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Quantitative trait loci for chemical body composition traits in pigs and their positional associations with body tissues, growth and feed intake

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Summary

In this study, quantitative trait loci (QTL) for chemical and physical body composition, growth and feed intake in pigs were identified in a three-generation full-sib population, developed by crossing Pietrain sires with a commercial dam line. Phenotypic data from 315 F_2 animals were available for protein and lipid deposition measured in live animals by the deuterium dilution technique at 30-, 60-, 90-, 120- and 140-kg body weight. At 140-kg body weight, carcass characteristics were measured by the AutoFOM grading system and after dissection. Three hundred and eighty-six animals from 49 families were genotyped for 51 molecular markers covering chromosomes SSC2, SSC4, SSC8, SSC9, SSC10 and SSC14. Novel QTL for protein (lipid) content at 60-kg body weight and protein (lipid) accretion from 120 to 140 kg were detected on SSC9 near several previously detected QTL for lean and fat tissue in neck, shoulder and ham cuts. Another QTL for lipid accretion was found on SSC8, closely associated with a QTL for intramuscular fat content. QTL for daily feed intake were detected on SSC2 and SSC10. The favourable allele of a QTL for food conversion ratio (FCR) on SSC2 was associated with alleles for increased lean tissue and decreased fat tissue. Because no QTL for growth rate were found in the region, the QTL for FCR is most likely due to a change in body composition. These QTL provide insights into the genomic regulation of chemical or physical body composition and its association with feed intake, feed efficiency and growth.

Keywords carcass characteristics, chemical body composition, feed intake, genomic markers, growth, pig, quantitative trait loci.

Introduction

At present, a large number of QTL in pigs have been detected for physical body composition traits, which are associated with lean and fat tissue characteristics (e.g. Bidanel *et al.* 2001; Milan *et al.* 2002; Geldermann *et al.* 2003). In contrast, QTL associated with protein and lipid deposition and their change during growth have only been reported in one study analysing chromosomes 1, 6, 7 and 13 (Mohrmann *et al.* 2006a). Knowledge of the deposition rates of chemical components is necessary to accurately estimate nutritional requirements of pigs during growth, to determine selection objectives for optimal development of body tissue growth and feed intake capacity and more generally, to provide parameters of a pig growth model that can be used to improve the efficiency of the entire pig production system (e.g. Schinckel & de Lange 1996; Knap *et al.* 2003; de Lange *et al.* 2003). Optimizing the efficiency of nutrient utilization will decrease the cost of food per unit gain, as feed is one of the largest cost factors involved in pig production (Quiniou & Noblet 1995; Quiniou *et al.* 1999). Additionally, the market price of the final product is based on carcass quality. Therefore, the association between chemical and physical body composition is of great economic interest.

Most QTL studies have been based on crosses of domestic breeds with the Meishan, Wild Boar or Iberian breed (e.g.

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Andersson-Eklund *et al.* 1998; Rohrer & Keele 1998a,b; Rohrer 2000). Favourable QTL alleles found in these less-improved breeds cannot be directly exploited within pig breeding due to the poor performance of these exotic breeds for traits of commercial interest. Alternatively, there is the potential to integrate QTL identified in commercial populations into existing pig breeding programmes. Information in the literature indicates that pig chromosomes 2, 4, 8, 9, 10 and 14 are associated with lean and fat tissue growth (e.g. Andersson *et al.* 1994; Malek *et al.* 2001a,b; Geldermann *et al.* 2003). These chromosomes were chosen in this study for analysis of physical and chemical body composition as well as feed intake, food conversion ratio (FCR) and growth rate in commercial breeds.

Materials and methods

Design and data

QTL mapping was based on data from a three-generation full-sib design. The resource family was created by mating seven unrelated Pietrain grandsires to 16 unrelated grandams from a crossbred dam line (Large White × Landrace × Leicoma). Pietrain sires were all heterozygous (*Nn*) at the *ryanodine receptor 1* (*RYR1*) locus. Eight F_1 boars and 40 F_1 sows were mated to produce 315 F_2 pigs of 49 families across 2 litters. Of these F_2 animals, 48 gilts and 46 barrows were housed individually in straw-bedded pens. These pigs were fed manually, and feed consumption was recorded weekly. The remaining 117 gilts and 104 barrows were housed in straw-bedded pens in groups of up to 15 pigs of both sexes. Food was supplied to these pigs by an electronic feeding station (ACEMA 48), which recorded feed consumption at each visit. Pigs were provided with one of three pelleted diets containing 13.8 MJ ME/kg and 1.2% lysine, 13.8 MJ ME/kg and 1.1% lysine or 13.4 MJ ME/kg and 1.0% lysine for weight ranges 30–60, 60–90 and 90–140 kg body weight respectively. Pigs reached maximal protein deposition because of *ad libtum* access to diets, which were formulated slightly above requirement. For a more detailed description of the management of this project, see Landgraf *et al.* (2006a,b) and Mohrmann *et al.* (2006a,b).

Physical body composition

Phenotypic measurements of physical body composition were collected from pigs slaughtered in a commercial abattoir at 140-kg body weight. Measurements of valuable carcass cuts were obtained using the AutoFOM device, which uses an automatic ultrasound scanning technique to produce a three-dimensional image of the pig (Brondum *et al.* 1998). Using this device, measurements were obtained for average fat thickness, belly weight, lean content, lean content of the belly and weights of entire and trimmed shoulder, loin and ham without bones. The right carcass side of each pig was then dissected into primal carcass cuts neck, shoulder, loin, ham and belly weights. The former four carcass cuts were further dissected into lean and fat tissue. Weights of jowl, thick rib, flank, front as well as hind hock, tail and claw were recorded. Additional measurements were obtained from the cold left carcass side, including carcass length; side fat thickness; loin eye area, fat area and thinnest fat measure (fat degree B) at the 13th/14th rib interface; fat content and area of the belly. Additional information about the dissection of carcasses is presented by Landgraf *et al.* (2006a).

Chemical body composition

Protein, lipid and ash content of the empty body was determined at target body weights of 30, 60, 90, 120 and 140 kg using deuterium dilution technique, an *in vivo* method of determining chemical body composition based on body water. The accuracy of this technique has been verified in previous studies using magnetic resonance imaging on live animals (Mohrmann *et al.* 2006b) and chemical analysis of serially slaughtered animals (Landgraf *et al.* 2006b). The deuterium dilution method determined the empty body water content, from which the percentage of fat-free substance of the empty body was estimated. Protein and ash contents of the empty body were estimated based on the percentage of fat-free substance. Lipid content was the difference of the fat-free content from 1.0. The equations for estimating these chemical components were developed in the study of Landgraf *et al.* (2006b) using the same data that was analysed here. Accretion rates of protein and lipid were calculated as the difference between lipid or protein composition at two consecutive target weights divided by days of growth between target weights. Protein content of loin and intramuscular fat content (IMF) were measured in the musculus longissimus thoracis et lumborum using near-infrared reflectance spectroscopy. Mean values and standard deviations of traits analysed in the present study are shown in Tables S1 & S2.

