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A genome scan reveals QTL for growth, fatness, leanness and meat quality in a Duroc-Pietrain resource population

G. Liu*,†, D. G. J. Jennen*, E. Tholen*, H. Juengst*, T. Kleinwächter*, M. Hölker*, D. Tesfaye*, G. Ün*, H.-J. Schreinemachers*, E. Murani‡, S. Ponsuksili‡, J.-J. Kim†, K. Schellander* and K. Wimmers‡

*Animal Breeding and Husbandry Group, Institute of Animal Science, University of Bonn, Endenicher Allee 15, 53115 Bonn, Germany. †School of Biotechnology, Yeungnam University, Gyeongsan, Korea. ‡Research Institute for the Biology of Farm Animals (FBN), Wilhelm-Stahl-Allee 2, 18196 Dummerstorf, Germany

Summary

We performed a genome-wide QTL scan for production traits in a line cross between Duroc and Pietrain breeds of pigs, which included 585 F_2 progeny produced from 31 full-sib families genotyped with 106 informative microsatellites. A linkage map covering all 18 autosomes and spanning 1987 Kosambi cM was constructed. Thirty-five phenotypic traits including body weight, growth, carcass composition and meat quality traits were analysed using least square regression interval mapping. Twenty-four QTL exceeded the genome-wide significance threshold, while 47 QTL reached the suggestive threshold. These QTL were located at 28 genomic regions on 16 autosomal chromosomes and QTL in 11 regions were significant at the genome-wide level. A QTL affecting pH value in loin was detected on SSC1 between marker-interval *S0312-S0113* with strong statistical support ($P < 3.0 \times 10^{-14}$); this QTL was also associated with meat colour and conductivity. QTL for carcass composition and average daily gain was also found on SSC1, suggesting multiple QTL. Seventeen genomic segments had only a single QTL that reached at least suggestive significance. Forty QTL exhibited additive inheritance whereas 31 QTL showed (over-) dominance effects. Two QTL for trait backfat thickness were detected on SSC2; a significant paternal effect was found for a QTL in the *IGF2* region while another QTL in the middle of SSC2 showed Mendelian expression.

Keywords pork quality, production traits, quantitative trait loci, resource population.

Introduction

Andersson *et al.* (1994) conducted the first genome-wide scan for growth and body composition in pigs using a wild boar × large white cross. Several other genome scans for QTL controlling a wide range of traits in pigs have been completed (http://www.animalgenome.org/QTLdb/pig.html; Hu *et al.* 2006). More recently the molecular genetic variation underlying QTL has been revealed in pigs and other farm animals (Grisart *et al.* 2002; Winter *et al.* 2002; van Laere *et al.* 2003; Takeda *et al.* 2006). Most of these studies have used exotic breeds or lines of swine, but an increasing number of QTL in pigs have been identified in commercial populations or crosses of commercial breeds (Nezer *et al.* 1999; Malek *et al.* 2001a,b; Stearns *et al.* 2005; Karlskov-Mortensen *et al.* 2006; Rohrer *et al.* 2006; van Wijk *et al.* 2006), suggesting that variation at the QTL still exists after long-term selection. In this study, we created a porcine F_2 resource population from a line cross between Duroc and Pietrain pigs. The Pietrain breed is used as a terminal sire due to exceptional muscularity and leanness, although Pietrain animals have relatively poor growth performance and meat quality. The Duroc has complementary features of Pietrain including lower carcass grade, fatter carcasses, faster growth, higher prolificacy, resistance to stress and superior meat quality (Rohrer *et al.* 2006).

Address for correspondence

K. Wimmers, Research Institute for the Biology of Farm Animals (FBN), Wilhelm-Stahl-Allee 2, 18196 Dummerstorf, Germany.
E-mail: wimmers@fbn-dummerstorf.de

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Materials and methods

Animals

The F_1 generation was produced by mating four Duroc boars to eight Pietrain sows and two Pietrain boars to five

Duroc sows. The F_1 animals were reciprocally assigned to produce F_2 animals, with 13 Duroc × Pietrain (DuPi) F_1 females mated to two Pietrain × Duroc (PiDu) F_1 boars and 14 PiDu F_1 females mated by three DuPi F_1 boars. All pigs were kept at the Frankenforst experimental research farm at the University of Bonn (Germany). Piglets were weaned at 28 days of age and placed in pens in the post-weaning unit until 10 weeks of age. Male piglets were castrated. All animals were individually weighed at birth, weaning, the beginning of the test and the end of the test. The F_2 pigs were given an *ad libitum* diet during the whole test period and were slaughtered at approximately 105 kg. The average age at slaughter was 177.6 ± 15.6 days. A total of 585 F_2 pigs from 31 full-sib families were produced from May 2000 to October 2003. The 19 founder animals were free of the *ryanodine receptor* mutation, which is responsible for the malignant hyperthermia syndrome (Fujii *et al.* 1991).

