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# Quantitative trait loci associated with AutoFOM grading characteristics, carcass cuts and chemical body composition during growth of *Sus scrofa*

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## Summary

A three-generation full-sib resource family was constructed by crossing two commercial pig lines. Genotypes for 37 molecular markers covering chromosomes SSC1, SSC6, SSC7 and SSC13 were obtained for 315 $F_2$ animals of 49 families and their parents and grandparents. Phenotypic records of traits including carcass characteristics measured by the AutoFOM grading system, dissected carcass cuts and meat quality characteristics were recorded at 140 kg slaughter weight. Furthermore, phenotypic records on live animals were obtained for chemical composition of the empty body, protein and lipid accretion (determined by the deuterium dilution technique), daily gain and feed intake during the course of growth from 30 to 140 kg body weight. Quantitative trait loci (QTL) detection was conducted using least-squares regression interval mapping. Highest significance at the 0.1% chromosome-wise level was obtained for five QTL: AutoFOM belly weight on SSC1; ham lean-meat weight, percentage of fat of primal cuts and daily feed intake between 60 and 90 kg live weight on SSC6; and loin lean-meat weight on SSC13. QTL affecting daily gain and protein accretion were found on SSC1 in the same region. QTL for protein and lipid content of empty body at 60 kg liveweight were located close to the *ryanodine receptor 1* (*RYR1*) locus on SSC6. On SSC13, significant QTL for protein accretion and feed conversion ratio were detected during growth from 60 to 90 kg. In general, additive genetic effects of alleles originating from the Piétrain line were associated with lower fatness and larger muscularity as well as lower daily gain and lower protein accretion rates. Most of the QTL for carcass characteristics were found on SSC6 and were estimated after adjustment for the *RYR1* gene. QTL for carcass traits, fatness and growth on SSC7 reported in the literature, mainly detected in crosses of commercial lines × obese breeds, were not obtained in the present study using crosses of only commercial lines, suggesting that these QTL are not segregating in the analysed commercial lines.

**Keywords** carcass characteristics, chemical body composition, markers, pig, quantitative trait loci.

## Introduction

Publication of genetic maps of porcine microsatellite markers (Rohrer *et al.* 1994,1996) enabled studies on quantitative trait loci (QTL) affecting economically important traits such as fatness and muscularity of pigs. Numerous QTL have been detected using crosses between commercial and obese breeds (e.g. Knott *et al.* 1998; Moser *et al.* 1998; Wada *et al.* 2000; Bidanel *et al.* 2001; Milan *et al.* 2002). Because of the inferior performance of the obese breeds for several economically important traits, these QTL are not of immediate interest in commercial pig breeding (Malek *et al.* 2001), and their use in other commercial populations requires additional QTL introgression (Bidanel & Rothschild 2002). Thus, detection of QTL using intercross designs with

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commercial lines will have more immediate use to the pig breeding industry. Several studies indicate the importance of porcine chromosomes 1, 6, 7 and 13 for the traits of carcass characteristics (e.g. Bidanel *et al.* 2001; Nezer *et al.* 2002; Beeckmann *et al.* 2003; Yue *et al.* 2003a,b). Therefore, these chromosomes were examined in the present study in crosses of Piétrain with a commercial dam line.

In Germany, commercial abattoirs are changing their payment system from a carcass-grading system based on lean content measured by the Fat-o-Meter (FOM) to a system based on the AutoFOM device (Tholen *et al.* 2001). Therefore, QTL associated with carcass characteristics of the AutoFOM carcass grading system are of high interest in selection programmes of pigs in order to maximize the market value of pork. Furthermore, there is a great interest in pig production and breeding to improve protein deposition and feed efficiency based on biological growth models (Schinckel & De Lange 1996). In this growth model, protein accretion rates and feed intake at different stages of growth have to be determined in the population of interest. Deuterium dilution technique is an *in vivo* method that accurately measures chemical composition of the empty body (Susenbeth 1984; Landgraf *et al.* 2006). Using this method, chemical body composition can be obtained on live animals during the course of growth. QTL for all these traits are expected to be used to improve carcass quality and to enhance feed efficiency by optimization of feed intake capacity using biological growth models.

## Materials and methods

### Animals

The experiment was based on a three-generation full-sib design. The resource family was created using seven unrelated Piétrain grandsires [which were heterozygous *Nn* for the *ryanodine receptor 1* (*RYR1*) locus] and 16 unrelated granddams of a crossbred dam line (created from Large White × Landrace × Leicoma). Eight boars and 40 sows were randomly selected within families from the $F_1$ litters, and they were mated avoiding inbreeding to produce two litters of $F_2$-generation pigs that were tested at a performance test station.