Genotypic data

Blood samples were collected from F_0, F_1 and F_2 animals from the vena jugularis, and genomic DNA was isolated. All animals were genotyped for 51 informative microsatellite markers selected from the published USDA linkage map (http://www.marc.usda.gov), of which 9, 9, 8, 9, 9 and 7 genomic markers were located on SSC2, SSC4, SSC8, SSC9, SSC10 and SSC14 respectively (Table S3). Average distance between markers was 16.5, 16.3, 18.4, 17.3, 16.0 and 17.4 cM and the largest gap between markers was 25.2, 26.5, 23.1, 21.7, 20.8 and 23.6 cM on SSC2, SSC4, SSC8, SSC9, SSC10 and SSC14 respectively.

Statistical analysis

The QTL analysis was performed with QTL EXPRESS (http://qtl.cap.ed.ac.uk; Seaton *et al.* 2002) using line-cross least squares multi-marker regression interval mapping for outbred lines (Haley *et al.* 1994). In this analysis, the additive estimate is defined as half of the difference between pigs homozygous for alleles from the grandpaternal sire line and pigs homozygous for alleles from the grandmaternal dam line. A positive additive genetic value indicates that the allele originating from the grandpaternal sire line (Pietrain) showed a higher effect than the allele from the grandmaternal dam line and vice versa. The dominance effect is defined as deviation of heterozygous animals from the mean of both types of homozygous animals. A positive dominance value indicates an increase in the trait of interest as a result of a heterozygous genotype and vice versa. Moreover, traits were tested for QTL expressing paternal or maternal imprinting. Fixed effects of sex, ryanodine receptor genotype (halothane genotype) and batch were fitted in the model for all traits. The effect of housing was significant for feed intake and FCR traits. For carcass characteristics and chemical body composition, linear regression on body weight at slaughter (140 kg) and at each target weight respectively was included in the model. Protein and lipid accretion, daily gain (DG), feed intake and FCR were adjusted for the small differences between target and actual body weight at the start and end of the weight range. Traits were analysed individually and thresholds to determine chromosome-wide statistical significance levels were obtained by permutation (Churchill & Doerge 1994) under 10 000 iterations.

Results

In the genomic analysis, five QTL were identified for carcass characteristics, 13 for lean tissue characteristics, seven for fat tissue characteristics, seven for chemical body composition and deposition and two each for DG, daily feed intake (DFI) and FCR (Table 1). QTL with significant imprinting effects were identified for 32 traits, of which 19 traits showed novel QTL not previously detected using the additive and dominance model (Table 2).

Carcass characteristics (lean and fat)

QTL were identified for valuable carcass cuts on SSC8, SSC9 and SSC14. The QTL with the highest *F*-ratio significant at the 0.1% chromosome-wide level was identified on SSC8 for ham weight at 11.7 cM between *SW2410* and *SW905* and explained 7.2% of the phenotypic variance. The additive genetic effect of the allele originating from the Pietrain grandpaternal breed was associated with 351 g higher ham weight and heterozygous animals showed 340 g higher ham weight due to dominance effects. In a similar region (3.7 cM), a QTL was identified for hind hock weight; it explained 3.5% of the phenotypic variance, but showed only significant additive genetic effects.

QTL were detected on SSC9 between *SW2401* and *SW2571* for shoulder weight measured by the AutoFOM device (68 cM) and by dissection (65 cM), explaining 4.8% and 5.8% of the phenotypic variance respectively. The allele originating from the Pietrain founder breed showed higher shoulder weight. An additional QTL for shoulder weight measured by the AutoFOM system was detected on SSC14 at 64.4 cM between *SW342* and *SW1081*. In this case, the Pietrain allele was associated with decreased shoulder weight. Furthermore, two QTL reaching the 5% chromosome-wide significance level were detected for shoulder weight measured by dissection on SSC9 at 23 cM and by the AutoFOM system on SSC14 at 37.4 cM (not shown in Table 1).

Lean tissue characteristics

QTL for lean tissue characteristics were detected on SSC2, SSC4, SSC8, SSC9, SSC10 and SSC14. On SSC2, QTL were identified for carcass cuts loin, ham and shoulder without external fat explaining 3.7%, 4.3% and 3.8% of the phenotypic variance respectively. QTL for weights of trimmed carcass cuts loin and ham were located at 10 and 15 cM respectively, close to *SW2623*. The allele originating from Pietrain founder parents was associated with higher lean tissue weights of both carcass cuts. The QTL for trimmed shoulder weight was located in a different region at 92 cM, close to *SWR2157*. Heterozygous animals were associated with significantly lower lean meat of the shoulder.

On SSC4, a single QTL was identified for lean content measured by the AutoFOM system accounting for 3.6% of the phenotypic variance. Additive genetic effects at this QTL indicate that alleles from the grandpaternal Pietrain breed were associated with decreased lean content.

QTL were identified on SSC8 for loin lean meat measured by the AutoFOM carcass grading system (5.7 cM) and dissection (15.7 cM), ham lean meat (12.7 cM) and loin eye area (11.7 cM). These QTL explained 6.0%, 4.5%, 5.2% and 4.0% of the phenotypic variance respectively and were located in the same region as QTL for entire ham weight and hind hock weight between *SW2410* and *SW905* (Fig. 1). Dominance and additive effects for these QTL indicate that heterozygous animals and Pietrain alleles were associated with higher loin and ham lean meat weight and higher loin eye area. In a different region of SSC8 (37.7 cM), a QTL for protein content of loin was identified with additive effects only.

On SSC9, QTL were detected for lean meat of the shoulder and neck cuts close to *SW2571*, explaining 5.6% and 4.7% of phenotypic variance respectively. At these QTL, the favourable allele originated from the Pietrain founder population.

Table 1 Evidence for QTL for AutoFOM (AF) grading characteristics, carcass cuts, growth, feed intake and chemical body composition or deposition.