Traits and phenotypes

The phenotypic data of F_2 animals were collected following the guidelines of the German performance test (ZDS 2003). The description of traits, numbers of records, means and standard deviation are summarised in Table S1. Meat pH value, meat conductivity and meat colour groups were measured using Star-series equipment (Rudolf Matthaeus Company, Germany). Muscle pH, conductivity and meat colour were also measured. Measures were taken at 45 min post-mortem (pH1, FF1) and 24 h post-mortem (pH24, FF24) respectively, on the M. longissimus dorsi between the 13th and 14th ribs (symbol: pH1ko, pH24ko, LF1ko, LF24ko) and in the ham (M. semimembranosus) (symbol: pH24si, LF24si) respectively. Muscle colour was measured at 24 h post-mortem by Opto-Star. Drip loss was scored using a bag method by a size-standardised sample from the l. dorsi that was collected at 24 h post-mortem. The sample was weighed, suspended in a plastic bag, held at 4 °C for 48 h and re-weighed at the end of the holding time (Honikel *et al.* 1986; Kauffman *et al.* 1986). Drip loss was calculated as a percentage of weight loss based on the start weight of a sample. To obtain cooking loss, a loin cube was taken from the l. dorsi, weighed, placed in a polyethylene bag and incubated in water at 75 °C for 50 min. The bag was then immersed in flowing water at room temperature for 30 min and the solid portion was reweighed. Cooking loss was obtained as the difference of the sample weights before and after the treatment. Thawing loss was determined similarly after at least 24 h freezing at −20 °C. Shear force was measured by the Instron-4310 equipment and replicated four times.

Genotypes

One hundred and six microsatellite markers primarily from the USDA-MARC map (http://www.marc.usda.gov) covering 87% of the porcine autosomes were genotyped on F_0, F_1 and F_2 animals (Table S2; Liu 2005). Genomic DNA was isolated from tail or ear samples that were collected at birth. Marker alleles were amplified by PCR, separated on a LICOR Model 4200 sequencer and scored using the ONEDSCAN software (Scanalytics). Singleplex reactions were performed for genotyping of the F_0 and F_1 generations whereas multiplexes were used for the F_2 generation. Detailed information on multiplex groups and reaction conditions is provided by Liu (2005).

Linkage analyses and map construction

Genotypic data were checked for genotyping errors using PEDCHECK (version 1.1) and CRIMAP (2.4 version). Marker orders and marker distances within linkage groups were determined using CRIMAP. Recombination units were converted to map distances using the Haldane mapping function. Marker information content and segregation distortion were tested by following Knott *et al.* (1998).

QTL analyses

QTL analyses were performed using the F2 option of QTL EXPRESS (Seaton *et al.* 2002). QTL were assumed fixed for alternative alleles in the founder animals (Haley *et al.* 1994). Models were fitted by an initial analysis of the phenotypes to determine significant fixed effects to be included in each set of analyses. The SAS 9.1 package PROC GLM was used to evaluate the relevant effects of birth-year-season, full-sib family, gender, carcass weight, date of slaughter and age at slaughter. Family was a significant factor for all traits; however, birth-year-season had more significant effects on body weight, ADG and carcass composition than family but not on meat quality traits. Birth-year-season and fill-sib family contained some similar information because the birth-year-season included information of the contemporary group (weaning period, period after weaning and fatting period). Family, sex, carcass weight and age at slaughter had significant effects on carcass composition traits. Date of slaughter had a significant effect on meat pH value, meat colour and especially on meat conductivity. Date of slaughter and the age at slaughter had no significant effects on drip loss, thaw loss and cooking loss; only family had a significant effect on shear force. Therefore, the final model included birth-year-season and sex as fixed effects, and carcass weight and age at slaughter as covariates for carcass composition traits. Full-sib family, sex and slaughter date were fixed effects, and carcass weight and age at slaughter were covariates for meat pH value, meat colour and conductivity. For drip loss, thaw loss, cooking loss and shear force, sex and family were included as fixed effects, and carcass weight and age at slaughter were included as covariates.

The basic model used in the present study was:

$$y_{ijk} = \mu + S_j + f_k + \beta COV_i + C_{ai}a + c_{di}d + e_{ijk} \qquad \text{(Model 1)}$$

where y_{ijk} was the phenotype of the i^{th} F_2 offspring; μ was the overall mean; s_j was the j^{th} fixed sex effect where $j = 1$, 2; f_k was the k^{th} fixed effect with birth-year-season (12 levels) for body weight, ADG and carcass composition traits and full-sib family ($k = 1$–31) for meat quality traits. β was the regression coefficient on the covariate; cov_i was covariate that varied according to the trait analysed: (i) total number born in a litter and sow parity, both as covariates for BWT; (ii) BWT, number of pigs weaned and age at weaning as covariates for WWT; (iii) WWT and the age at beginning of test, both as covariates for TSW; (iv) BWT and the number of piglets weaned in a litter, both as covariates for ADG_1; (v) WWT as a covariate for ADG_2; (vi) TSW as a covariate for ADG_3; (vii) BWT as a covariate for ADG_4; (viii) TSW and age at end, both as covariates for FCS and FCR; (ix) BWT and age, both as covariates for live weight (i.e. body weight at slaughter). c_{ai} was the additive coefficient of the i^{th} individual at a putative QTL location in the genome calculated as half of the difference of the trait value between homozygous carriers of the Duroc and the Pietrain alleles; c_{di} was the dominant coefficient of the i^{th} individual at a putative QTL location in the genome estimated as the difference between the trait value of heterozygous individuals and the mean trait value observed for homozygous animals; a and d were the additive and dominant effects of a putative QTL respectively; e_{ijk} was the residual error. The regression model was fitted at 1-cM intervals along each chromosome and the *F*-value for the QTL effect was calculated at each point. The position reaching the highest *F*-value was considered as the position of the QTL.

Evidence for any QTL on a chromosome led to further analyses. First, we tested a model with two linked QTL on that chromosome (model 2). The best model for two linked QTL was identified by a grid search of all possible combinations of two QTL at 1 cM resolution; the two positions were chosen that maximised the joint *F*-value testing the model of two QTL vs. no QTL. The significance of the second QTL was determined by the *F*-value for the comparison of the best two QTL model vs. the best single QTL for that linkage group.