In the present study, 315 pigs of the $F_2$ generation were used. Among these $F_2$ pigs, 49 gilts and 46 barrows were single-housed in straw-bedded pens, whereas 112 gilts and 108 barrows were housed in straw-bedded pens with groups up to 15 pigs and not separated by sex. Single-housed pigs were manually fed with weekly determination of feed consumption. Group-housed pigs were fed by electronic feeding station of type ACEMA 48 (Acemo, Rennes, France), which recorded feed consumption for every single visit. Pigs were allowed *ad libitum* access to a series of three pelleted diets with 13.8 MJ ME/kg and 1.2% lysine, 13.8 MJ ME/kg and 1.1% lysine, as well as 13.4 MJ ME/kg and 1.0% lysine in the weight ranges of 30–60, 60–90 and 90–140 kg body weight respectively. *Ad libitum* access and diet formulation slightly above requirement provided a performance at the individual maximum protein deposition capacity of the pigs (Landgraf *et al.* 2006). At body weight of 140 kg, pigs were slaughtered in a commercial abattoir where an AutoFOM device was used in the online carcass-grading system.

### Traits

Besides the estimation of lean-meat percentage, separate weights of valuable carcass cuts were measured using the AutoFOM device. This device produced a digitized three-dimensional scanning, provided by 16 ultrasonic transducers embedded in a fixed stainless steel transducer array. A cross-section image at every 5 mm in the whole length of the carcass resulted in approximately 200 measurements on every ultrasonic transducer. Therefore, about 3200 measurements were potentially obtained from each carcass. Each measurement consisted of external fat thickness and muscle thickness. Using the slices from all 16 transducers, the system provided a three-dimensional image of the backside of the carcass to estimate the carcass composition (Brøndum *et al.* 1998). The AutoFOM device measured 10 traits including average fat thickness, lean-meat percentage of the carcass, and the entire and lean weights of shoulder, loin and ham, as well as belly weight and its lean-meat content. Furthermore, the right carcass side of each pig was dissected into the primal cuts ham, shoulder, loin, belly and neck. Ham, shoulder, loin and neck were further dissected into fat and lean. In addition, weight of jowl, hind hock and caudal vertebrae, as well as tail musculature, were measured. Standard performance traits recorded on test stations such as carcass length, pH value of ham and loin, conductivity, back fat and side fat thickness, as well as loin eye area, fat area and thinnest fat measure (fat degree B) at the 13th/14th rib interface, were measured on the cold left carcass side according to the principles of test stations (ZDS 1992). Intramuscular fat content of the musculus longissimus thoracis et lumborum was measured using near-infrared transmission analysis. The FOM device provided both measures of back fat and longissimus muscle depth perpendicular to the muscle between the 3rd and 4th ribs cranial to the last ribs.

Chemical body composition of the empty body was determined at the target body weights of 30, 60, 90, 120 and 140 kg using a deuterium dilution technique. Equations for estimation of chemical body composition from empty body water determined by the deuterium dilution technique were developed based on chemical analysis of pigs slaughtered in a previous serial slaughter trial. The prediction equations and the measurement technique using deuterium are described in detail by Landgraf *et al.* (2006) and Mohrmann *et al.* (2006). Protein and lipid accretion rates were calculated based on chemical body composition at two adjacent target weights and time of growth. Further details about performance of the

$F_2$ pigs in traits of feed intake, feed conversion, chemical body composition and protein and lipid deposition are presented in Tables S1 and S2.

### Markers

Blood samples were collected from all animals of the $F_0$, $F_1$ and $F_2$ generations from the vena jugularis and used for isolation of genomic DNA. Markers on SSC1 (10), SSC6 (9), SSC7 (10) and SSC13 (8) were selected from the MARC pig map (http://www.marc.usda.gov) because of their expected associations with carcass characteristics. For SSC1, SSC6, SSC7 and SSC13, the average distances between two adjacent markers were 16, 21, 17 and 18 cM respectively, and the largest gaps were 28, 29, 26 and 24 cM respectively (Table 1).

### Statistical analysis

Regression analysis of the $F_2$ population was computed with QTL Express (http://latte.cap.ed.ac.uk) using the line-cross least-squares multi-marker regression interval mapping program developed by Haley *et al.* (1994). Marker information was used to calculate the probabilities of individuals to inherit two grandpaternal alleles, two grandmaternal alleles or one of each for a putative QTL at each 1-cM position. A least-squares regression model was used for QTL analysis, adjusting the phenotypes for fixed effects and covariates affecting the corresponding trait. Phenotypic data were adjusted for fixed effect of sex (barrows and gilts), *RYR1* genotype (*NN*, *Nn* and *nn*) and batch effect (1–9). For carcass characteristics and chemical body composition, a linear regression on body weight at day of slaughter or the target weight was fitted. In contrast, for traits such as growth rate, accretion rates and feed intake, linear regression on body weight at the start and end of the considered target weight range were used as covariables. The housing type significantly affected feed intake and feed conversion ratio and was considered for these traits in the analysis. The additive effect was defined as half of the phenotypic difference between pigs that were homozygous for Piétrain (sire-line) alleles and pigs that were homozygous for the dam-line alleles. The dominance effect was defined as the phenotypic deviation of heterozygous animals from the mean of both genotypes of homozygous animals. To test for a putative segregating QTL on a particular chromosome, an *F*-test was applied. Critical values of chromosome-wise statistics were obtained for 10 000 permutations (Churchill & Doerge 1994). De Koning *et al.* (2001) suggested that a chromosome is a candidate for carrying a putative QTL when the chromosome-wise error probability was below or equal to 0.05. Estimates for additive and dominance effects were calculated at the location on the chromosome with the highest *F*-ratio. Information content along each location at one chromosome was calculated as the proportion of the variance of the considered coefficient on the variance for a fully informative marker with the same frequencies of observed genotypes as expected frequencies (Knott *et al.* 1998). Markers, their positions, number of alleles and the information contents for the additive and dominance coefficients at the marker locations are shown in Table 1.