		Results of the present study					Other studies confirming the QTL
SSC	Trait	*F*-ratio	Pos[1]	% Var[2]	a ± SE[3]	d ± SE[3]	References[4]
Carcass characteristics (lean and fat)							
8	Hind hock weight (kg)	5.29*	3.7	3.5	**0.044 ± 0.014**	0.011 ± 0.025	–
8	Entire ham weight (kg)	11.43***	11.7	7.2	**0.351 ± 0.082**	**0.340 ± 0.149**	Beeckmann *et al.* (2003) and Geldermann *et al.* (2003)
9	Entire shoulder weight (kg)	9.03**	65	5.8	**0.182 ± 0.043**	0.002 ± 0.077	–
9	AF entire shoulder weight (kg)	7.53**	68	4.8	**0.099 ± 0.030**	**−0.113 ± 0.053**	–
14	AF entire shoulder weight (kg)	5.15*	64.4	3.3	**−0.100 ± 0.031**	0.055 ± 0.050	–
Lean tissue characteristics							
2	Loin weight without external fat (kg)	5.7*	10	3.7	**0.166 ± 0.051**	0.060 ± 0.077	Andersson-Eklund *et al.* (1998), Geldermann *et al.* (2003) and Lee *et al.* (2003)
2	Ham weight without external fat (kg)	6.66*	15	4.3	**0.333 ± 0.091**	−0.018 ± 0.149	
2	Shoulder weight without external fat (kg)	5.75*	92	3.8	0.014 ± 0.047	**−0.252 ± 0.074**	Geldermann *et al.* (2003) and Lee *et al.* (2003)
4	AF lean content (kg)	5.62*	33	3.6	**−1.213 ± 0.420**	−1.262 ± 0.737	Cepica *et al.* (2003b), Geldermann *et al.* (2003) and Edwards *et al.* (2006)
8	AF loin lean meat weight (kg)	9.59**	5.7	6.0	**0.089 ± 0.030**	**0.179 ± 0.055**	Beeckmann *et al.* (2003), Geldermann *et al.* (2003) and Andersson-Eklund *et al.* (1998)
8	Loin weight without external fat (kg)	6.96*	15.7	4.5	0.106 ± 0.054	**0.297 ± 0.093**	
8	Ham weight without external fat (kg)	8.02**	12.7	5.2	**0.304 ± 0.091**	**0.376 ± 0.163**	
8	Loin eye area m.l.t.l.[5] (cm^2)	6.21*	11.7	4.0	**1.734 ± 0.611**	**2.397 ± 1.105**	
8	Protein content of loin (%)	5.14*	37.7	3.3	**−0.212 ± 0.076**	0.210 ± 0.124	–
9	Shoulder weight without external fat (kg)	8.63**	73	5.6	**0.184 ± 0.044**	0.003 ± 0.075	–
9	Neck weight without external fat (kg)	7.13*	86	4.7	**0.115 ± 0.032**	−0.072 ± 0.053	
10	Protein content of loin (%)	6.17*	94	4.0	**−0.193 ± 0.072**	**−0.279 ± 0.120**	–
14	AF ham lean meat weight (kg)	6.24*	68.4	4.0	**−0.273 ± 0.083**	0.174 ± 0.128	Dragos-Wendrich *et al.* (2003) and Geldermann *et al.* (2003)
Fat tissue characteristics							
2	External neck fat weight (kg)	7.07*	6	4.6	**−0.089 ± 0.027**	−0.071 ± 0.041	de Koning *et al.* (2001), Milan *et al.* (2002) and Sanchez *et al.* (2006)
2	External ham fat weight (kg)	7.42**	11	4.8	**−0.128 ± 0.041**	**−0.133 ± 0.063**	
8	Intra muscular fat content (%)	5.19*	48.7	3.4	**0.129 ± 0.046**	−0.114 ± 0.069	Rohrer & Keele (1998a)
9	Fat area of belly (cm^2)	6.57*	30	4.3	−0.834 ± 0.573	**3.440 ± 1.047**	Rohrer & Keele (1998a)
9	External ham fat weight (kg)	6.81*	86	4.4	**−0.131 ± 0.036**	0.064 ± 0.060	Karlskov-Mortensen *et al.* (2006)
9	External shoulder fat weight (kg)	7.48**	86	4.9	**−0.047 ± 0.021**	**0.111 ± 0.034**	
14	AF average fat thickness (cm)	5.53*	69.4	3.6	**0.930 ± 0.391**	**−1.436 ± 0.599**	Malek *et al.* (2001a), Dragos-Wendrich *et al.* (2003) and Geldermann *et al.* (2003)
Chemical body composition and deposition							
8	LAR, 60–90 kg (kg/day)	5.42*	49.7	3.7	**0.015 ± 0.005**	0.005 ± 0.007	Rohrer & Keele (1998a), de Koning *et al.* (2001) and Malek *et al.* (2001a)
9	PAR, 120–140 kg (kg/day)	6.22*	92	4.3	−0.003 ± 0.003	**0.014 ± 0.004**	–
9	LAR, 120–140kg (kg/day)	5.37*	93	3.8	−0.017 ± 0.009	**0.042 ± 0.015**	–

Table 1 Continued.

SSC	Trait	Results of the present study					Other studies confirming the QTL
		F-ratio	Pos[1]	% Var[2]	a ± SE[3]	d ± SE[3]	References[4]
9	Protein cont empty body, 60 kg (%)	5.64*	115	3.7	0.002 ± 0.003	**0.018 ± 0.006**	–
9	Protein cont FFS_{EB}, 60 kg (%)	5.63*	116	3.7	−0.017 ± 0.029	**−0.161 ± 0.048**	–
9	Lipid cont empty body, 60 kg (%)	5.63*	115	3.7	−0.072 ± 0.142	**−0.785 ± 0.235**	–
10	PAR, 90–120 kg (kg/day)	5.25*	4	3.6	**−0.006 ± 0.002**	0.001 ± 0.003	–
Daily gain, feed intake and food conversion ratio							
2	FCR, 90–120 kg (kg feed/kg gain)	5.95*	3	3.9	**−0.143 ± 0.044**	−0.076 ± 0.068	–
2	DFI, 120–140 kg (kg/day)	6.59*	79	4.3	−0.062 ± 0.040	**0.214 ± 0.063**	Rohrer (2000) and Malek *et al.* (2001a)
4	FCR, 90–120 kg (kg feed/kg gain)	6.07*	20	4.0	**0.149 ± 0.043**	0.013 ± 0.074	–
9	DG, 120–140 kg (kg/day)	6.5*	89	4.2	−0.020 ± 0.015	**0.087 ± 0.025**	–
10	DFI, 60–90 kg (kg/day)	7.3**	44	4.7	**−0.108 ± 0.028**	0.011 ± 0.046	Knott *et al.* (1998)
10	DG, 90–120 kg (kg/day)	5.08*	4	3.3	**−0.037 ± 0.012**	0.000 ± 0.018	–

Values in bold represent significant additive or dominance effects.

m.l.t.l., musculus longissimus thoracis et lumborum; LAR, lipid accretion rate; PAR, protein accretion rate; FFS_{EB}, fat-free substance of the empty body; FCR, food conversion ratio calculated as kg feed/kg gain; DFI, daily feed intake; DG, daily gain.

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

[1]Positions of the QTL in cM.

[2]Percentages of F_2 variance explained by the QTL calculated as the proportion of residual sum of squares due to the QTL effect on the residual sum of squares excluding the QTL effect.

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

[4]References of other studies reporting QTL for similar traits in similar regions of the genome.

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

A QTL for protein content of loin was detected on SSC10, showing both additive and dominance effects. An additional QTL was detected for ham lean meat weight measured by the AutoFOM carcass grading system on SSC14 between *SW342* and *SW1081*. The Pietrain allele for this QTL was associated with lower ham lean meat weight.