The presence of imprinting effects was investigated as described by Knott *et al.* (1998) by adding a third effect into model 1, which compared the two classes of heterozygotes, defined according to the paternal or maternal origin of grandparental alleles. This model, denoted model 3 in the text below, was first contrasted with no QTL model (*F*-ratio with 3 df in the numerator). When significant, it was compared with model 1 to test the significance of imprinting effects (*F*-ratio with 1 df in the numerator). When imprinting effects reached the threshold (see below), then paternal and maternal effects (de Koning *et al.* 2002) were tested further by *t*-test. We also explored the two QTL model with imprinting effect, denoted model 4. The procedure was similar to that described above. For further details on the models, see Liu (2005).

Significance thresholds were determined by data permutation (Churchill & Doerge 1994) of 10 000 permutations including 5% chromosome-wide level (CW level, *); 5% genome-wide level (GW, **); 1% genome-wide (GW ***). The 5% chromosome-wide threshold corresponds approximately to the suggestive linkage threshold proposed by Lander & Kruglyak (1995) and ranged from 4.38 to 5.42 for different chromosomes. Average significance thresholds were derived based on 16 representative traits (BFT-av, BFT-sh, F1314, sidefat, fat area, loin eye area (LEA), FMR, pH24ko, pH24si, pH1ko, LF24si, colour, Drip, CL, EBLC and ECLC). A list of average thresholds (F_{2df}) by chromosome is shown in Table 1. For the two QTL model, the *F*-value was tested against significance thresholds derived for the test of one QTL vs. no QTL, as previously described (Knott *et al.* 1998). The threshold *F*-value obtained from the null hypothesis simulations was converted into a probability of the *F*-value under a standard *F* distribution with two df in the numerator. Thresholds for parent-of-origin effects (F_{3df}) were obtained by permutation test for each trait individually (Table 2).

The empirical 95% confidence intervals (CI) and flanking markers for the QTL positions were obtained by applying the bootstrapping approach with 1000 iterations proposed by Visscher *et al.* (1996).

Results and discussion

One hundred and six microsatellite markers spread across the 18 autosomes were assigned to a swine sex-averaged map which spanned 1987 Kosambi cM (Table S2). Order of all markers agreed with the published USDA-MARC2 swine map (Rohrer *et al.* 1996). Twenty-four QTL exceeded the genome-wide significance thresholds while 47 QTL reached the suggestive threshold and these QTL were assigned to 28 genomic regions on all autosomal chromosomes except SSC11 and SSC17. Among these regions, 11 regions contained QTL significant at the genome-wide level. Up to five QTL were detected for 32 of 35 traits, while no QTL were identified for carcass weight, LF1ko or thaw loss.

QTL for meat quality

Convincing evidence for QTL affecting pH24ko and pH24si were found on SSC1, and these QTL explained 11.84% and 9.08% of the phenotypic variation respectively (Table 1, Fig. 1). The CI for both QTL were between 51 and 58 cM (flanking markers: *S0312-S0113*), which is in close proximity to the QTL region described by Geldermann *et al.* (2003) in a wild boar × Pietrain family. In the same region, QTL significant at the 5% genome-wide level were identified for meat colour, conductivity (LF24si) and pH1ko and a suggestive QTL for conductivity (LF24ko). The CI and the *F*-value profiles for meat colour and conductivity indicated

Table 1 QTL on swine chromosomes 1–18 identified with an F2 model.

