Exclusion of the SLA as candidate region and reduction of the position interval for the porcine chromosome 7 QTL affecting growth and fatness

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Abstract: Pig chromosome 7 (SSC7) has been shown to be rich in quantitative trait loci (QTL) affecting performance and quality traits. Most studies mapped the QTL close to the Swine Leukocyte Antigens (SLA), which has a large impact on adaptability and natural selection. Previous comparative mapping studies suggested that the 15 cM region limited by markers *LRA1* (mapped at 55 cM) and *S0102* (mapped at 70 cM) contains hundreds of genes. To reduce the number of candidate genes, we improved the mapping resolution with a genetic chromosome dissection through a backcross recombinant progeny test program between Meishan (MS) and European (EU, i.e. Large White or Landrace) breeds. Three first generation backcross - (EU x MS) x EU – and 2 second generation backcross ((EUxMS))xEU)xEU sires carrying a recombination in the QTL mapping interval were progeny tested, i.e. measured for a total of 44 growth, fatness, carcass and meat quality traits. Progeny family size varied from 29 to 119 pigs. Animals were genotyped for markers covering the region of interest. Progeny test results allowed the QTL interval to be reduced from 15-20 cM to 10 cM and even less than 6 cM if we assume that the EU pigs used in this study share only one QTL allele. Except for a putative QTL affecting some carcass composition traits, the SLA is excluded as a candidate region, suggesting that it might be possible to apply a marker assisted selection strategy for this QTL while controlling SLA allele diversity. The strong QTL effects remaining in animals with only 12.5% (issued from first generation backcross boars) and 6.25 % (issued from second generation backcross boars) Meishan genetic background shows that epistatic interactions are likely to be limited. Finally, the QTL does not have strong effects on meat quality traits.

Introduction

In different studies, pig chromosome 7 (SSC7) has been shown to be rich in QTL affecting economical and quality traits such as growth (Walling et al., 1998; Bidanel et al., 2001; de Koning et al., 2001), backfat thickness (Rohrer and Keele, 1998; Bidanel et al., 2001; Malek et al., 2001), carcass composition (Milan et al., 2002) and meat quality (Grindflek et al., 2001; Quintanilla et al., 2003). Most of these studies mapped the QTL close to the Swine Leukocyte Antigens (SLA), with a most likely position in the SSC7p12-q12 region. In all studies, Meishan alleles at the SSC7 QTL were associated with better performances and had dominant effects over European alleles.

Previous comparative mapping studies suggested that the 15 cM region limited by *LRA1* and *S0102* contains hundreds of genes (Genet et al., 2001; Demeure et al., 2003). As many of these genes can be considered as good candidates, reducing the QTL location interval appeared as a necessity. In addition, the QTL effects evidenced on different traits in this interval could be associated with one pleiotropic gene or different co-localized genes. Genetic chromosome dissection through a backcrossing program has been shown as a successful approach to confirm QTL effects and improve mapping resolution (Marklund et al., 1999).

A backcross program was developed as described by Sanchez et al. (2005) to improve the resolution of QTL located on several chromosomal regions and in particular on SSC7. More specifically on chromosome 7 the precise mapping of the QTL relative to the SLA complex is of particular interest, due to its impact on adaptability and natural selection. The use of a backcross program also allowed epistatic effects to be estimated in animals with a European genetic background. Finally, effects of the QTL on additional traits were investigated. In this study, 44 different meat quality, growth and fatness traits were measured.

Materials and Methods

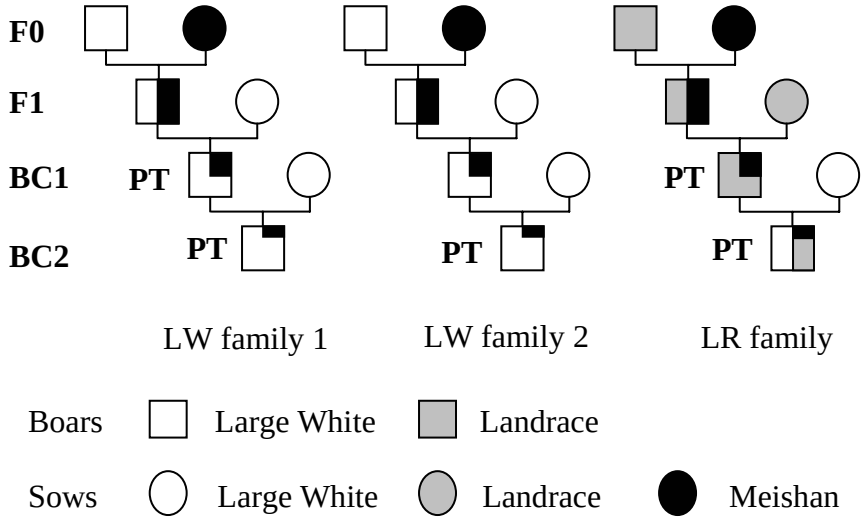
Animals and measurements

The recombinant animals were obtained with three different designs, using animals from