Fat tissue characteristics

QTL were identified for fat tissue characteristics on SSC2, SSC8, SSC9 and SSC14. QTL were identified for external fat weights of ham and neck cuts explaining 4.8% and 4.6% of the phenotypic variance respectively in the same region of SSC2 as QTL identified for lean weights of loin and ham cuts. The allele originating from the Pietrain grandpaternal breed was associated with significantly less external fat in both cuts. A QTL was identified on SSC8 for IMF at 48.7 cM between *SWR1101* and *SW444*. The Pietrain allele at this QTL was associated with higher IMF. On SSC9, a QTL was identified for fat area of the belly at 30 cM, between *SW21* and *SW911* explaining 4.3% of the phenotypic variance. Heterozygous animals showed 3.44 cm^2 larger fat area of the belly. In a different region of SSC9 (86 cM) close to *S0019*, QTL were identified for external fat weights of ham and shoulder cuts explaining 4.4% and 4.9% of the phenotypic variance respectively. At these QTL, the Pietrain allele was associated with significantly less external fat in both cuts, but only the shoulder showed significantly more external fat in heterozygous animals. These QTL were in the same region as QTL for lean tissue characteristics.

An additional QTL reaching 5% chromosome-wide significance was identified for external fat weight of the shoulder at 12 cM on SSC9 (not shown in Table 1). A QTL was detected for average fat thickness measured by the AutoFOM device in the same region as QTL on SSC14 for shoulder weight and ham lean meat weight measured by the AutoFOM device. Heterozygous animals showed a dominance effect of 1.4-mm less average fat thickness, whereas the additive genetic effect of Pietrain allele yielded in 0.9-mm higher average fat thickness than that from the crossbred dam line.

Table 2 Evidence for QTL expressing imprinting effects on 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]	i ± SE[3]
Carcass characteristics (*lean and fat*)							
2	Entire ham weight[5] (kg)	4.44*	10	4.3	**0.165 ± 0.078**	−0.188 ± 0.116	**0.182 ± 0.070**
4	Thick rib[5] (kg)	5.27*	13	5.2	−0.025 ± 0.018	**−0.075 ± 0.031**	**0.059 ± 0.020**
9	Entire shoulder weight (kg)	7.33**	73	7.0	**0.159 ± 0.041**	0.052 ± 0.069	**0.099 ± 0.045**
10	Tail weight[5] (kg)	4.29*	88	4.2	0.014 ± 0.013	−0.001 ± 0.020	**0.040 ± 0.012**
14	AF entire shoulder weight (kg)	5.79**	73.4	5.5	**−0.086 ± 0.029**	0.041 ± 0.044	**0.081 ± 0.028**
Lean tissue characteristics							
2	AF shoulder lean meat weight[5] (kg)	8.36***	0	7.8	0.007 ± 0.034	−0.041 ± 0.050	**0.158 ± 0.032**
2	AF lean content[5] (%)	5.52*	0	5.3	0.590 ± 0.411	0.148 ± 0.604	**1.451 ± 0.387**
2	Loin eye area m.l.t.l.[4,5] (cm^2)	7.81***	0	7.3	0.749 ± 0.540	−0.281 ± 0.792	**2.316 ± 0.507**
2	Loin weight without external fat (kg)	11.01***	2	10.2	**0.153 ± 0.049**	−0.002 ± 0.074	**0.216 ± 0.046**
2	Ham weight without external fat (kg)	9.73***	10	9.0	**0.307 ± 0.083**	−0.074 ± 0.124	**0.297 ± 0.075**
8	AF lean content of belly[5] (%)	4.38*	1.7	4.2	0.453 ± 0.619	**3.300 ± 1.125**	**1.332 ± 0.655**
8	AF loin lean meat weight (kg)	7.78***	7.7	7.3	**0.090 ± 0.030**	**0.191 ± 0.056**	**0.061 ± 0.030**
9	Loin eye area m.l.t.l.[4,5] (cm^2)	5.25*	71	5.0	**1.049 ± 0.519**	−1.199 ± 0.908	**1.698 ± 0.579**
9	Shoulder weight without external fat (kg)	8.52***	73	8.1	**0.176 ± 0.044**	0.006 ± 0.074	**0.135 ± 0.048**
9	AF lean content[5] (%)	5.58**	115	5.3	0.493 ± 0.390	**1.846 ± 0.641**	**1.093 ± 0.411**
10	Shoulder weight without external fat[5] (kg)	4.46*	84	4.4	0.102 ± 0.052	−0.087 ± 0.086	**0.132 ± 0.048**
14	AF lean content of belly[5] (%)	5.4**	68.4	5.2	**−1.591 ± 0.580**	1.361 ± 0.901	**1.407 ± 0.562**
14	AF ham lean meat weight (kg)	6.19**	71.4	5.9	**−0.260 ± 0.078**	0.151 ± 0.116	**0.188 ± 0.076**
14	AF shoulder lean meat weight[5] (kg)	4.44*	75.4	4.3	**−0.090 ± 0.034**	0.060 ± 0.054	**0.081 ± 0.034**
Fat tissue characteristics							
2	External ham fat weight (kg)	11.28***	0	10.3	**−0.090 ± 0.038**	−0.008 ± 0.056	**−0.188 ± 0.036**
2	External loin fat weight[5] (kg)	6.63**	0	6.4	−0.064 ± 0.052	−0.036 ± 0.076	**−0.206 ± 0.049**
2	Thinnest fat measure[4,5] (cm)	8.54***	0	7.9	−0.067 ± 0.044	−0.009 ± 0.064	**−0.196 ± 0.041**
2	Fat area m.l.t.l.[4,5] (cm^2)	6.2**	0	5.9	−0.670 ± 0.486	−0.461 ± 0.713	**−1.824 ± 0.456**
2	Fat area of belly[5] (cm^2)	5.64**	0	5.5	−0.567 ± 0.556	0.264 ± 0.808	**−2.029 ± 0.517**
9	External loin fat weight[5] (kg)	7.62***	75	7.3	−0.080 ± 0.048	−0.007 ± 0.084	**−0.234 ± 0.054**
9	External ham fat weight (kg)	5.94**	86	5.7	**−0.132 ± 0.036**	0.061 ± 0.059	**−0.077 ± 0.038**
9	Fat area of belly (cm^2)	4.63*	87	4.6	**−1.217 ± 0.516**	−0.097 ± 0.843	**−1.587 ± 0.543**
9	Sidefat thickness[4,5] (cm)	6.12**	67	6.3	**−0.149 ± 0.067**	0.136 ± 0.122	**−0.238 ± 0.075**
10	External loin fat weight[5] (kg)	4.46*	0	4.4	−0.049 ± 0.050	−0.106 ± 0.080	**−0.153 ± 0.049**
14	AF average fat thickness (mm)	5.27*	69.4	5.1	**0.934 ± 0.389**	**−1.382 ± 0.596**	**−0.810 ± 0.377**
Chemical body composition and deposition							
9	LAR, 120–140 kg (kg/day)	5.4*	87	5.6	−0.018 ± 0.009	**0.036 ± 0.014**	**−0.023 ± 0.009**
Daily gain, feed intake and food conversion ratio							
9	DG, 120–140 kg (kg/day)	6.83**	86	6.5	−0.022 ± 0.015	**0.082 ± 0.025**	**−0.044 ± 0.016**

Values in bold represent significant additive, dominance or imprinting effects.

m.l.t.l., musculus longissimus thoracis et lumborum; LAR, lipid accretion rate; DG, daily gain.