SSC[1]	Trait[2]	*F*-ratio[3]	Nominal *P*	Position (CI)[4]	Flanking markers[5]	Additive (SE)[6]	Dominance (SE)[7]	Variation (%)[8]
1	pH24ko	33.18***	3.0×10^{-14}	53.5 (51–58)	*S0312-S0113*	0.04 (0.01)	−0.02 (0.01)	11.84
1	pH24si	24.66***	6.2×10^{-11}	55.2 (51–58)	*S0312-S0113*	0.05 (0.01)	−0.02 (0.01)	9.08
1	pH1ko	14.10***	1.1×10^{-6}	55.8 (53–58)	*S0312-S0113*	−0.04 (0.01)	0.06 (0.02)	5.40
1	Colour	12.59***	4.6×10^{-6}	59.0 (51–73)	*S0312-SW1957*	1.66 (0.35)	−0.82 (0.56)	4.85
1	LF24ko	7.79*	4.7×10^{-4}	55.7	*S0312-S0113*	0.16 (0.04)	−0.09 (0.06)	3.06
1	LF24si	8.80**	1.8×10^{-4}	63.5 (45.3–88.3)	*S0312-SW373*	0.36 (0.13)	−0.70 (0.23)	3.46
1	BFT-av	10.59***	3.1×10^{-5}	42.0 (6.5–71)	*SW1824-S0155*	0.06 (0.02)	0.01 (0.02)	3.59
1	BFT-sh	10.05***	5.2×10^{-5}	40.2 (7–73.5)	*SW1824-SW1957*	0.11 (0.02)	0.04 (0.04)	3.42
1	BFT-10	5.78*	3.3×10^{-3}	44.5	*SW1851-SW2166*	0.06 (0.02)	0.01 (0.02)	1.99
1	BFT-lo	6.16*	2.3×10^{-3}	70.4	*S0113-SW1957*	0.05 (0.02)	−0.04 (0.02)	2.12
1	F1314	9.26***	1.1×10^{-3}	71.5 (20–79.8)	*SW1515-SW1957*	0.05 (0.01)	−0.04 (0.02)	3.16
1	Side fat	7.47*	6.3×10^{-4}	50.7	*SW1851-SW2166*	0.14 (0.04)	−0.04 (0.06)	2.56
1	Fat area	16.05***	1.7×10^{-7}	44.5 (28.7–70.4)	*SWR2300-S0155*	0.75 (0.13)	−0.01 (0.18)	5.35
1	FMR	10.02***	5.3×10^{-5}	74.0 (19.4–79.8)	*SW1515-SW1957*	0.02 (0.00)	−0.01 (0.01)	3.47
1	ECLC	10.04***	5.4×10^{-5}	72.0 (15–78.8)	*SW1515-SW1957*	−0.56 (0.12)	0.35 (0.20)	3.42
1	EBLC	10.35***	3.9×10^{-5}	45.5 (15–75.1)	*SW1515-SW1957*	−0.70 (0.15)	−0.03 (0.22)	3.52
1	ADG3	9.01***	1.4×10^{-4}	90.6 (11–96.3)	*SW1824-SW1301*	17.87 (5.60)	−29.11 (10.0)	3.17
1	ADG4	12.69***	4.1×10^{-6}	93.2 (66.1–97.4)	*S0113-SW1301*	12.66 (3.22)	−18.51 (5.74)	4.27
2	pH24si	7.46*	6.4×10^{-4}	61.8	*SW1564-S0226*	−0.02 (0.01)	−0.02 (0.01)	2.94
2	Drip loss	6.03*	2.7×10^{-3}	20.1	*SW2623-S0141*	−0.18 (0.10)	−0.59 (0.20)	3.75
2	Shear	6.53*	1.7×10^{-3}	65.5	*SW834-S0226*	−1.82 (0.49)	−0.51 (0.74)	4.52
2	F1314	9.51**	8.7×10^{-5}	55.2 (39–101.4)	*S0141-SWR308*	−0.07 (0.02)	−0.02 (0.02)	3.24
2	Side fat	6.51*	1.6×10^{-3}	51.3	*SW240-SW1564*	−0.12 (0.04)	−0.13 (0.07)	2.24
2	Dressing	6.02*	2.6×10^{-3}	25.0	*SW2623-S0141*	0.28 (0.12)	0.68 (0.25)	2.08
2	LEA	8.52**	2.3×10^{-4}	23.7 (5–77.2)	*SW2443-SWR2157*	1.17 (0.34)	1.73 (0.71)	2.91
2	FMR	8.48**	2.4×10^{-4}	54.6 (9.5–101.4)	*SW2443-SWR308*	−0.01 (0.00)	0.00 (0.00)	2.90
2	EBLC	8.97**	1.5×10^{-4}	53.0 (27.7–101.4)	*SW2623-SWR308*	0.67 (0.17)	0.51 (0.30)	3.07
2	ECLC	9.67**	7.5×10^{-5}	55.2 (21–101.4)	*SW2623-SWR308*	0.63 (0.15)	0.22 (0.25)	3.31
3	Drip	4.66*	1.0×10^{-2}	0.0	*SW72-S0164*	0.24 (0.08)	−0.07 (0.11)	2.92
3	Side fat	8.32**	2.8×10^{-4}	70.4 (25.6–70.4)	*SW72-S0002*	−0.11 (0.04)	0.34 (0.11)	2.85
3	BWT	5.80*	3.2×10^{-3}	0.0	*SW72-S0164*	−0.04 (0.02)	0.06 (0.03)	2.02
4	F1314	5.55*	4.1×10^{-3}	27.0	*S0227-S0001*	−0.05 (0.02)	−0.09 (0.05)	1.92
4	BFT-10	4.98*	7.2×10^{-3}	31.0	*S0227-S0001*	−0.07 (0.02)	−0.02 (0.05)	1.72
5	Drip	6.42*	1.8×10^{-3}	20.0	*SW491-SW1482*	0.22 (0.08)	−0.32 (0.13)	3.98
6	LEA	6.77*	1.2×10^{-3}	17.9	*S0035-S0087*	−0.14 (0.42)	−4.31 (1.17)	2.32
6	ADG3	5.66*	3.7×10^{-3}	0.0	*S0035-S0087*	12.19 (5.23)	25.75 (10.32)	2.02
7	CL	10.95***	2.2×10^{-5}	64.5 (38–73.5)	*S0064-S0115*	0.71 (0.15)	0.17 (0.28)	3.72
7	BFT-10	5.43*	4.6×10^{-3}	68.8	*SW175-S0115*	−0.06 (0.02)	0.03 (0.03)	1.88
8	BFT-av	5.86*	3.0×10^{-3}	102.9	*S0144-SW61*	0.05 (0.02)	−0.04 (0.02)	2.06
8	BFT-sh	5.47*	4.4×10^{-3}	102.9	*S0144-SW61*	0.06 (0.02)	−0.08 (0.03)	1.89
8	LEA	9.49**	8.9×10^{-5}	86.5 (40.6–92.8)	*SW2611-S0144*	−1.24 (0.30)	−0.87 (0.53)	3.23
8	FMR	6.24*	2.1×10^{-3}	86.0	*S0086-S0144*	0.01 (0.00)	0.01 (0.01)	2.15
8	EBLC	5.54*	4.2×10^{-3}	102.9	*S0144-SW61*	−0.46 (0.15)	0.31 (0.22)	1.92
8	ECLC	7.22*	8.0×10^{-4}	86.0	*S0086-S0144*	−0.53 (0.15)	−0.42 (0.26)	2.50
8	ADG4	5.55*	4.1×10^{-3}	92.2	*S0144-SW61*	8.47 (3.06)	10.55 (5.44)	1.91
8	Dressing	4.96*	7.2×10^{-3}	98.8	*S0144-SW61*	−0.23 (0.11)	−0.41 (0.18)	1.72
9	LEA	6.72*	1.3×10^{-3}	67.2	*S0109-S0295*	−1.26 (0.38)	0.92 (0.76)	2.31
9	WWT	7.12*	8.8×10^{-4}	10.0	*SW21-SW911*	0.35 (0.10)	−0.25 (0.18)	2.49
9	ADG1	7.72*	4.9×10^{-4}	9.2	*SW21-SW911*	12.56 (3.47)	−8.52 (6.05)	2.67
9	ADG5	5.06*	6.6×10^{-3}	0.0	*SW21-SW911*	10.10 (3.32)	−4.30 (4.89)	1.80
10	ADG2	9.02**	1.4×10^{-4}	79.3 (52–91)	*SW830-SW951*	17.46 (4.91)	−17.08 (8.22)	3.18
10	ADG5	4.95*	7.4×10^{-3}	59.2	*SW830-S0070*	13.92 (5.53)	−25.36 (14.63)	1.76
12	CL	5.51*	4.3×10^{-3}	41.5	*S0143-SW874*	−0.81 (0.25)	0.53 (0.69)	1.90
12	BWT	5.40*	4.8×10^{-3}	101.9	*SW874-SW605*	−0.08 (0.03)	0.11 (0.13)	1.88
13	BFT-av	5.06*	6.6×10^{-3}	26.4	*S0219-SW344*	−0.09 (0.03)	0.08 (0.09)	1.75
13	BFT-10	4.70*	9.5×10^{-3}	28.4	*S0219-SW344*	−0.10 (0.03)	−0.01 (0.10)	1.63