experimental farms or breeding companies (Figure 1). All QTL in this study presented favorable dominant effects of Meishan (MS) alleles over Large White (LW) alleles, making it interesting to test the effects of Meishan alleles in a European genetic background. In the first design (LW family 1), backcross animals were obtained by crossing Large White x Meishan F1 boars used in the INRA QTL program (Bidanel et al., 2001) with Large White females located in two INRA experimental herds (Avord, Cher and Le Magneraud, Charente-Maritime). Fathers from the second and third designs came from commercial crosses of the ADN breeding company (Pleyben, France). First generation backcross pigs (BC1) were obtained by crossing either Large White x Meishan F1 males with Large White females (LW family 2) or Landrace x Meishan F1 males with Landrace females (LR family). For both LW family 2 and LR family, a second generation of backcross pigs (BC2) was produced by crossing BC1 boars with Large White sows from INRA herd.

To confirm and pinpoint the QTL location, one animal completely heterozygous and four animals for which recombination events occurred in the QTL interval were selected for progeny testing (Figure 2). Due to the different Meishan regions conserved, these animals permit testing the QTL location in the chromosomal regions represented in black on Figure 2. Only two different Meishan haplotypes (called A and B) were segregating in the five tested animals. Both Meishan haplotypes were previously tested in the INRA F2 QTL program families and they showed similar effects on growth and fatness in contrast to Large White haplotypes. The progeny testing principle is detailed in Sanchez et al. (2005). Briefly, it is based on a comparison of piglets performances depending on which allele they received from the tested sire. A sire is considered to be heterozygous for the QTL if the paternal allele significantly affects the value of the trait in his progeny ($P<0.05$), and homozygous for the QTL if the probability of such an effect is weak ($P>0.05$).

Figure 1. Pedigrees of the animals used to study quantitative trait locus on Swine chromosome 7. Boars which were progeny tested were noted PT.

