differ for the two sexes (Knott et al. 1998), separate effects for the two sexes were calculated for each model. Analysis in castrated males (Table 2, part b) revealed QTL for seven fat deposition traits (with F-ratio values up to 25.9 and VF<sub>2</sub> up to 13.6%) and QTL for two muscling traits (with *F*-ratio values up to 18.5 and VF<sub>2</sub> up to 9.9%). In the males. OTL for fat deposition traits mapped to a chromosome interval flanked by SW2476 and SW259, encompassing the AR gene, while OTL for two muscling traits were located in the vicinity of the ACSL4 gene. OTL for traits in the females (Table 2, part c) were detected with F-ratio values ranging from 9.5 to 11.7 and accounting for 9.8 to 12.1% of the VF<sub>2</sub>. Most of the QTL maxima were located at position 90 cM (ACSL4). Exceptions were QTL for ham meat weight and ham weight, which mapped about 15 cM proximally to the SW2456 and SW2476 interval. For fat deposition traits, only that for ham external fat weight, which explained for 10.0% of the VF<sub>2</sub>, exceeded genomewide threshold.

The QTL analysis in a  $W \times M F_2$  family was performed here with the same number of F<sub>2</sub> animals and the same trait data as in previous calculations (Čepica et al. 2003) but average marker spacing was 2.7 cM within the QTL region flanked by microsatellites SW2476 and SW1943. QTL for ten fat deposition, four muscling and three growth traits all mapped to 90 cM on the  $W \times M$  F<sub>2</sub> linkage map, corresponding to the ACSL4 gene, whereas QTL for ham and ham meat weight mapped 6 cM proximally to the chromosome interval flanked by SW2456 and AR. The other OTL affecting ham weight is located between SW2456 and AR. Pérez-Enciso et al. (2005) reported a proximal location for QTL affecting ham weight compared with QTL affecting fatness traits. Analyses done separately for female and male F<sub>2</sub> animals located QTL for fatness traits proximal to QTL affecting growth and muscling traits in males with these QTL at about 75, 84 and 90 cM (Table 2). QTL for fat traits at *ACSL4* that had low significance in the female analysis were highly significant in the combined analysis. The most prominent QTL affecting fat deposition traits was located in the proximity of *AR*, and the QTL affecting growth and muscling traits mapped at *ACSL4*.

Analysis of the QTL was limited due to a lack of recombination in the chromosome region flanked by genes RPS4X and SERPINA7 that corresponds to 34 Mb on the human chromosome X. Several genes can be considered positional candidates for all or some of the influenced traits. ACSL4 (Mercadé et al. 2006), AR (Trakooljul et al. 2004) and SERPINA7 (previously known as TBG; Nonneman et al. 2005; Ponsuksili et al. 2005; Kuehn et al. 2007) have already been studied in pigs as candidate genes for different traits. Studies conducted in humans and mice indicate that several other genes located within the porcine chromosome region flanked by SW2456 and SW1943 can also be considered as positional candidate genes for fat deposition traits. For example, IRS4 is located at human chromosome (HSA) HSAq22.3 (http://www. ncbi.nlm.nih.gov; York et al. 1997; Fantin et al. 2000; Schreyer et al. 2003), MED12 at Xq13, AGTR2 at HSAXq22-q23, SLC6A14 at HSAXq23-q24 and HTR2C at HSAXq24 (reviewed by Rankinen et al. 2006). Further studies using outbred populations with segregating loci in the QTL region may help to localize the gene effects.

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## Supplementary material

The following supplementary material is available for this article online from http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2052.2007.01661.x

Table S1 Markers, SNPs, their NCBI dbSNP ss numbers, recombination fractions, distances in Kosambi cM and LOD scores between markers and their position on the wild boar  $\times$  Meishan linkage map.

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