Table 1 (Continued)

SSC[1]	Trait[2]	*F*-ratio[3]	Nominal *P*	Position (CI)[4]	Flanking markers[5]	Additive (SE)[6]	Dominance (SE)[7]	Variation (%)[8]
13	Fat area	5.59*	4.0×10^{-3}	47.9	*SW344-SW398*	−0.61 (0.18)	0.00 (0.50)	1.93
13	ADG4	5.56*	4.1×10^{-3}	0.0	*S0219-SW344*	−6.96 (3.60)	21.03 (8.27)	1.92
14	FCS	4.57*	1.1×10^{-2}	23.6	*SW857-S0007*	0.04 (0.02)	−0.15 (0.06)	1.78
15	pH24si	5.86*	3.1×10^{-3}	52.5	*SW1111-SW1119*	0.03 (0.01)	0.01 (0.01)	2.32
15	BFT-av	4.80*	8.6×10^{-3}	29.7	*SW1111-SW936*	−0.02 (0.02)	−0.09 (0.03)	1.66
15	BFT-10	8.18**	3.2×10^{-4}	27.0 (17.5–64)	*S0355-SW1119*	−0.03 (0.02)	−0.10 (0.03)	2.80
15	LEA	7.23*	8.0×10^{-4}	53.0	*SW936-SW1119*	−0.92 (0.28)	0.76 (0.44)	2.49
15	FCS	5.08*	6.5×10^{-3}	67.2	*SW936-SW1119*	0.01 (0.02)	−0.08 (0.02)	1.97
16	BFT-av	7.68*	5.1×10^{-4}	62.9	*S0026-S0061*	0.05 (0.02)	0.11 (0.04)	2.63
16	BFT-sh	5.83*	3.1×10^{-3}	62.4	*S0026-S0061*	0.07 (0.03)	0.14 (0.05)	2.01
16	BFT-lo	6.62*	1.4×10^{-3}	64.0	*S0026-S0061*	0.05 (0.02)	0.13 (0.04)	2.28
16	Dressing	6.79*	1.2×10^{-3}	61.8	*S0026-S0061*	−0.33 (0.12)	−0.55 (0.21)	2.32
16	FCR	6.63*	1.4×10^{-3}	0.0	*S0111-S0026*	0.06 (0.02)	−0.01 (0.02)	2.64
18	Drip	6.19*	2.3×10^{-3}	56.4	*S0062-SWR414*	−0.29 (0.08)	−0.08 (0.13)	3.84
18	CL	4.75*	9.0×10^{-3}	53.0	*S0062-SWR414*	−0.35 (0.15)	−0.56 (0.26)	1.62

[1]*Sus scrofa* chromosome.

[2]Trait abbreviations: ADG_1 = average daily gain from birth to weaning (g/day); ADG2 = average daily gain from weaning to test start (g/day); ADG3 = average daily gain from test start to slaughter (g/day); ADG4 = average daily gain from birth to slaughter (g/day); ADG5 = average daily gain from birth to test start (g/day); BFT = back fat thickness on loin at 13–14th rib ($F_{13/14}$) (cm); BFT-10 = BFT at 10th rib (cm); BFT-av = average BFT (cm); BFT-lo = loin BFT (cm); BFT-sh = shoulder BFT (cm); BWT = birth weight (kg); CL = carcass length (cm); colour = meat colour; cook = cooking loss (%); CW = carcass weight (kg); dressing = dressing percentage (%); drip = drip loss (%); EBLC = estimated belly lean content (%); ECLC = estimated carcass lean content (%); FA = fat area (cm^2); FCR = food conversion ratio [(kg/kg), weight of consumed food per live weight in the fatting period]; FCS = food consumption [(kg/day), in the fatting period]; FMR = ratio of fat area to meat area (%); LEA = loin eye area in Musculus longissimus dorsi (M.l.d.) at 13th-14th rib (cm^2); LF1 ko = conductivity 1 h M.l.d.; LF24 ko = conductivity 24 h M.l.d.; LF24si = conductivity 24 h Musculus semimembranosus (M.sm.); pH1ko = pH 45 min M.l.d.; pH24 ko = pH 24 h M.l.d.; pH24si = pH 24 h M.sm.; shear = shear force (N); sidefat = side fat thickness (cm); thaw = thaw loss (%); TSW = test start weight (kg); WWT = weaning weight (kg).