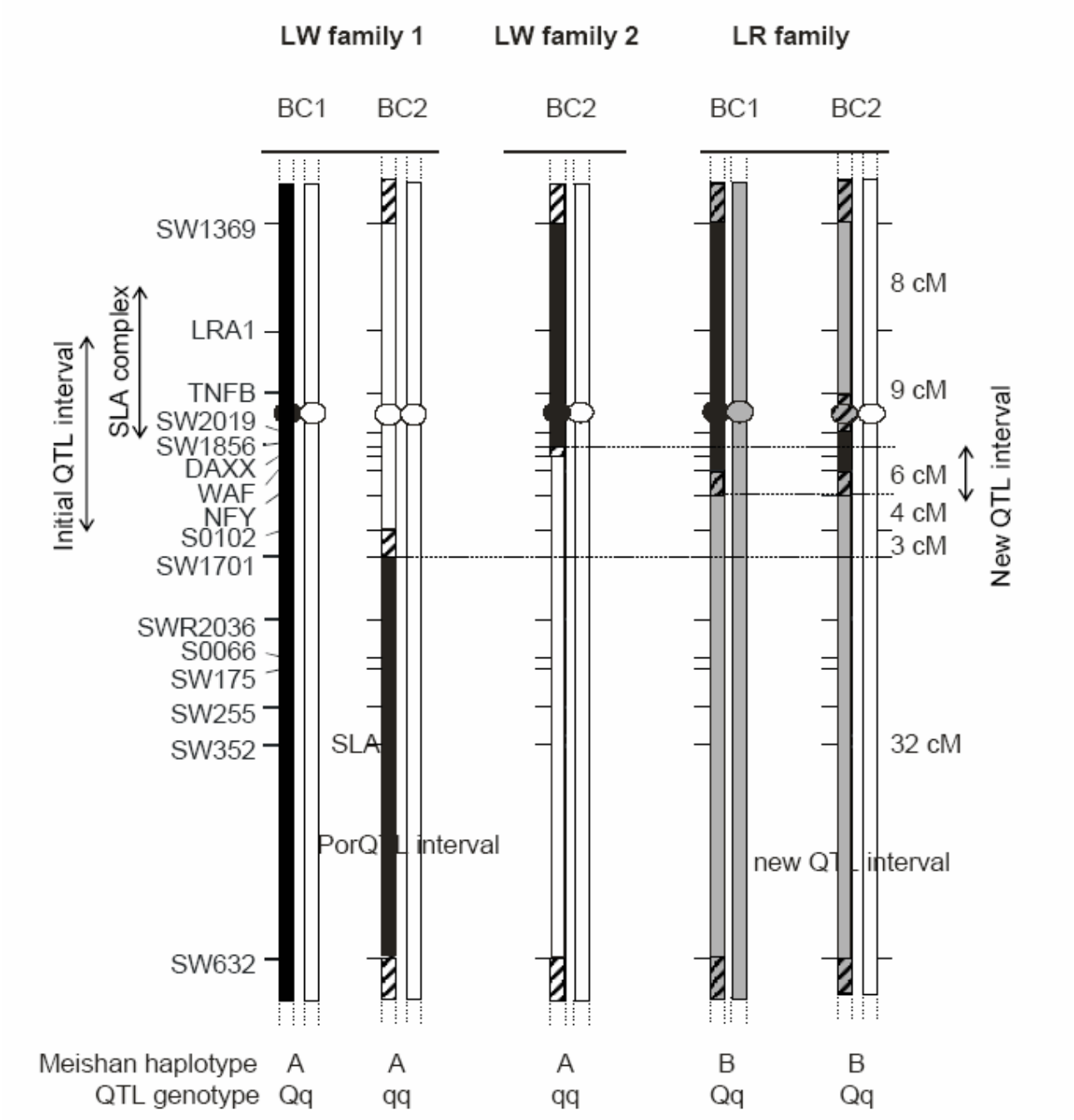


All backcross piglets were individually weighed at birth. Piglets were weaned at 28 days of age and placed in postweaning collective pens until 10 weeks of age. They were then transferred to a fattening unit, weighed and submitted to a performance test until approximately 20 weeks of age. Animals were weighed again at 3, 10 and 22 weeks and average daily gains were estimated for 0 to 3 weeks (ADG1), 3 to 10 weeks (ADG2) and 10 to 22 weeks (ADG3) intervals. At the end of the test period six ultrasonic backfat measurements (US-BFT values) were recorded on each side of the spine at 4 cm from the mid-dorsal line at the levels of the shoulder (neck), the last rib (back) and the hip joint (rump). Pigs were slaughtered at approximately 105 kg in a commercial slaughterhouse. Carcass weight and length as well as carcass fat depths at the shoulder, the last rib and the hip joint were measured shortly after slaughter (BFT values). Additional fat (G1, G2) and lean depths (M2, M6) were taken using a “Fat-o-Meater” probe. G1 was measured between the 3rd and the 4th lumbar vertebrae at 8 cm from the mid-dorsal line. G2,

M2 (loin eye) and M6 (loin eye + intercostals muscles) were measured at the 11 and 12 rib junction, at 6 cm from the mid-dorsal line. Lean meat content (LMC) was estimated using G1, G2 and M2 measurements.

Figure 2. Backcross animals haplotypes in the QTL region.

Meishan alleles are represented in black, Large White alleles in white and Landrace alleles in grey. Regions with unknown race origin are in dashed pattern, using the colors of the two possible race origin. The two Meishan haplotypes are defined by A or B. Qq and qq are attributed to the heterozygous and homozygous animals respectively, with Q for the favorable allele associated with better growth and lower fatness. Circles on the chromosome represents the centromere.



The day after slaughter, the whole carcass was weighed. The leaf fat was removed and weighed and the right half-carcass was divided into seven cuts: front and back feet, ham, loin, belly, shoulder and backfat, which were individually weighed. Different meat quality criteria were also controlled on several muscles. Ultimate pH measurements were taken on *Adductor*,

Longissimus dorsi, *Gluteus superficialis* and *Biceps femoris* muscles. Water holding capacity (WHC) and color were also evaluated in *Gluteus superficialis* and *Biceps femoris* muscles. WHC was measured using a piece of filter paper put on the freshly cut surface of the muscle and was defined as the time for the paper to become wet (a higher value is associated with a better WHC). Color was measured as three coordinates according to the Minolta L* a* b* system (Konica Minolta, Tokyo, Japan). Values of L* indicates lightness of the meat (a lower value is associated with a darker meat) while a* and b* represent the degrees of green-redness and blue-yellowness of the meat, respectively.