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

[1]Positions of the QTL in cM.

[2]Percentages of F_2 variance explained by the QTL calculated as the proportion of residual sum of squares due to the QTL effect on the residual sum of squares excluding the QTL effect.

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

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

[5]New QTL only identified when the imprinting effect is included in the model.

Chemical body composition and deposition

QTL for protein accretion rate (PAR) from 90 to 120 kg was identified on SSC10. QTL for PAR for a later growth period (120–140 kg) was found on SSC9 at 92 cM explaining 4.3% of the phenotypic variance. In the same region of SSC9, a QTL for lipid accretion rate (LAR) was identified for the same growth period. These were located in the same

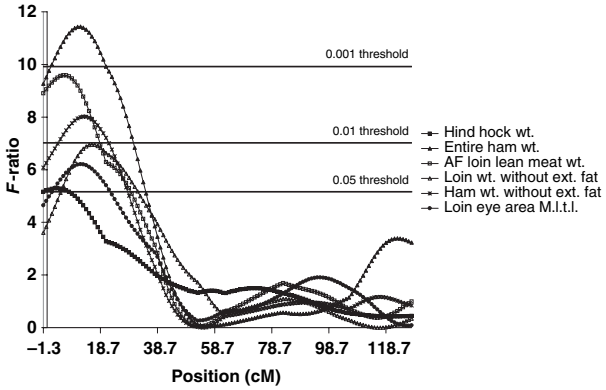

Figure 1 *F*-ratio curves for evidence of QTL for carcass, AutoFOM (AF) and lean traits on SSC8. Horizontal lines indicate the chromosome-wide significance levels.

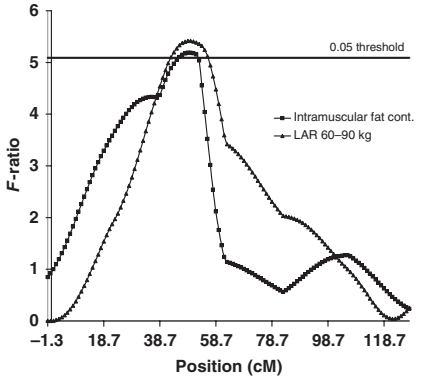

Figure 3 *F*-ratio curves for evidence of QTL for intramuscular fat content and lipid accretion 60–90 kg on SSC8. Horizontal line indicates the chromosome-wide significance level. LAR, lipid accretion rate.

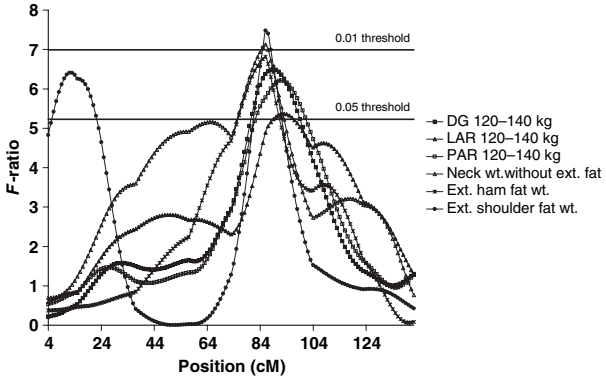

Figure 2 *F*-ratio curves for evidence of QTL for chemical body composition, lean and fat tissue on SSC9. Horizontal lines indicate the chromosome-wide significance levels. DG, daily gain; LAR, lipid accretion rate; PAR, protein accretion rate.

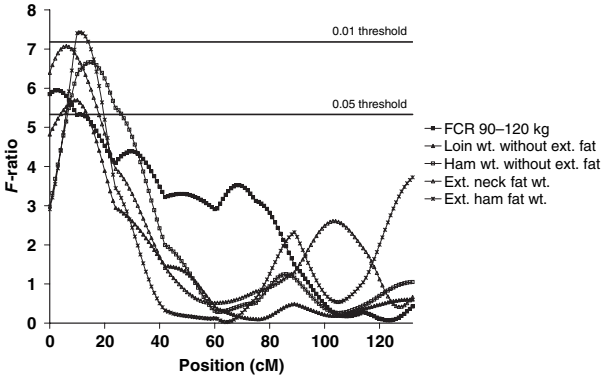

Figure 4 *F*-ratio curves as evidence of QTL for food conversion ratio, lean and fat tissue on SSC2. Horizontal lines indicate the chromosome-wide significance levels. FCR, food conversion ratio.

region of SSC9 as QTL for lean and fat tissue (Fig. 2). A second QTL for LAR for an earlier growth period (60–90 kg) was identified on SSC8 close to *SW444*, positioned very close to the QTL for IMF (Fig. 3). Alleles from the Pietrain breed are associated with higher LAR between 60 and 90 kg and decreased PAR from 90 to 120 kg. Heterozygous animals were associated with higher PAR and LAR at the later growth stage (120–140 kg). QTL for protein and lipid content of the empty body and protein content of the fat free substance at 60 kg were identified on SSC9 between *SW2093* and *SW174*. Heterozygous animals were associated with significantly higher protein content of the empty body and significantly lower protein content of the fat free substance and lipid content of the empty body at 60 kg.

Feed intake, daily gain and food conversion ratio

A QTL for FCR from 90 to 120 kg was detected on SSC2 in the same region as QTL for lean and fat tissue characteristics between *SWR2516* and *SW2623* (Fig. 4). The Pietrain allele was associated with higher feed efficiency, i.e. 143 g less food per 1-kg gain. An additional QTL for FCR from 90 to 120 kg was detected on SSC4 between *SW489* and *S0301*. In contrast, the Pietrain allele was associated with lower feed efficiency at this QTL. On SSC10, QTL for DFI for 60–90 kg was identified at the same position as *SW2195*, and for a later growth stage (120–140 kg) on SSC2 between *SW1370* and *SWR2157*. Pietrain alleles were associated with 108 g less DFI at 60–90 kg body weight and heterozygous animals were associated with 214 g higher DFI at heavier weights. A QTL for DG (120–140 kg) was detected on SSC9 in the same region as QTL for PAR, LAR, lean and fat tissue (Fig. 2). An additional QTL was detected on SSC10 for DG 90–120 kg at the same position as the QTL detected in this study for PAR at the same stage of growth.