**Table 1** Markers used in the quantitative trait loci mapping project, their relative map positions using the MARC pig map and the information contents for the additive (a) and dominance (d) coefficients.

| Marker | SSC | Position (cM) | Number of alleles | Information content of coefficients | |
|---|---|---|---|---|---|
| | | | | a | d |
| *SW1514* | 1 | 0 | 8 | 0.91 | 0.73 |
| *SW1515* | 1 | 16.4 | 8 | 0.86 | 0.69 |
| *SW1332* | 1 | 29.2 | 4 | 0.77 | 0.55 |
| *SW1851* | 1 | 44.6 | 4 | 0.81 | 0.68 |
| *SW1430* | 1 | 58.5 | 6 | 0.78 | 0.64 |
| *SWR982* | 1 | 86.2 | 6 | 0.89 | 0.79 |
| *SW1311* | 1 | 100.8 | 6 | 0.78 | 0.62 |
| *SW1828* | 1 | 118.5 | 7 | 0.90 | 0.81 |
| *SW1301* | 1 | 140.5 | 5 | 0.86 | 0.84 |
| *SW2512* | 1 | 144.0 | 6 | 0.86 | 0.84 |
| *MP35* | 6 | 0 | 6 | 0.58 | 0.45 |
| *SW2406* | 6 | 21.4 | 8 | 0.74 | 0.56 |
| *SW1841* | 6 | 41.5 | 15 | 0.96 | 0.79 |
| *S0087* | 6 | 62.8 | 5 | 0.88 | 0.76 |
| *SW122* | 6 | 83.3 | 7 | 0.94 | 0.80 |
| *S0228* | 6 | 105.2 | 6 | 0.79 | 0.64 |
| *SW1881* | 6 | 121.1 | 8 | 0.84 | 0.80 |
| *SW322* | 6 | 149.8 | 8 | 0.80 | 0.70 |
| *SW2052* | 6 | 164.6 | 9 | 0.83 | 0.72 |
| *SW2564* | 7 | 0 | 5 | 0.71 | 0.60 |
| *SWR1343* | 7 | 12.2 | 4 | 0.72 | 0.65 |
| *SW2155* | 7 | 32.9 | 4 | 0.66 | 0.53 |
| *SW1369* | 7 | 48.2 | 8 | 0.75 | 0.67 |
| *SW1856* | 7 | 61.5 | 5 | 0.73 | 0.59 |
| *SWR2036* | 7 | 78.2 | 9 | 0.80 | 0.67 |
| *SW632* | 7 | 104.4 | 6 | 0.78 | 0.57 |
| *SWR773* | 7 | 117.3 | 3 | 0.75 | 0.50 |
| *SW2537* | 7 | 139.5 | 7 | 0.85 | 0.64 |
| *SW764* | 7 | 156.0 | 5 | 0.76 | 0.62 |
| *S0282* | 13 | 0 | 8 | 0.89 | 0.83 |
| *SWR1941* | 13 | 14.1 | 7 | 0.93 | 0.87 |
| *SW1407* | 13 | 27.2 | 11 | 0.84 | 0.87 |
| *SW864* | 13 | 43.1 | 5 | 0.72 | 0.77 |
| *S0068* | 13 | 62.2 | 9 | 0.60 | 0.70 |
| *SW398* | 13 | 79.3 | 6 | 0.62 | 0.64 |
| *SW2440* | 13 | 102.2 | 6 | 0.84 | 0.84 |
| *S0291* | 13 | 126.2 | 8 | 0.81 | 0.69 |

## Results and discussion

The results of the genomic analyses are presented for each of the four chromosomes in Table 2 and described and discussed as follows:

**Table 2** Evidence for quantitative trait loci (QTL) for AutoFOM (AF) grading characteristics, carcass cuts, growth, feed intake and chemical body composition or deposition.