A total of 44 traits, i.e., seven growth, 12 fatness, 17 carcass composition and eight meat quality traits were measured (Table 1).

Table 1. Traits measured on backcross offspring

Growth[a]	**Fatness**[a]
Birth weight	US BFT - average - 100d
Weaning weight	US BFT - rump - 100d
Weight at the beginning of the test	US BFT - back - 100d
Weight at the end of the test	US BFT - neck - 100d
ADG1 (0 to 3 weeks)	US BFT - average - 120d
ADG2 (3 to 10 weeks)	US BFT - rump - 120d
ADG3 (10 to 22 weeks)	US BFT - back - 120d
Carcass composition[a]	US BFT - neck - 120d
Carcass length	US BFT - average - 140d
Foot weight	US BFT - rump - 140d
Ham weight	US BFT - back - 140d
Belly weight	US BFT - neck - 140d
Shoulder weight	**Meat quality**
Backfat weight	pH24 Adductor
Loin weight	pH24 Gluteus superficialis
Head weight	pH24 Longissimus dorsi
BFT - average	pH24 Biceps femoris
BFT - rump	Water holding capacity of gluteus superficialis
BFT - back	Water holding capacity of biceps femoris
BFT - neck	Gluteus superficialis color (L* a* b*)
Lean meat content (LMC)	Biceps femoris color (L* a* b*)
G1 – 3rd to 4th lumbar vertebrae	
G2 – 11 and 12 rib junction	
M2 – loin eye	
M6 – loin eye + intercostals muscles	

[a] US: ultrasonic; BFT: backfat thickness; ADG: average daily gain; G1 and G2: Additional fat measures; M2 and M6: lean depths measures at the 11 and 12 rib junction.

Genetic Markers and Genotyping

The microsatellites markers used were mostly public markers available on the USDA web site (http://www.marc.usda.gov/genome/genome.html) . Information about the DAXX, WAF and NFY microsatellites are available in Demeure et al. (2003). Those three markers have been integrated in the genetic map by genotyping 245 animals from the INRA QTL program families. Mapping analyses were realized with the 2.4 version of CriMap software (Green et al., 1990). The amplifications were performed on ABI9700 PCR machines (Applied Biosystems, Foster City, CA). Thermal cycling parameters were denaturation at 95°C for 5 min, followed by 30 cycles of 95°C for 30s / annealing temperature for 30s / 72°C for 45s; a final amplification was performed at 72°C for 15 min. The PCR amplification analysis was done on ABI377 automatic sequencer (Applied Biosystems, Foster City, CA). Results were analyzed with ABI Genescan and Genotyper (Applied Biosystems, Foster City, CA) and scored and validated in GEMMA (Iannuccelli et al., 1996).

Statistical analysis

The data were first adjusted for environmental effects using the GLM procedure of SAS (1999). A contemporary group (i.e., a slaughter date effect for meat quality traits and a batch effect for the other traits) and a sex (except for Minolta coordinates) were included in the model for all traits. Some traits were additionally corrected for a covariate: birth weight for ADG1, weaning weight for ADG2, weight at the beginning of the test for ADG3, weight at the measurement for backfat thickness and body composition traits.

These adjusted data were then used to test within each sire family the presence of a QTL in the chromosomal region investigated. Analyses were performed with the half full-sib (HFS) model developed by Le Roy et al. (1998). The hypothesis of one QTL (H1) linked to the set of markers considered was compared with the hypothesis of no QTL (H0) at the same location. Under the H1 hypothesis, a QTL with a gene substitution effect for each sire and for each dam was fitted to the data. Likelihoods were then maximised under each hypothesis and the test statistic was computed as the ratio of likelihoods (L-ratio). The location with the highest L-ratio was considered as the most likely position of the QTL. Approximate confidence intervals of QTL position were determined empirically using the "Drop-off" method. More details on the model and methodology can be found in Le Roy et al. (1998) and Bidanel et al. (2001). Chromosome-wide (CW) significance thresholds were determined assuming a polygenic infinitesimal model and a Normal distribution of performance (Le Roy et al., 1998). A total of 1000 simulations were achieved for each sire x trait combination. Because many tests were carried out, two experiment-wide thresholds were defined in addition to those corresponding to usual 5% and 1% CW significance levels. As traits were correlated, an equivalent number of independent traits was estimated through a canonical decomposition of the correlation matrix. The first 20 eigenvalues explained more than 95 % of the total variability, leading to an approximate number of 100 independent tests (20 traits x 5 sires). A Bonferroni correction was used to compute probabilities corresponding to 10% and 5% experiment-wide significance levels, i.e., 10-3 and 5.10-4. A total of 5, 1, 0.1 and 0.05 false positives were expected from 0.05, 0.01, 0.001 and 5.10-4 significance levels, respectively.