Imprinting

For several carcass cuts, lean tissue and fat tissue characteristics, QTL expressing paternal imprinting effects were

identified on SSC2 close to *SWR2516* and *SW2623*. On SSC8, QTL expressing paternal imprinting were detected for lean tissue traits at 1.7 and 7.7 cM between *SW2140* and *SW905*. SSC9 harboured a large number of QTL showing paternal imprinting for carcass, lean tissue, fat tissue characteristics, LAR and DG between *SW2401* and *S0019* or 67 and 87 cM. An additional QTL showing paternal imprinting effects for lean content was identified in a different region of SSC9 (115 cM). Furthermore, QTL with paternal imprinting effects associated with carcass characteristics and lean tissue were detected on SSC10 close to *SW2043* and for fat tissue at the same position as *SW830*. For carcass characteristics, lean tissue and fat tissue measured by the AutoFOM device, QTL expressing maternal imprinting were detected on SSC14 close to *SW1081*.

Discussion

QTL for important carcass cuts have high economic value and were identified in the present study on SSC8, SSC9 and SSC14. The most significant QTL detected in this study at the 0.1% chromosome-wide level was for ham weight on SSC8, in agreement with other reports in the literature (cited in Table 1). QTL for shoulder weight identified in this study on SSC9 and SSC14 have not been reported before.

QTL have been reported for lean weights of carcass cuts shoulder, loin and neck as well as lean meat content measurements in the same region of SSC2 as the QTL detected for loin and ham lean meat weight in the present study (cited in Table 1). Additionally, QTL have been reported in this region for weight gain (Lee *et al.* 2003; Thomsen *et al.* 2004) as well as for carcass cuts and lean tissue characteristics around 0 cM (Milan *et al.* 2002; Nezer *et al.* 2002; Stearns *et al.* 2005; Sanchez *et al.* 2006). In a different region of SSC2, there is evidence in the literature (cited in Table 1) supporting the QTL identified in the present study for shoulder lean meat weight. Additional QTL have been reported in this region for weight gain (Malek *et al.* 2001a) and growth rate (Knott *et al.* 1998).

Numerous QTL were identified in this study between 5.7 and 15.7 cM on SSC8 for lean tissue characteristics in the same region as QTL were detected in the present study for ham weight and hind hock weight (Fig. 1). This is supported with reports in the literature (cited in Table 1) for loin, neck, ham and shoulder meat weights as well as bone/lean meat ratio in ham. A single QTL for protein content of loin was identified in a different region of SSC8 where no QTL have been reported for lean tissue. QTL were also identified in this study for shoulder and neck lean meat weight in a region of SSC9 where no QTL for lean tissue have been reported. However, one QTL has been reported for live weight at slaughter in this region (Cepica *et al.* 2003a). There is evidence in the literature (cited in Table 1) for QTL associated with lean meat of shoulder, loin, neck and ham in the same region of SSC14 as the QTL identified in the present study for ham lean meat weight measured by the AutoFOM device.

Surprisingly, in the present F_2 population only one QTL was detected for lean tissue on SSC4. In the literature, a large number of QTL have been reported for growth and fatness on SSC4 (e.g. Andersson *et al.* 1994; Marklund *et al.* 1999; Cepica *et al.* 2003b). Most QTL from these studies have been detected in F_2 populations at least partly derived from exotic breeds. Therefore, these QTL may not be segregating within the commercial lines used in the present study. Nonetheless, there is evidence in the literature (cited in Table 1) to support the location of the QTL identified in the present study on SSC4 for lean content.

QTL were identified for fat weights of carcass cuts neck and ham in the same region of SSC2 as QTL identified for lean meat weights of important carcass cuts in the present study. There is substantial evidence in the literature (cited in Table 1) for a QTL influencing fat tissue in this area. Additionally, a large number of QTL have been identified for backfat around 0 cM (e.g. Knott *et al.* 1998; Milan *et al.* 2002; Stearns *et al.* 2005). In a similar region, an imprinted QTL has been mapped to the *IGF2* locus with large effects on fat deposition and muscle mass (Nezer *et al.* 1999).

A novel QTL for IMF on SSC8 was identified in the present study. Although no QTL have been reported before for intramuscular fat in this genomic region, QTL have been reported for fat tissue (Table 1). The Pietrain allele for this QTL is associated with increased IMF. This may have implications for meat quality as IMF is a major factor affecting meat quality and consumer satisfaction.

QTL were identified in the present study for external fat weights of carcass cuts ham and shoulder in the same region as QTL identified for lean meat weights of neck and shoulder on SSC9 (Fig. 2). There is limited information supporting a QTL in this region for growth and fatness, however, a QTL has been reported for weight of fat in ham (cited in Table 1). In a different region of this chromosome, a QTL for fat area of the belly was identified in the present study in the same region as a QTL previously reported in the literature for leaf fat weight (cited in Table 1). Additionally, a QTL for average fat thickness measured by the AutoFOM system was identified in the present study in the same region of SSC14 as for ham lean meat weight and entire shoulder weight measured by the same device. There is much evidence in the literature for a QTL influencing fatness in this region of SSC14 (cited in Table 1). As discussed, several genomic regions contained QTL for both leanness and fatness (SSC2, SSC9 and SSC14), indicating their close relationships when animals are slaughtered at almost the same finishing weight.

From the present study, it was found that the allele originating from Pietrain founder parents was generally associated with increased lean and decreased fat as expected for a breed, which has been intensively selected for lean content. This was not the case for the QTL on SSC14 where the Pietrain allele (cryptic) was associated with decreased weight of ham lean meat and higher average fat thickness. It is also surprising to find that Pietrain alleles were associated with decreased lean content at the QTL identified on SSC4.

The present study is the first to report QTL for PAR on SSC9 and SSC10 for different stages of growth. In conjunction with the study by Mohrmann *et al.* (2006a), QTL for PAR have now been detected for all observed growth periods (30–60 kg, SSC1; 60–90 kg, SSC13; 90–120 kg, SSC1 and SSC10; 120–140 kg, SSC9). A novel QTL for LAR was identified in the present study on SSC9 for the same growth period as PAR around numerous QTL for lean and fat tissue growth (Fig. 2). A second QTL for LAR for a different growth stage was identified on SSC8 positioned at the same location as the QTL for IMF detected in this study (Fig. 3). QTL have been previously reported in this region for fat tissue, growth and length of small intestine, weight gain and carcass weight (cited in Table 1). Additionally, this study is the first to report QTL for protein and lipid content on SSC9. In a previous study by Mohrmann *et al.* (2006a), QTL for protein and lipid content at early stages of growth (30, 60 and 90 kg) were detected in a different genomic region (SSC6). As QTL for chemical body composition and accretion rates were identified in different genomic regions for different growth stages, it is likely that these components are regulated by more than one genomic region and regulated differently throughout growth.