| SSC | Trait | *F*-ratio | Pos[1] | %Var[2] | a ± SE[3] | d ± SE[3] |
|---|---|---|---|---|---|---|
| 1 | Entire loin weight (kg) | 6.92** | 119 | 3.7 | 0.04 ± 0.06 | −0.30 ± 0.08 |
| 1 | Entire neck weight (kg) | 6.63* | 29 | 3.7 | −0.07 ± 0.04 | −0.22 ± 0.07 |
| 1 | Jowl weight (kg) | 8.25** | 101 | 4.7 | −0.05 ± 0.02 | −0.12 ± 0.04 |
| 1 | External loin fat weight (kg) | 6.49* | 119 | 3.6 | −0.03 ± 0.05 | −0.25 ± 0.07 |
| 1 | AF average fat thickness (cm) | 6.50* | 87 | 3.5 | −1.03 ± 0.36 | −1.16 ± 0.55 |
| 1 | AF belly weight (kg) | 12.19*** | 83 | 6.9 | −0.17 ± 0.04 | −0.15 ± 0.06 |
| 1 | DG, 30–60 kg (kg) | 5.36* | 101 | 2.7 | −0.026 ± 0.01 | 0.031 ± 0.015 |
| 1 | DG, 90–120 kg (kg) | 6.56* | 115 | 3.5 | −0.036 ± 0.011 | −0.025 ± 0.017 |
| 1 | PAR, 30–60 kg (kg) | 6.25* | 100 | 3.5 | −0.005 ± 0.002 | 0.005 ± 0.002 |
| 1 | PAR, 90–120 kg (kg) | 7.55** | 114 | 4.4 | −0.006 ± 0.002 | −0.005 ± 0.003 |
| 6 | Average back fat thickness (cm) | 7.59** | 160 | 4.2 | −0.11 ± 0.04 | 0.16 ± 0.06 |
| 6 | Fat area on m.l.t.l.[4] ($cm^2$) | 7.50** | 157 | 4.2 | −0.71 ± 0.49 | 2.90 ± 0.81 |
| 6 | Back fat depth (FOM device, cm) | 6.44* | 87 | 3.5 | −1.43 ± 0.47 | 1.39 ± 0.71 |
| 6 | Thinnest fat measure[4] (cm) | 7.62** | 154 | 4.2 | −0.10 ± 0.04 | 0.23 ± 0.07 |
| 6 | Intramuscular fat content (%) | 7.83** | 138 | 4.4 | −0.07 ± 0.05 | 0.32 ± 0.08 |
| 6 | Side fat thickness[4] (cm) | 7.28** | 84 | 4.0 | −0.22 ± 0.07 | 0.22 ± 0.10 |
| 6 | Belly weight (kg) | 6.01* | 86 | 3.3 | −0.19 ± 0.06 | 0.13 ± 0.09 |
| 6 | External loin fat weight (kg) | 7.20** | 140 | 4.0 | −0.09 ± 0.06 | 0.33 ± 0.09 |
| 6 | Loin weight without ext. fat (kg) | 5.96* | 83 | 3.3 | 0.14 ± 0.05 | −0.15 ± 0.07 |
| 6 | Ham weight without ext. fat (kg) | 9.35*** | 135 | 5.3 | 0.22 ± 0.09 | −0.56 ± 0.15 |
| 6 | Entire ham weight (kg) | 8.9** | 51 | 5.1 | 0.26 ± 0.07 | 0.30 ± 0.13 |
| 6 | External shoulder fat weight (kg) | 6.42* | 84 | 3.6 | −0.08 ± 0.02 | 0.05 ± 0.03 |
| 6 | Shoulder wt. without ext. fat (kg) | 6.26* | 155 | 3.5 | 0.09 ± 0.05 | −0.23 ± 0.08 |
| 6 | Loin eye area m.l.t.l.[4] ($cm^2$) | 7.44** | 90 | 4.1 | 2.03 ± 0.60 | −1.83 ± 0.94 |
| 6 | Hind hock weight (kg) | 7.47** | 31 | 4.2 | 0.004 ± 0.013 | 0.09 ± 0.02 |
| 6 | AF average fat thickness (cm) | 8.34** | 114 | 4.7 | −0.55 ± 0.42 | 2.41 ± 0.64 |
| 6 | AF entire loin weight (kg) | 5.53* | 121 | 2.9 | −0.06 ± 0.03 | −0.10 ± 0.04 |
| 6 | AF entire ham weight (kg) | 5.80* | 110 | 3.1 | −0.03 ± 0.07 | −0.35 ± 0.10 |
| 6 | AF ham lean-meat weight (kg) | 5.52* | 117 | 2.9 | −0.01 ± 0.09 | −0.42 ± 0.13 |
| 6 | AF entire shoulder weight (kg) | 8.11** | 122 | 4.5 | −0.04 ± 0.03 | −0.16 ± 0.04 |
| 6 | AF shoulder lean-meat weight (kg) | 7.47** | 0 | 4.1 | 0.08 ± 0.04 | −0.21 ± 0.06 |
| 6 | Fat cuts percentage (%) | 11.70*** | 85 | 6.9 | −0.39 ± 0.09 | 0.34 ± 0.14 |
| 6 | Loin and ham lean meat% (%) | 8.91** | 82 | 5.1 | 0.32 ± 0.09 | −0.25 ± 0.13 |
| 6 | Protein cont. $FFS_{EB}$, 30 kg (%) | 5.99* | 42 | 3.3 | 0.006 ± 0.034 | −0.18 ± 0.05 |
| 6 | Protein cont. $FFS_{EB}$, 60 kg (%) | 6.17* | 84 | 3.4 | −0.06 ± 0.03 | 0.14 ± 0.05 |
| 6 | Protein cont. empty body, 30 kg (%) | 5.84* | 42 | 4.3 | −0.001 ± 0.004 | −0.02 ± 0.01 |
| 6 | Protein cont. empty body, 60 kg (%) | 6.17* | 84 | 3.9 | 0.007 ± 0.004 | −0.019 ± 0.007 |
| 6 | Lipid cont. empty body, 30 kg (%) | 5.69* | 42 | 3.1 | 0.06 ± 0.18 | −0.97 ± 0.29 |
| 6 | Lipid cont. empty body, 60 kg (%) | 6.15* | 84 | 3.4 | −0.31 ± 0.16 | 0.67 ± 0.23 |
| 6 | DFI, 60–90 kg (kg) | 8.99*** | 138 | 5.1 | −0.025 ± 0.03 | 0.205 ± 0.049 |
| 6 | DFI, 90–120 kg (kg) | 5.6* | 130 | 3.0 | 0.012 ± 0.032 | 0.164 ± 0.049 |
| 13 | Loin and ham lean meat% (%) | 5.72* | 69 | 3.1 | 0.26 ± 0.10 | 0.23 ± 0.14 |
| 13 | Loin weight without ext. fat (kg) | 8.53*** | 71 | 4.9 | 0.19 ± 0.06 | 0.16 ± 0.08 |
| 13 | PAR, 60–90 kg (kg) | 5.46* | 0 | 3.0 | −0.006 ± 0.002 | 0.001 ± 0.003 |
| 13 | FCR, 60–90 kg (kg:kg) | 6.56* | 0 | 3.6 | 0.108 ± 0.031 | −0.027 ± 0.045 |