Results

The DAXX, WAF and NFY microsatelittes markers have been integrated in the genetic map by genotyping 245 animals from the INRA QTL program families. The Sw1856-DAXX-WAF-NFY-S0102 order confirms the results previously obtained by radiated hybrid mapping (Demeure et al., 2003). The distances calculated under the Kosambi formula for Sw1856-DAXX, DAXX-WAF, WAF-NFY and NFY-S0102 intervals are 0.8cM; 1cM; 3.7cM and 4.1cM respectively.

The LW family 1 BC1 (LW1-BC1) boar had an entire Meishan chromosome (with an haplotype called A) and a full LW chromosome (Figure 2). This animal allowed QTL effects to be tested and estimated in a 7/8 Large White background. Under an additive model, QTL effects were expected to be roughly similar to those detected in F2 pigs as Meishan alleles were found to be dominant over LW alleles. Indeed, QTL effects were identified for several fatness and carcass composition traits. However in contrast to F2 results, no significant effects were found for growth and meat quality traits (Table 2).

The LW male from family 1 BC2 (LW1-BC2), son of boar LW1-BC1 was the first animal tested to reduce the QTL interval. Male LW1-BC2 only partly received MS haplotype A from his father - from *Sw1701* (73 cM) to *Sw632* (105 cM) - as a recombination occurred between *S0102* and *Sw1701* (Figure 2). The next chromosomal region tested was the distal part of the QTL position confidence interval obtained in F2 pigs. As shown in Table 2, only two traits (ADG3 and BFT)

showed chromosome wide significant QTL effects, suggesting that this animal does not carry the MS allele of the QTL identified in its father.

The LW family 2 BC2 (LW2-BC2) boar carried the same MS haplotype (A) as LW family 1 pigs. The associated QTL allele was thus assumed to be the same. Again, only suggestive QTL effects were found for a limited number of traits (LMR, G2, M6 and head weight), with QTL locations estimated around 50 cM. The lack of effect on growth and fatness traits observed in LW1-BC2 and LW2-BC2 progeny led us to reduce the QTL position to the *Sw1856 – Sw1701* interval. However, as this interval was deduced from homozygous animals, we had to confirm it, by testing animals heterozygous for QTL in this region.

Table 2: Traits affected by QTL segregation in backcross populations – Large White families.

Traits[a]	Number of animals	P value[b]	Position[c]	Estimated effect[d]
LW family 1 – BC1				
Carcass lenght (mm)	29	+	56 (54-88)	-17,10
US BFT – rump – 140d (mm)	28	**	58 (54-85)	2,26
US BFT – average - 140d (mm)	28	**	57 (56-87)	1,76
US BFT - neck - 140d (mm)	28	*	54 (54-61)	2,06
`BFT - rump (mm)	28	**	62 (54-82)	2,24
BFT - back (mm)	28	**	87 (60-101)	1,92
BFT - neck (mm)	28	+	77 (64-96)	2,08
LMC (%)	28	+	94 (80-110)	-1,02
G1 (mm)	28	+	89 (54-97)	2,25
G2 (mm)	28	+	89 (82-96)	2,68
LW family 1 – BC2				
ADG3 from 10 to 22 weeks (kg)	64	+	114 (102-126)	-0,02
BFT - rump (mm)	40	+	98 (87-108)	1,10
False teats (units)	37	++	118 (110-127)	0,15
LW family 2 – BC2				
LMC (%)	49	+	47 (47-57)	0,18
G2 (mm)	49	+	47 (47-54)	-0,15
M6 (mm)	49	+	47 (47-53)	-1,16
Head weight (kg)	49	+	51 (47-61)	-0,08

[a] US: ultrasonic measurement; BFT: backfat thickness; ADG: average daily gain; LMC: lean meat content.
[b] +; ++ = 0.05 and 0.01 chromosomal significance levels. *; ** = 0.10 and 0.05 experiment-wide significance levels. [c] Haldane mapping function [d] in trait units