QTL for FCR, DFI and DG were identified in the present study on SSC2, SSC4, SSC9 and SSC10. The QTL for FCR identified on SSC2 is probably caused by a change in body composition because it is positionally associated with QTL in which the Pietrain allele resulted in an increase in lean tissue and a decrease in fat tissue, and in this region, no growth QTL were detected (Fig. 4). In contrast, the QTL for FCR 60–90 kg on SSC13 identified in the previous study by Mohrmann *et al.* (2006a) is probably caused by a QTL associated with protein accretion, which was located at the same chromosomal position. No reports confirm the QTL identified in the present study for FCR on SSC4, although QTL have been reported in a different region of SSC4 for food consumption and FCR (Cepica *et al.* 2003b). QTL for early body weight and weight gain have been reported in the same genomic region as the QTL identified in the present study for DFI on SSC2 (cited in Table 1). QTL have not been reported for DFI in this region, however significant and suggestive QTL for this trait have been found in two other genomic regions by Houston *et al.* (2005), one of which was located at the same position as a QTL for DG reported by Lee *et al.* (2003). No QTL have been reported confirming the QTL for DFI on SSC10; however, a QTL has been reported for early growth rate in a similar region (cited in Table 1). At these QTL in the present study, Pietrain alleles are associated with lower DFI and heterozygous animals are associated with higher DFI. This is likely to be a result of long-term selection of the Pietrain breed for increased lean content and reduced backfat, known to have an unfavourable genetic association with feed intake (e.g. Roehe *et al.* 2003). At the QTL for DG on SSC9, heterozygous animals showed significantly higher DG (87 g/day) due to dominance, which is important because growth of purebred Pietrain are often restricted due to limited feed intake capacity (Roehe 2006). In contrast, the QTL identified on SSC10 for DG showed additive effects where Pietrain alleles are associated with decreased DG.

A large number of QTL with significant imprinting effects were identified in the present study, of which some QTL were not detected using an additive and dominance model. For several lean and fat tissue traits, QTL expressing paternal imprinting were identified in the same region of SSC2 where an imprinted QTL has been mapped to the paternally expressed *IGF2* locus (Nezer *et al.* 1999). Therefore, the *IGF2* locus is the most probable candidate for the effects detected in this study. A maternally expressed QTL for early growth has been detected close to the QTL showing paternal imprinting effects identified in the present study on SSC8 for lean tissue characteristics (de Koning *et al.* 2001). Milan *et al.* (2002) reported a QTL on SSC9 expressing imprinting for (ham + loin)% near the QTL showing paternal imprinting in the present study for carcass characteristics, lean tissue, fat tissue, LAR and DG. Additionally on SSC9, QTL with imprinting effects for liveweight, average DG and belly weight have been reported in the same region as the QTL for lean content showing paternal imprinting identified in the present study (Milan *et al.* 2002; Quintanilla *et al.* 2002). de Koning *et al.* (2001) found a paternally expressed QTL for early growth rate on SSC10 in the same region as the QTL showing paternal imprinting detected in the present study for tail weight and shoulder lean meat weight. Thomsen *et al.* (2004) reported maternally expressed QTL on SSC10 for fat tissue and meat quality traits and a paternally expressed QTL for lean tissue in the same region as the paternally expressed QTL detected in the present study for external loin fat weight. On SSC14, a paternally expressed QTL for growth was detected by de Koning *et al.* (2001) close to the QTL detected in the present study showing maternal imprinting effects for carcass, lean tissue and fat tissue characteristics. Additionally, Rohrer *et al.* (2005) identified paternally expressed QTL in this region for meat quality traits. Therefore, imprinting effects are likely to play an important role in the regulation of physical and chemical body composition.

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References

Andersson L., Haley C.S., Ellegren H. *et al.* (1994) Genetic mapping of quantitative trait loci for growth and fatness in pigs. *Science* **263,** 1771–4.

Andersson-Eklund L., Marklund L., Lundstrom K., Haley C.S., Andersson K., Hansson I., Moller M. & Andersson L. (1998) Mapping quantitative trait loci for carcass and meat quality traits in a Wild Boar × Large White intercross. *Journal of Animal Science* **76,** 694–700.

Beeckmann P., Moser G., Bartenschlager H., Reiner G. & Geldermann H. (2003) Linkage and QTL mapping for *Sus scrofa* chromosome 8. *Journal of Animal Breeding and Genetics* **120** (Suppl. 1), 66–73.

Bidanel J.P., Milan D., Iannuccelli N. *et al.* (2001) Detection of quantitative trait loci for growth and fatness in pigs. *Genetics Selection Evolution* **33,** 289–309.

Brondum J., Egebo M., Agerskov C. & Busk H. (1998) On-line pork carcass grading with the autofom ultrasound system. *Journal of Animal Science* **76,** 1859–68.

Cepica S., Schroffel J., Stratil A. *et al.* (2003a) Linkage and QTL mapping for *Sus scrofa* chromosome 9. *Journal of Animal Breeding and Genetics* **120**(Suppl. 1), 74–81.

Cepica S., Stratil A., Kopecny M. *et al.* (2003b) Linkage and QTL mapping for *Sus scrofa* chromosome 4. *Journal of Animal Breeding and Genetics* **120**(Suppl. 1), 28–37.

Churchill G.A. & Doerge R.W. (1994) Empirical threshold values for quantitative trait mapping. *Genetics* **138,** 963–71.

Dragos-Wendrich M., Sternstein I., Brunsch C., Moser G., Bartenschlager H., Reiner G. & Geldermann H. (2003) Linkage and QTL mapping for *Sus scrofa* chromosome 14. *Journal of Animal Breeding and Genetics* **120**(Suppl. 1), 111–8.

Edwards D.B., Ernst C.W., Raney N.E., Tempelman R.J., Hoge M.D. & Bates R.O. (2006) QTL mapping in an F_2 Duroc × Pietrain resource population: I. Growth traits. *Journal of Animal Science* **84**(Suppl. 2), 108.

Geldermann H., Muller E., Moser G. *et al.* (2003) Genome-wide linkage and QTL mapping in porcine F_2 families generated from Pietrain, Meishan and Wild Boar crosses. *Journal of Animal Breeding and Genetics* **120,** 363–93.

Haley C.S., Knott S.A. & Elsen J.M. (1994) Mapping quantitative trait loci in crosses between outbred lines using least-squares. *Genetics* **136,** 1195–207.

Houston R.D., Haley C.S., Archibald A.L. & Rance K.A. (2005) A QTL affecting daily feed intake maps to chromosome 2 in pigs. *Mammalian Genome* **16,** 464–70.

Karlskov-Mortensen P., Bruun C.S., Braunschweig M.H. *et al.* (2006) Genome-wide identification of quantitative trait loci in a cross between Hampshire and Landrace I: carcass traits. *Animal Genetics* **37,** 156–62.

Knap P.W., Roehe R., Kolstad K., Pomar C. & Luiting P. (2003) Characterization of pig genotypes for growth modeling. *Journal of Animal Science* **81**(E Suppl. 2), E187–95.