PAR, protein accretion rate; DG, daily gain; FOM, Fat-o-Meter; DFI, daily feed intake; FCR, food conversion ratio calculated as feed intake divided by gain; m.l.t.l., musculus longissimus thoracis et lumborum; $FFS_{EB}$, fat-free substance of the empty body.

*, ** and *** implies significance at the 5%, 1% or 0.1% chromosome-wise levels respectively.

[1]Positions of the QTL in cM.

[2]Percentages of $F_2$ variance explained by the QTL.

[3]Estimated additive (a) and dominance (d) effects and their standard errors (SE).

[4]Measured at the 13th/14th rib interface.

## Chromosome 1

As shown in Table 1, the number of alleles for the 10 markers on SSC1 ranged between four (*SW1332*, *SW1851*) and eight (*SW1514*, *SW1515*). Observed heterozygosity in $F_1$-generation parents ranged between 0.58 (*SW1311*) and 0.90 (*SW1828*). Average observed heterozygosity was 0.77 for SSC1. QTL were detected for belly weight and average fat thickness (as measured by the AutoFOM carcass grading system) at 83 and 87 cM, close to the marker *SWR982*. For AutoFOM belly weight, the QTL was significant at the 0.1% chromosome-wise level (Fig. 1). Piétrain alleles tended to be associated with lower belly weight and with thinner average fat thickness at the QTL on SSC1. Heterozygous pigs showed smaller bellies and thinner back fat as indicated by negative estimates for the dominance coefficients (Table 2).

The AutoFOM device is relatively new for carcass grading of pigs so that information about QTL associated with these traits is presently not available in the literature. However, several QTL have been reported for fatness on SSC1 (De Koning *et al.* 1999; Nezer *et al.* 2002; Varona *et al.* 2002; Geldermann *et al.* 2003). The *melanocortin-4 receptor* (*MC4R*) locus is located close to *SWR982* (86 cM) on SSC1 and is significantly associated with growth and fatness (Kim *et al.* 2000; Park *et al.* 2002). This receptor is implicated in mediating the effect of leptin, which is a protein secreted from white adipocytes and influences energy metabolism and lipid accretion (Ramsey 2001). Close to this region, Malek *et al.* (2001) reported QTL for last rib and lumbar back fat thickness; Nezer *et al.* (2002) found a QTL for back fat thickness; and Geldermann *et al.* (2003) detected a QTL for external fat of shoulder. Bidanel & Rothschild (2002) pointed out that *MC4R* is significantly associated with 5–8% differences in back fat.

Significant QTL were detected at 119 cM (close to *SW1828*) for the weights of the carcass cuts entire loin and external loin fat, explaining 4.2% and 3.6% of phenotypic variance respectively (Table 2). Again, Piétrain alleles and heterozygotes showed lesser fat weight. For loin fat weight, Bidanel & Rothschild (2002) and Beeckmann *et al.* (2003) also reported a QTL distally located on SSC1, whereas the significant QTL found for entire neck weight at 29 cM (close to *SW1332*) is not reported in the literature. For weight of the jowl, a significant QTL at the 1% significance level was detected at 101 cM (close to *SW1311*). This QTL explained 4.7% of phenotypic variance. Milan *et al.* (2002) detected a significant QTL on SSC1 for head weight, which is an indicator of skeletal development and should be closely associated with jowl weight. The QTL for head weight was detected next to *S0113* (80.5 cM) close to the QTL for jowl weight in this study.