The two Landrace backcross pigs that were progeny tested shared the B MS haplotype. The Landrace BC1 (LR-BC1) male had a MS haplotype from *Sw1369* to *WAF* and a Landrace haplotype from *NFY* to *Sw632*. The progeny test revealed very important QTL effects on many growth, fatness and carcass composition traits (Table 3, Figure 3), leading us to conclude that the boar was heterozygous for QTL with most likely positions around 65 cM. Suggestive QTL effects were also found on meat quality, with positive effects of MS allele on water holding capacity (+3.8s, $p < 0.05$) and Longissimus dorsi ultimate pH (+0.1 units, $p < 0.05$). The second Landrace backcross boar (LR-BC2) was the son of LR-BC1. Its MS haplotype was reduced to a small region from *Sw2019* to *WAF*. LR-BC2 boar also appeared as heterozygous for the main QTL effects (Table 3, Figure 3). These two progeny testing gave a new QTL interval reduced from *TNFβ* to *NFY* (around 10 cM). Considering the LW2-BC2 progeny testing, the proximal limit might even be *Sw1856*, defining thus a 6 cM interval. Only further experiments on complementary animals could definitively exclude the *TNFβ* - *Sw1856* region.

Table 3: Traits affected by the QTL segregation in backcross populations – Landrace family

Traits[a]	Number of animals	P value[b]	Position[c]	Estimated effect[d]
LR family - BC1				
ADG3 from 10 to 22 weeks (kg)	118	+	24 (10-44)	-0,02
US BFT - average - 100d (mm)	119	+	66 (64-69)	0,52
US BFT - rump - 100d (mm)	119	**	66 (64-69)	0,72
US BFT - average - 120d (mm)	119	+	70 (64-81)	0,86
US BFT - rump - 120d (mm)	119	**	66 (62-68)	1,09
US BFT - neck - 120d (mm)	119	+	133 (125-135)	0,31
US BFT - average - 140d (mm)	119	**	65 (62-67)	1,41
US BFT - rump - 140d (mm)	119	**	65 (62-67)	1,41
US BFT - back - 140d (mm)	119	*	65 (62-67)	1,25
US BFT - neck - 140d (mm)	119	**	64 (62-66)	1,57
BFT - average (mm)	91	**	63 (61-66)	3,01
BFT - rump (mm)	91	**	63 (61-66)	3,17
BFT - back (mm)	91	**	62 (51-65)	3,01
BFT - neck (mm)	91	++	65 (62-68)	3,05
LMC (%)	91	**	63 (61-66)	-1,25
G1 (mm)	91	++	64 (61-66)	2,01
G2 (mm)	91	**	63 (62-65)	2,61
Ham weight (kg)	91	+	135 (126-135)	-0,29
Backfat weight (kg)	91	+	68 (67-78)	0,34
pH24 Longissimus dorsi (units)	73	+	65 (60-69)	-0,10
Water holding capacity of gluteus superficialis (s)	90	+	99 (89-115)	-3,77

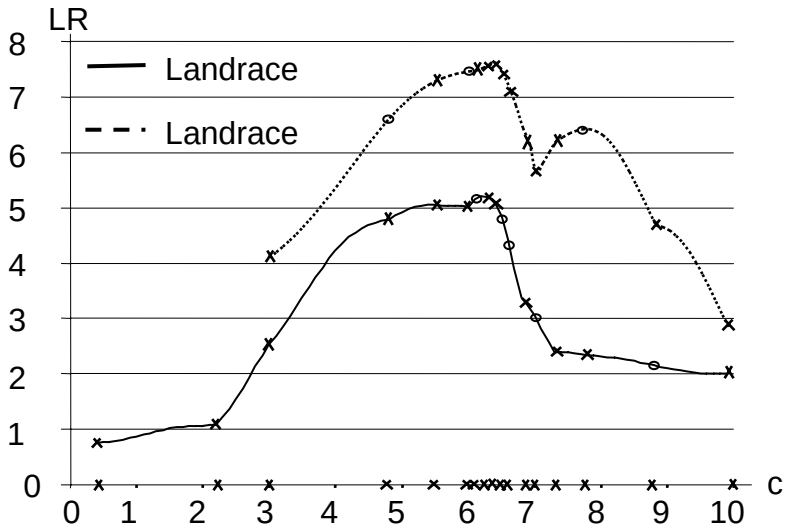
Table 3: Traits affected by the QTL segregation in backcross populations – Landrace family (following).