[3]Three significance levels were used: 5% chromosome-wide significance level, i.e. suggestive level (*), where the critical value varied by chromosome: (1) 5.39, (2) 5.42, (3) 4.55, (4) 4.81, (5) 5.29, (6) 4.97, (7) 5.06, (8) 4.72, (9) 4.55, (10) 4.90, (11) 4.55, (12) 4.55, (13) 4.78, (14) 4.51, (15) 4.70, (16) 4.46, (17) 4.44, (18) 4.69; 5% genome-wide significance level ($F = 8.02$**, nominal $P = 3.7 \times 10^{-4}$); and 1% genome-wide significant level ($F = 9.76$***, nominal $P = 6.8 \times 10^{-5}$) respectively.

[4]Position in Kosambi cM, with the 95% confidence interval (CI) given in parentheses according to the bootstrapping approach when the QTL reached the 5% and 1% genome-wide significance level.

[5]Two methods for flanking makers were used: when the QTL reached the genome-wide significance threshold, the flanking makers were given according to the CI derived by bootstrapping; when the QTL was only suggestive, the flaking markers were those makers around the peak, as near as possible.

[6]Additive effects, expressed as the deviation of the Duroc-Pietrain alleles in units presented in Table S1. SE = standard error.

[7]Dominance effects, expressed as the deviation of the Duroc-Pietrain alleles in units presented in Table S1. SE = standard error.

[8]Fraction of phenotypic variance explained by a QTL as a percentage of the residual variance in the F_2 population.

possible existence of multiple QTL on this chromosome. The position of these QTL corresponds with QTL for meat colour reported by de Koning *et al.* (2001) and the CI overlapped with QTL for Hunter L* reported by Rohrer *et al.* (2006). On SSC2, one suggestive QTL for pH24 in ham in the present study was consistent with the result found by Geldermann *et al.* (2003); Su *et al.* (2004) and Rohrer *et al.* (2006). Alleles from the Duroc breed were favourable for both pH and colour.

A QTL for pH24si was obtained on SSC15 near marker *SW936* with higher pH values for Duroc alleles. This QTL corresponded to previously described QTL for meat pH value, glycogen content, glycolytic potential, reflectance, tenderness and flavour score (Ciobanu *et al.* 2001; Malek *et al.* 2001b). *PRKAG3* (RN) that was assigned to this region showed association with glycogen content in the muscle (Ciobanu *et al.* 2001).

Four suggestive QTL for drip loss were detected on SSC2, SSC3, SSC5 and SSC18 (Table 1), which jointly explained 14.48% of the phenotypic variance in the resource population. QTL on SSC2 and SSC5 exhibited overdominance effects, with heterozygotes having less drip loss compared with both homozygotes. On SSC3, Duroc QTL alleles were associated with more drip loss, while Pietrain alleles on SSC18 were associated with higher drip loss. The suggestive QTL on SSC2 for drip loss was located between *SW2623* and *S0141*, which confirmed findings by Thomsen *et al.* (2004) and van Wijk *et al.* (2006). In this region of SSC2, Sanchez *et al.* (2006) also showed evidence for meat quality traits such as water-holding capacity and meat colour. The QTL

Table 2 Imprinted QTL analyses including multiple effects.

SSC[1]	Trait[2]	QTL model[3]	*F*-ratio[4]	Position (cM)[5]	Additive (SE)[6]	Dominance (SE) [7]	Imprinting (SE)[8]	Variation (%)[9]
2	F1314	Model 3	7.17** (5.98)	83 (0–169)	−0.0674 (0.0155)	−0.0113 (0.0253)	−0.0242 (0.0153)	3.66
		Model 3 with cofactor at 83 cM	4.01 (4.25)	12	−0.0187 (0.0185)	−0.0316 (0.0298)	−0.0562 (0.0175)	2.09
		Model 3 with cofactor at 12 cM	5.75** (5.46)	92 (70–169)	−0.0557 (0.0138)	0.0099 (0.0192)	−0.0135 (0.0133)	2.97
		Model 3 with cofactor at 92 cM	5.00* (4.09)	11	−0.0299 (0.0179)	−0.0330 (0.0307)	−0.0620 (0.0172)	2.59
		Model 3 with cofactor at 11 cM	5.77** (5.70)	92 (56–169)	−0.0577 (0.0138)	−0.0099 (0.0192)	−0.0137 (0.0133)	2.98
		Model 4	$F_{6df} = 5.96$***	QTL_1:11	−0.0299 (0.0179)	−0.0330 (0.0307)	−0.0620 (0.0172)	5.97
			$F_{3df} = 4.62$*	QTL_2:92	−0.0577 (0.0138)	−0.0099 (0.0192)	−0.0137 (0.0133)	
18	Cook	Model 3	5.40* (4.01)	4	0.3670 (0.1934)	−0.2623 (0.3150)	−0.6216 (0.1864)	4.97

[1]*Sus scrofa* chromosome.
[2]Trait abbreviations are given in Table 1.
[3]Model 3 is the single imprinted QTL model; model 4 is the two-QTL model with imprinting effect.
[4]The *F*-ratios of this column have different degrees of freedom according to each model. The numbers in parentheses indicate the threshold for this time test obtained by 1000 permutations.
[5]Position in Haldane cM, with the 95% confidence interval (CI) given in parentheses according to the bootstrapping approach when the QTL reached the 5% and 1% genome-wide significance level.
[6]Additive effects.
[7]Dominance effects.
[8]Imprinting effects.
[9]Fraction of phenotypic variance explained by a QTL as a percentage of the residual variance in the F_2 population
*, ** and *** refer to 5% chromosome-wide level, 5% genome-wide level, and 1% genome-wide significance, respectively.