Four QTL for growth traits were detected on SSC1, explaining between 2.7% and 4.4% of the phenotypic variance. All these QTL were located between the markers *SW1311–SW1828* at 100–115 cM. However, the detected QTL affecting daily gain and protein accretion rates were only significant in the weight ranges from 30 to 60 kg and 90 to 120 kg. The QTL for protein accretion rate between 90 and 120 kg was significant at the 1% level. Piétrain alleles decreased daily protein accretion rates, which is consistent with the lower level of daily gain of purebred Piétrain pigs. The QTL associated with protein accretion rate seems to mainly regulate growth, because no QTL associated with protein or lipid content were found on SSC1. In addition, the larger phenotypic variance explained by the QTL for protein accretion compared with those of daily gain suggests that this QTL is mainly associated with lean growth.

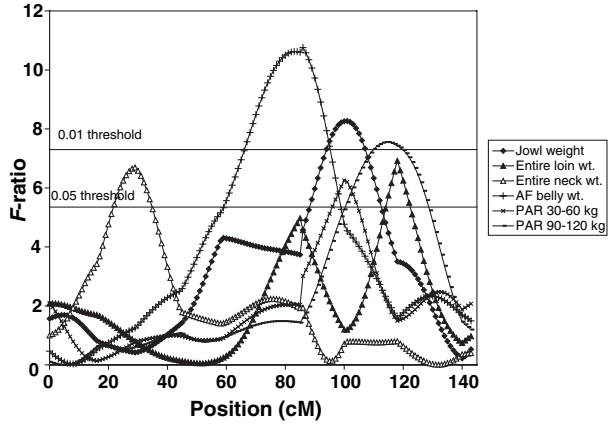


**Figure 1** *F*-ratio curves for evidence of quantitative trait loci for carcass, AutoFOM (AF) and growth traits on SSC1. Horizontal lines indicate the chromosome-wise significance levels. PAR, protein accretion rate.

## Chromosome 6

Nine markers on SSC6 were used, with 5–15 alleles for markers *S0087* and *SW1841* respectively. Observed heterozygosity was high, ranging between 0.71 (*MP35*) and 0.98 (*SW1841*). The mutation at the *RYR1* locus is associated with malignant hyperthermia syndrome (Fujii *et al.* 1991) and is located on SSC6 within the *S0087–SW122* interval at 63–83 cM (Rohrer *et al.* 1996). According to Hanset *et al.* (1995), this mutation accounts for up to 100% of phenotypic differences between Piétrain and Large White. Because phenotypic data were adjusted for the *RYR1* genotypes in the present study, QTL were not detected for traits associated with stress syndrome such as conductivity and pH. However, without adjustment for the *RYR1* genotypes, a QTL analysis for conductivity 24 h post-mortem was detected, indicating a major QTL located in the immediate vicinity of *RYR1* with an *F*-ratio of 30.6 that explained 16.4% of phenotypic variance (data not shown). Even with adjustment for *RYR1* genotypes, significant evidence was found for QTL close to *RYR1* for several fatness traits including side fat thickness (13th/14th rib interface),

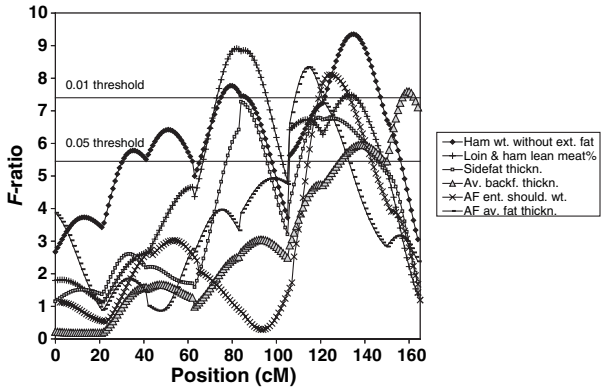


**Figure 2** *F*-ratio curves for evidence of quantitative trait loci for carcass and AutoFOM (AF) traits on SSC6. Horizontal lines indicate the chromosome-wise significance levels.

external shoulder fat weight, belly weight and loin fat depth (FOM device). In this region, a QTL explaining 6.9% of phenotypic variance was found for percentage of fat of carcass cuts (neck, shoulder, loin, ham and belly fat) on body weight. Furthermore, significant evidence was found for loin weight without external fat at 83 cM, loin eye area on musculus longissimus thoracis et lumborum (m.l.t.l.; 13th/14th rib interface) at 90 cM and loin and ham lean-meat percentage at 82 cM (Fig. 2) explaining 3.3%, 4.1% and 5.1% of phenotypic variance respectively. Generally, Piétrain alleles decreased fat and increased lean-meat measurements. These findings indicate that additional loci closely linked to the *RYR1* locus are involved in the phenotypic variation in these traits. In agreement with these results, Yue *et al.* (2003a) detected several QTL for fatness (e.g. external shoulder, back and ham fat weight, loin fat depth) and lean-meat traits (e.g. shoulder, loin and ham lean-meat weight, lean-meat area) in a Meishan × Piétrain resource family. Grindflek *et al.* (2001) found a muscling QTL close to *RYR1*. Varona *et al.* (2002) detected a QTL for belly bacon weight close to the region of the belly weight QTL in the present study.