Trait[a]	Number of animals	P value[b]	Position[c]	Estimated effect[d]
LR family – BC2				
ADG3 from 10 to 22 weeks (kg)	89	+	73 (71-82)	-0,03
US BFT - average - 140d (mm)	97	+	41 (30-60)	0,71
US BFT - rump - 140d (mm)	97	**	64 (61-66)	0,71
US BFT - back - 140d (mm)	97	+	47 (33-60)	0,58
BFT - average (mm)	80	**	55 (45-65)	2,04
BFT - rump (mm)	80	**	83 (78-88)	2,57
BFT - back (mm)	80	**	64 (57-66)	2,89
G2 (mm)	80	++	64 (53-67)	1,16
M6 (mm)	80	+	69 (67-72)	2,31
Carcass lenght (mm)	80	**	66 (54-78)	-20,74
Foot weight (kg)	80	+	62 (51-67)	-0,08
Backfat weight (kg)	80	+	64 (51-66)	0,17
Head weight (kg)	80	**	98 (94-103)	-0,48
Biceps femoris L* (units)	80	+	64 (58-67)	-1,91

[a] US: ultrasonic measurement; BFT: backfat thickness; ADG: average daily gain; LMC: lean meat content.
[b] +; ++ = 0.05 and 0.01 chromosomal significance levels. *; ** = 0.10 and 0.05 experiment-wide significance levels.
[c] Haldane mapping function
[d] in trait units

Figure 3. Results of a backfat thickness measured after slaughter QTL analysis in the two backcross Landrace family.

The different used markers, which locations are represented by crosses, are, by position order: S0025; Sw1354; S0064; Sw1369; LRA1; TNFb; BMP5; Sw2019; Sw1856; DAXX; WAF; NFY; S0102; Sw1701; S0078; Sw352 and Sw632. For each family, the genotyped markers are represented on curves by a cross. When the marker was not genotyped in a family, a circle represents it. LRT, likelihood ratio test.



Discussion

When backcross animals were assigned as heterozygous for the QTL, the QTL was considered to be located in the heterozygous Meishan / European chromosomal region. This interpretation was based on the assumption that QTL alleles are fixed in purebred parental pigs. This appeared to be the case in F2 pigs, where all Meishan QTL alleles were clearly associated with higher performances than Large White QTL alleles (Bidanel et al., 2001, Milan et al., 2002).

The first backcross (LW1-BC1) boar confirmed the existence of SSC7 QTL effects on fatness and carcass composition traits in a Large White genetic background. Conversely, no significant QTL effects could be found for growth traits, which was quite surprising as the Meishan haplotype of this animal came from the F2 design (Bidanel et al., 2001). This is likely to be due to the limited progeny size (only 29 offspring), which was large enough to detect the very strong effects of the chromosomal region on fatness traits, but not for the more moderate effects on growth rate. This hypothesis seems to be confirmed by progeny test results from Landrace BC1 and BC2 boars, where larger sizes (118 and 89 offsprings) allowed significant effects to be observed on at least some growth traits.

Only few meat quality traits were found to be significantly affected by the chromosomal region investigated, most of them being only suggestive QTL ($p < 0.05$). In addition, none of the detected QTL was located in the previously defined interval, except the pH24 *Longissimus dorsi* (in the Landrace BC1 boar progeny) and the *Biceps femoris* L* (in the Landrace BC2 boar progeny) QTL, mapped at 65 cM and 64 cM respectively. Previous studies found significant effects of this chromosomal region on meat quality, but in different crossbred populations, i.e., (Duroc x Landrace) x (Landrace x Yorkshire) pigs (Grinflek et al., 2001) and Meishan x Wild boar F2 pigs (Yue et al., 2003). It can thus be concluded that the chromosomal region investigated in this study has little or no effect on meat quality traits in crosses between Meishan and Large White or Landrace breeds.

The backcross experimental design also allowed to test the hypothesis that several loci can affect traits as different as growth and fatness. Indeed, comparing the observed QTL effects in the progenies of different sires makes it possible to evaluate if a recombination event has broken up a QTL haplotype resulting in markedly reduced QTL effects in some families. Results from the progeny of boar LW1-BC2 suggests that no additional major QTL segregates in the region distal from *Sw1701* excepted for ADG3 and BFT, 60 cM away from the other QTL most likely positions. The effect on ADG might be due to the segregation in our crosses of a QTL affecting ADG similar to the one previously described in a Pietrain x Large White intercross around *Sw352* (Nezer et al., 2002).