Knott S.A., Marklund L., Haley C.S. *et al.* (1998) Multiple marker mapping of quantitative trait loci in a cross between outbred Wild Boar and Large White pigs. *Genetics* **149,** 1069–80.

de Koning D.J., Rattink A.P., Harlizius B., Groenen M.A.M., Brascamp E.W. & van Arendonk J.A.M. (2001) Detection and characterization of quantitative trait loci for growth and reproduction traits in pigs. *Livestock Production Science* **72,** 185–98.

Landgraf S., Susenbeth A., Knap P.W., Looft H., Plastow G., Kalm E. & Roehe R. (2006a) Developments of carcass cuts, organs, body tissues and chemical body composition during growth of pigs. *Animal Science* **82,** 889–99.

Landgraf S., Susenbeth A., Knap P.W., Looft H., Plastow G.S., Kalm E. & Roehe R. (2006b) Allometric association between *in vivo* estimation of body composition during growth using deuterium dilution technique and chemical analysis of serial slaughtered pigs. *Animal Science* **82,** 223–31.

de Lange C.F.M., Morel P.C.H. & Birkett S.H. (2003) Modeling chemical and physical body composition of the growing pig. *Journal of Animal Science* **81**(E Suppl. 2), E159–65.

Lee S.S., Chen Y., Moran C., Cepica S., Reiner G., Bartenschlager H., Moser G. & Geldermann H. (2003) Linkage and QTL mapping for *Sus scrofa* chromosome 2. *Journal of Animal Breeding and Genetics* **120**(Suppl. 1), 11–9.

Malek M., Dekkers J.C.M., Lee H.K., Baas T.J. & Rothschild M.F. (2001a) A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. I. Growth and body composition. *Mammalian Genome* **12,** 630–6.

Malek M., Dekkers J.C.M., Lee H.K., Baas T.J., Prusa K., Huff-Lonergan E. & Rothschild M.F. (2001b) A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. II. Meat and muscle composition. *Mammalian Genome* **12,** 637–45.

Marklund L., Nystrom P.E., Stern S., Andersson-Eklund L. & Andersson L. (1999) Confirmed quantitative trait loci for fatness and growth on pig chromosome 4. *Heredity* **82,** 134–41.

Milan D., Bidanel J.P., Iannuccelli N., Riquet J., Amigues Y., Gruand J., Le Roy P., Renard C. & Chevalet C. (2002) Detection of quantitative trait loci for carcass composition traits in pigs. *Genetics Selection Evolution* **34,** 705–28.

Mohrmann M., Roehe R., Knap P.W., Looft H., Plastow G.S. & Kalm E. (2006a) Quantitative trait loci associated with AutoFOM grading characteristics, carcass cuts and chemical body composition during growth of *Sus scrofa*. *Animal Genetics* **37,** 435–43.

Mohrmann M., Roehe R., Susenbeth A., Baulain U., Knap P.W., Looft H., Plastow G.S. & Kalm E. (2006b) Association between body composition of growing pigs determined by magnetic resonance imaging, deuterium dilution technique and chemical analysis. *Meat Science* **72,** 518–31.

Nezer C., Moreau L., Brouwers B., Coppieters W., Detilleux J., Hanset R., Karim L., Kvasz A., Leroy P. & Georges M. (1999) An imprinted QTL with major effect on muscle mass and fat deposition maps to the *IGF2* locus in pigs. *Nature Genetics* **21,** 155–6.

Nezer C., Moreau L., Wagenaar D. & Georges M. (2002) Results of a whole genome scan targeting QTL for growth and carcass traits in a Pietrain × Large White intercross. *Genetics Selection Evolution* **34,** 371–87.

Quiniou N. & Noblet J. (1995) Prediction of tissular body composition from protein and lipid deposition in growing pigs. *Journal of Animal Science* **73,** 1567–75.

Quiniou N., Noblet J., Dourmad J.Y. & van Milgen J. (1999) Influence of energy supply on growth characteristics in pigs and consequences for growth modelling. *Livestock Production Science* **60,** 317–28.

Quintanilla R., Milan D. & Bidanel J.P. (2002) A further look at quantitative trait loci affecting growth and fatness in a cross between Meishan and Large White pig populations. *Genetics Selection Evolution* **34,** 193–210.

Roehe R. (2006) Molecular and quantitative genetic determination of protein and lipid deposition during growth of pigs. *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production 13-06*. Belo Horizonte, MG, Brazil. (On CD: e-mail secretariat@wcgalp8.org.br)

Roehe R., Plastow G.S. & Knap P.W. (2003) Quantitative and molecular genetic determination of protein and fat deposition. *Homo – Journal of Comparative Human Biology* **54,** 119–31.

Rohrer G.A. (2000) Identification of quantitative trait loci affecting birth characters and accumulation of backfat and weight in a Meishan-White composite resource population. *Journal of Animal Science* **78,** 2547–53.

Rohrer G.A. & Keele J.W. (1998a) Identification of quantitative trait loci affecting carcass composition in swine: I. Fat deposition traits. *Journal of Animal Science* **76,** 2247–54.

Rohrer G.A. & Keele J.W. (1998b) Identification of quantitative trait loci affecting carcass composition in swine: II. Muscling and wholesale product yield traits. *Journal of Animal Science* **76,** 2255–62.

Rohrer G.A., Thallman R.M., Shackelford S., Wheeler T. & Koohmaraie M. (2005) A genome scan for loci affecting pork quality in a Duroc-Landrace F_2 population. *Animal Genetics* **37,** 17–27.

Sanchez M.P., Riquet J., Iannuccelli N. *et al.* (2006) Effects of quantitative trait loci on chromosomes 1, 2, 4, and 7 on growth, carcass and meat quality traits in backcross Meishan × Large White pigs. *Journal of Animal Science* **84,** 526–37.

Schinckel A.P. & de Lange C.F.M. (1996) Characterization of growth parameters needed as inputs for pig growth models. *Journal of Animal Science* **74,** 2021–36.

Seaton G., Haley C.S., Knott S.A., Kearsey M. & Visscher P.M. (2002) QTL EXPRESS: mapping quantitative trait loci in simple and complex pedigrees. *Bioinformatics* **18,** 339–40.

Stearns T.M., Beever J.E., Southey B.R., Ellis M., McKeith F.K. & Rodriguez-Zas S.L. (2005) Evaluation of approaches to detect quantitative trait loci for growth, carcass, and meat quality on swine chromosomes 2, 6, 13 and 18. I. Univariate outbred F_2 and sib-pair analyses. *Journal of Animal Science* **83,** 1481–93.

Thomsen H., Lee H.K., Rothschild M.F., Malek M. & Dekkers J.C.M. (2004) Characterization of quantitative trait loci for growth and meat quality in a cross between commercial breeds of swine. *Journal of Animal Science* **82,** 2213–28.

Supplementary material

The following supplementary material is available for this article online from http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2052.2007.01689.x.

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.

Table S3 Markers used in the present QTL mapping project, their relative map positions using MARC pig map, number of different alleles and the information contents for the additive (a) and dominance (d) F_2 coefficients and heterozygosity (H) in the F_1 generation.

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