For AutoFOM carcass characteristics, QTL were detected within the *S0228–SW1881* interval at 105–121 cM. Additive effects of these QTL were small, whereas overdominance was detected for all traits. A QTL for shoulder lean-meat weight was detected at a different location (0 cM; close to marker *MP35*) than those of the other AutoFOM characteristics. Óvilo *et al.* (2000) and Varona *et al.* (2002) detected significant QTL for several fat thickness traits and intramuscular fat content as well as for muscle area on loin eye located between the markers *S0228–SW1881* (105–121 cM).

Similar to De Koning *et al.* (1999) and Malek *et al.* (2001), who detected QTL for back fat thickness more distally, a number of QTL for fatness traits such as average back fat thickness, fat area on musculus longissimus thoracis et lumborum (13th/14th rib interface), fat degree B, intramuscular fat content (IMF) and external loin fat weight were detected on SSC6 close to *SW322* (150 cM), explaining up to 4.2% of phenotypic variance. At all QTL, Piétrain alleles were associated with lower fatness and lower intramuscular fat content, whereas the dominance effects were unfavourable for these traits. Furthermore, a highly significant QTL was detected for the weight of ham without external fat within the *SW1881–SW322* interval at 121–150 cM. For entire ham and hind hock weight, QTL were detected within the *SW2406–SW1841* interval at 21–42 cM. The estimated positive additive effects indicate an increase in amount of lean ham weight because of Piétrain alleles.

Although results are reported in the literature associating markers on SSC6 with growth, no QTL for daily gain, protein or lipid accretion rates were detected in the present study. However, QTL associated with protein and lipid content of the empty body were detected on SSC6 at 42 and 84 cM for target weight 30 and 60 kg respectively. Because these traits within a weight class are closely correlated, protein and lipid content of the empty body showed almost similar QTL profiles (Fig. 3). The QTL for protein content at 60 kg target weight were located close to *SW122* (83 cM) and explained 3.9% of phenotypic variance of chemical empty body composition in the $F_2$ generation. For chemical body composition at 30 kg body weight, the QTL showed significant dominance effects. Although these dominance effects were unfavourable for protein content of the fat-free substance they were slightly favourable for protein content of the empty body. This is because of the highly unfavourable dominance effects on lipid content as component of the empty body. At 60 kg body weight, there was a tendency that Piétrain alleles increased the empty body protein content whereas these alleles reduced protein content of the fat free substance. At this target weight, Piétrain alleles decreased the empty body lipid content as expected. Dominance effects were unfavourable and resulted in lower empty body protein and higher empty body lipid content at 60 kg body weight. For these QTL associated with chemical body composition, dominance effects were substantially higher than additive effects, thereby indicating overdominance. The QTL detected for body composition at 60 kg body

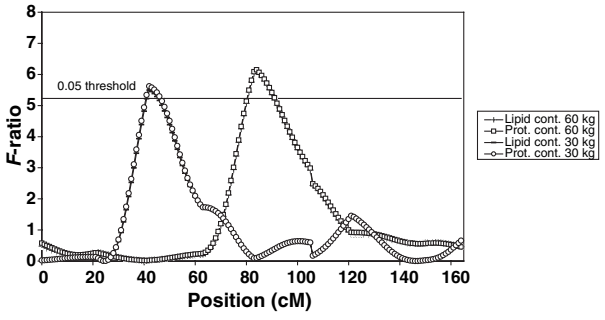


**Figure 3** *F*-ratio curves for evidence of quantitative trait loci for protein and lipid content of the empty body at 60 kg liveweight on SSC6. Horizontal line indicates the chromosome-wise significance level.

weight correspond to a number of QTL reported for physical body composition in the region of the *RYR1* locus (e.g. Grindflek *et al.* 2001; Yue *et al.* 2003a).

For daily feed consumption in the weight ranges 60–90 and 90–120 kg, two significant QTL were detected within the *SW1881–SW322* marker interval at 121–150 cM. These QTL accounted for 5.1% and 3.0% of phenotypic variance respectively. Additive effects were small, whereas overdominance effects substantially increased daily feed consumption. QTL for feed consumption on SSC6 have not been reported in literature.

### Chromosome 7

The number of alleles of the markers on SSC7 ranged between three (*SWR773*) and nine (*SWR2036*) and were generally lower compared with the other three chromosomes analysed in this study. Moreover, the observed heterozygosity and the average information contents of additive and especially of the dominant coefficients were lower in comparison to the other analysed chromosomes.