The SLA region was a particularly interesting target because, in humans, the HLA heterozygosity confers a selective advantage against multiple-strain infections (Penn et al., 2002). Selecting QTL located in the SLA region might reduce its variability and result in a reduced animal adaptability, with dramatic consequences for breeders. The progeny test of LW2-BC2 boar revealed possible additional QTL in the SLA region or on the p arm of SSC7 for few carcass composition traits but no QTL affecting growth or fatness traits has been detected. Wada et al. (2000) and Rohrer (2000) pointed out that it is likely that an additional region on the p arm should contain a QTL influencing also fatness traits. Results from the progeny of Landrace boars BC1 and BC2 showed similar QTL effects on fatness traits in both families (see Figure 3 for backfat thickness measured after slaughter), except for the QTL affecting fatness at 100 and 120 days of age, that was lost in boar LR-BC2. This could be due to the loss of a second QTL located in the *TNFb-Sw2019* interval or to the progeny size difference, the QTL significance levels being globaly lower for the LR-BC2. On the opposite, results for carcass composition traits are different between the two boars, with a loss of the effect on the lean meat content (LMC) in the LR-BC2 progeny while this same male has a new and strong QTL effect ($P<0.01$) on carcass length. The loss of the QTL effect on LMC might be explained by an epistatic effect or by a second QTL proximal to *Sw2019*. The effect on carcass length observed in the LR-BC2 progeny indicates that the QTL involved in its control could be segregating in the LW and/or LR breeds. Globally the large effect on fatness traits observed both in the Large White families (where Meishan haplotype A segregates) and Landrace families (where Meishan haplotype B segregates) were similar. This confirms that both Chinese haplotypes also studied in the INRA F2 original cross have similar effects on fatness. We could not however exclude that the limited differences observed among the different families could be due to the segregation of additional QTL within European Large white and Landrace herds or limited difference among Meishan haplotype A and B.

In the analysis of the results of this backcross program we should not exclude formally the risk

that the favorable QTL allele of Meishan origin could also segregate within European Large White or Landrace herds. In that case, the observation of a contrast of effects between the two chromosomes of a tested sire will lead to a false conclusion about the location of the studied QTL. To limit that risk of a false conclusion on the localization of the QTL, we based mainly our deduction on the analysis of sires found heterozygous at the QTL and carrying part of a Meishan haplotype whose effect has already been evaluated in other families. Indeed, when a sire is identified as heterozygous, the shape of the likelihood ratio test curve, the estimate of the QTL effect and their comparison with previous results allow to increase the confidence in the reliability of results. Considering both animals identified as heterozygous and homozygous at QTL, we reduce the QTL region to a 6 cM interval (*Sw1856 – NFY*), but if we only wish to consider animals identified as heterozygous at QTL, the QTL is located in a larger interval: *TNFβ – NFY*. A recent multiQTL study, performed on the INRA QTL program, revealed that three QTL might be located in the *Sw1856 – Sw1701* interval (H. Gilbert, unpublished data). The next generations of backcross animals will allow to confirm the 6 cM interval, to refine it, and to test the multi loci determinism of growth and fatness traits suggested by the Gilbert et al. (unpublished data) results. In parallel, recent high throughput and low costs for SNP genotyping methods should facilitate new approaches. In particular, fine mapping strategies based on linkage disequilibrium will be evaluated. The first one is based on the study of allele frequency evolution in a population submitted to a selection for growth and fatness traits. A second approach would be a progeny test using animals from different commercial or experimental programs, in order to find fragments that are identical by descent (IBD).

Implications

Our results give new insights on the SSC7 QTL: First, based on the assumption of a unique European QTL allele, this two generation backcross program allowed the QTL interval to be reduced from 15-20 cM to 6 cM. Even if the assumptions concerning the Large White x Meishan boar are not correct, the Landrace BC2 boar defines a *TNFβ – NFY* interval of less than 10 cM. Secondly, excepted for a possible QTL affecting few carcass composition traits, the SLA is excluded as a candidate region, suggesting that it might be possible to apply a marker assisted selection strategy for this QTL with limited consequences on SLA allele diversity. Third, the fact that QTL effects are still strong with a Meishan genetic contribution of only 12.5% indicates that this Meishan allele keeps its large favorable effect on animals of a genetic background close to slaughter pigs; this also shows that the probability of epistatic effects is low. Fourth, the QTL does not have strong effects on meat quality traits.

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