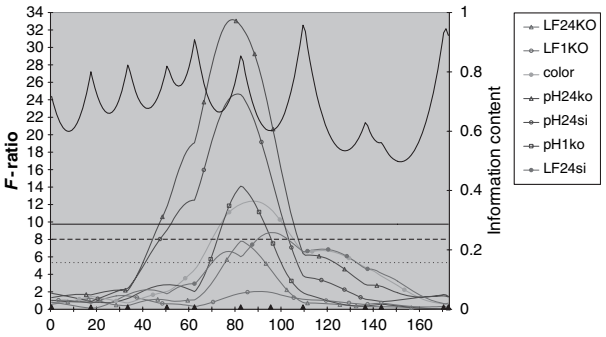

Figure 1 QTL results for meat quality on SSC1 by model 1. Three threshold levels are shown: the short dashed line is the chromosome-wide significance ($F = 5.39$*), the longer dashed line is the genome-wide significance ($P < 0.05$, $F = 8.02$**), and the thick solid line is the genome-wide significance level ($P < 0.01$, $F = 9.76$***). Genetic distances in Haldane cM are given on the *x*-axis, where black triangles indicate marker positions: *SW1824, SW1515, SWR2300, SW1851, S0312, SW2166, S0113, S0155, SW1957, SW373, SW1301* and *SW2512* respectively. The thin solid black curve represents the information content of multiple markers. Trait abbreviations are given in Table 1.

for drip loss on SSC3 was not identified before. The suggestive QTL on SSC5 in marker interval *SW491-SWR453*, corresponded with QTL reported by Thomsen *et al.* (2004); however, the latter showed paternal expression. The QTL on SSC18 was bracketed by markers *S0062* to *SWR414*, so different from QTL found by de Koning *et al.* (2001). Geldermann *et al.* (2003) reported a genome-wide significant QTL for pH24 in ham in this region. A suggestive QTL for shear force found on SSC2 near marker *SW1517* was identical with that found in a Duroc-Berkshire population (Stearns *et al.* 2005) and is also in good agreement with the QTL for slice shear force 2-day post-mortem (Rohrer *et al.* 2006).

QTL for fat deposition

The QTL for back fat traits jointly explained from 4.4% to 11.7% of the phenotypic variance in the F_2 population (Table 1); however, some traits were closely correlated. Our results indicated that Duroc alleles tended to be associated with more fat for QTL on SSC1; Pietrain alleles tended to be associated with more fat on SSC2, SSC7 and SSC13; and QTL on SSC3, SSC16 and SSC15 exhibited overdominance effects.

A series of genome-wide significant QTL affecting fatness traits was detected on SSC1 (Table 1, Fig. 2) within 0.0–80 cM (flanking markers: *SW1851-SW1957*), overlapping the CI of QTL for meat quality. The peaks of the *F*-value profiles of the fatness QTL were located at both sides of the peaks of meat quality QTL, i.e. the peaks of average BFT, shoulder BFT and fat area were proximal (flanking markers: *SW1851-SW2166*), and the other peaks of e.g.

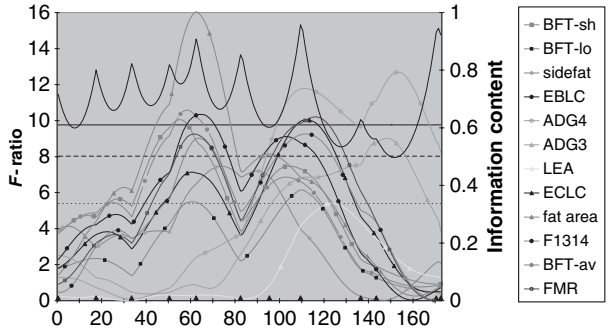

Figure 2 QTL for carcass composition on SSC1 by model 1. Three threshold levels are shown: the short dashed line is the chromosome-wide significance ($F = 5.39$*), the longer dashed line is the genome-wide significance ($P < 0.05$, $F = 8.02$**), and the thick solid line is the genome-wide significance level ($P < 0.01$, $F = 9.76$***). Genetic distances in Haldane cM are given on the *x*-axis where black triangles indicate marker positions: *SW1824, SW1515, SWR2300, SW1851, S0312, SW2166, S0113, S0155, SW1957, SW373, SW1301* and *SW2512* respectively. The thin solid black curve represents the information content of multiple markers. Trait abbreviations are given in Table 1.

F1314, BFT at loin were distal (flanking markers: *S0113-SW373*). The QTL for average BFT, BFT at shoulder and fat area confirmed the results described for SSC1 by Malek *et al.* (2001a) and Grapes & Rothschild (2006). Furthermore, they were localised near QTL for shoulder external fat weight found by Geldermann *et al.* (2003) in the Meishan × Pietrain family. The QTL for F1314 and BFT at loin were at similar position as those found by Nezer *et al.* (2002) and corresponded with results of Geldermann *et al.* (2003) in three families, especially with results from the wild boar × Pietrain family. Malek *et al.* (2001a) reported QTL for last rib BFT and lumbar BFT consistent with our results, showing a similar shape of QTL plots for BFT as ours. Interestingly, Grapes & Rothschild (2006) reported refined QTL mapping on SSC1 in the Berkshire × Yorkshire population analysed by Malek *et al.* (2001a), showing that the likely position of the QTL for average BFT moved from the interval *S0312-SW2166* to the interval *S0113-SW373*. The peaks of QTL for side fat depth overlapped with QTL found by Geldermann *et al.* (2003). In addition, the position of QTL for ratio of fat area to meat area (FMR) was identical with the mapping results in the Meishan × Pietrain family and near to the genomic region in wild boar × Meishan family reported by Geldermann *et al.* (2003).