Significant QTL for body composition (especially fatness), growth, and feed intake were not detected on SSC7 in the present study. Numerous QTL have been found for these traits, usually based on crosses between obese and commercial lines. In particular, a highly significant QTL for back fat traits on SSC7 was detected at the *swine leukocyte antigen* (*SLA*) locus (Rothschild *et al.* 1995; Rohrer 2000; Wada *et al.* 2000; Bidanel *et al.* 2001). As suggested by Nezer *et al.* (2002), this lack of QTL in our study may be due to use of crosses of commercial lines. They used crosses between Piétrain × Large White and also did not detect QTL for back fat thickness on SSC7. Using a Duroc × Norwegian Landrace intercross, Grindflek *et al.* (2001) found no QTL for back fat thickness on SSC7 but identified a QTL for fat-smell intensity at the *SLA* complex. Moreover, Evans *et al.* (2003) could not confirm previously detected QTL for back fat thickness on SSC7 in a commercial pig population. However, they confirmed a QTL for growth rate on SSC7 in Hampshire. In contrast, Nagamine *et al.* (2003) confirmed a segregating QTL affecting back fat in a region on SSC7 in several commercial lines.

### Chromosome 13

As shown in Table 1, the number of alleles for markers on SSC13 ranged between five (*SW864*) and 11 (*SW1407*), and information contents generally exceeded 0.6. Their lowest observed heterozygosity was 0.63. Several researchers reported evidence for fatness QTL on SSC13 in exotic line crosses (Rohrer & Keele 1998; Yu *et al.* 1999; Bidanel *et al.* 2001) as well as in commercial line crosses (Malek *et al.* 2001; Nezer *et al.* 2002). As represented in Fig. 4, there was significant evidence of QTL for loin lean-meat weight and percentage of loin and ham lean meat of

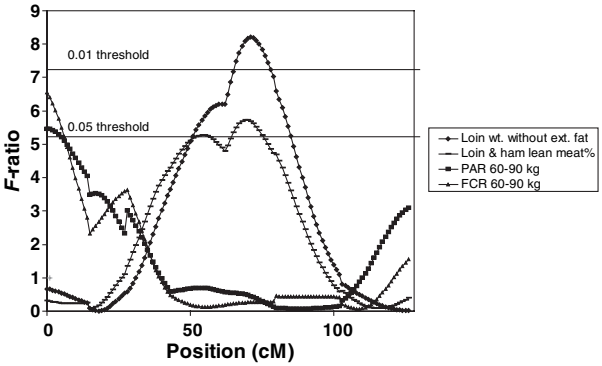


**Figure 4** *F*-ratio curves for evidence of quantitative trait loci for the traits on SSC13. Horizontal lines indicate the chromosome-wise significance levels. PAR, protein accretion rate; FCR, food conversion ratio.

body weight at slaughter day within the *S0068–SW398* interval at 62–79 cM. In agreement with these findings, Yue *et al.* (2003b) detected a QTL for ham and shoulder lean-meat weight located at *S0068* in a Wild Boar × Meishan cross. Malek *et al.* (2001) found a QTL showing overdominance that was associated with last rib back fat and located within the *SW344–S0068* (35–62 cM) interval. In general, Piétrain alleles were associated with higher weight of loin lean meat and with higher percentages of ham and loin lean meat.

Concerning growth and feed conversion, two significant QTL at the 5% chromosome-wise level were detected on SSC13. A QTL for daily protein accretion rate between 60 and 90 kg body weight was detected at the *S0282* marker position (0 cM; Fig. 4) and it explained 3.0% of phenotypic variance in the $F_2$ generation. Piétrain alleles resulted in lower rates of daily gain and protein accretion, whereas dominance effects increased these traits. Several reported QTL for daily gain on SSC13 were based on crosses with obese breeds. Yu *et al.* (1999) detected QTL for daily gain at different stages of growth at *PIT1*; De Koning *et al.* (2001) detected QTL for growth between 25 to 90 kg body weight within the *S0076–S0068* interval; and Yue *et al.* (2003) found QTL for early growth distally on SSC13. Using commercial founder lines, Malek *et al.* (2001) did not detect QTL for growth traits on SSC13.

A QTL for feed conversion ratio during growth from 60 to 90 kg body weight was detected at the same marker position (*S0282*) as for protein accretion rate (Fig. 4). Alleles from Piétrain resulted in unfavourable higher feed conversion ratios. QTL for feed efficiency on SSC13 have not been reported in the literature.

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## Supplementary Material

The following supplementary material is available for this article online from http://www.blackwell-synergy.com:

**Table S1** Means and standard deviations (SD) of carcass characteristics measured on pigs of the $F_2$ generation.

**Table S2** Means and standard deviations (SD) of chemical body composition, accretion rates, daily gain, daily feed intake and food conversion ratio measured on pigs of the $F_2$ generation.