A QTL significant at the 5% genome-wide level was found on SSC3 for side fat thickness, corresponding to Knott *et al.* (1998); Su *et al.* (2002) and Geldermann *et al.* (2003) using the wild boar × Pietrain family. Suggestive QTL for BFT-10 and BFT-13/14 were detected on SSC4 at 31 and 27 cM respectively, which confirmed results of many previous studies. In the distal region on SSC8, which was not previously associated with fatness, new suggestive QTL for average BFT and shoulder BFT were identified. Suggestive QTL for fat area, BFT-av and BFT-10 were found on SSC13, which confirmed the results of previous studies (Malek *et al.* 2001a; Nezer *et al.* 2002). QTL for BFT-10 and BFT-av were mapped on SSC15 that were consistent with results of Knott *et al.* (1998) and Su *et al.* (2004). Three new suggestive QTL were obtained on SSC16 affecting average BFT, shoulder BFT and loin BFT.

QTL for LEA

We detected five QTL for LEA on SSC2, SSC6, SSC8, SSC9 and SSC15, which jointly explained 10.35% of the phenotypic variance in the F_2 population (Table 1). Pietrain QTL alleles on SSC8, SSC9 and SSC15 tended to produce pigs with larger LEA. Heterozygotes for the SSC2 QTL had the biggest LEA, whereas heterozygotes for the SSC6 QTL had the smallest LEA.

The QTL on SSC2 overlapped with that found in Duroc × Berkshire population by Stearns *et al.* (2005), as the first marker used by them was *SW1201*, which is near *SW240* in the present study. The QTL on SSC8 was consistent with findings by Varona *et al.* (2002). A QTL for LEA on SSC9 was reported by Rohrer *et al.* (2006). The QTL for LEA on SSC6 and SSC15 were not described in previous studies.

QTL for carcass length (CL)

A QTL significant at the 1% genome-wide level was found on SSC7, with the Duroc alleles associated with longer carcasses compared with Pietrain alleles (Table 1). The CI of this QTL was consistent with or overlapped with the QTL found by Nezer *et al.* (2002) and Geldermann *et al.* (2003). In the Meishan × Duroc and wild boar × Meishan families (Geldermann *et al.* (2003), the correspondence was especially high with similar QTL profiles and significance levels. Sato *et al.* (2003) and Mikawa *et al.* (2005) both found QTL for the number of vertebrae around marker *SW252* where our QTL had a similar profile, but with greater statistical support. In this region, where the SLA genes are located, the candidate gene *CYP21A2* is of particular interest as it belongs to a family of genes affecting steroid metabolism. Functionally different alleles at this locus could underlie the largest QTL effects, especially for body conformation. Suggestive QTL found on SSC12 overlapped with that reported by Karlskov-Mortensen *et al.* (2006). A novel suggestive QTL was detected on SSC18 in the present study.

QTL for estimated carcass lean content (ECLC) and for estimated belly lean content (EBLC)

QTL for ECLC were detected on SSC1, SSC2 and SSC8, which jointly explained 9.2% of the phenotypic variation in the DUPI population (Table 1). QTL for EBLC were detected

on SSC1, SSC2 and SSC8, which jointly explained 9.1% of the phenotypic variance in the DUPI population. Pietrain alleles increased lean content at QTL on SSC1 and SSC8, whereas Duroc alleles increased lean content at QTL on SSC2. Geldermann *et al.* (2003) and Karlskov-Mortensen *et al.* (2006) mapped QTL for lean percentage in the same region on SSC1 and SSC2. Milan *et al.* (2002) described genome-wide significant QTL for 'ECLC' on SSC1 that overlapped our QTL; however, the definition of this trait was somewhat different from ours. In this study, no overlap was detected between QTL for CL and QTL for lean content; however, a positive correlation of CL and leanness has been found (Jonsson 1975; Perez-Enciso *et al.* 2005).

QTL for weight and average daily gain

Two suggestive QTL for BWT were identified on SSC3 and SSC12, and QTL heterozygotes had higher birth weights (Table 1). The QTL on SSC3 might overlap with the QTL of Malek *et al.* (2001a) and Quintanilla *et al.* (2002). A suggestive QTL for WWT was located on SSC9, at the same region where a suggestive QTL for ADG1 was obtained. The Duroc was associated with higher WWT and faster growth rate during the suckling period. A suggestive QTL for ADG2 was observed on SSC10. Two QTL for ADG3 were detected on SSC1 and SSC6. Three QTL affecting ADG4 were located on SSC1, SSC8 and SSC13.

On SSC1 a genome-wide significant QTL for ADG4 was obtained between *S0312-SW1301*. A QTL affecting ADG3 reached the genome-wide significance level in the same region and showed the same shape of *F*-value profile (Fig. 2). There were no QTL for ADG1 and ADG2 on this chromosome. Heterozygotes for the QTL had a slower growth rate than the homozygotes. The profile of the *F*-ratio under model 1 revealed two peaks; the highest peak was distal and the second peak was within the QTL region affecting F1314, BFT at loin, FMR and meat content, between interval *SW2166-SW373*. QTL affecting ADG were reported in the distal end of SSC1 by Paszek *et al.* (1999); Rohrer (2000) and Bidanel *et al.* (2001). Sanchez *et al.* (2006) also provided evidence for this QTL in two BC_1 boar families. Quintanilla *et al.* (2002) reported two QTL segregated in a Meishan × large white population on SSC1 affecting growth traits (weight at 10, 13 and 17 weeks, ADG2): one QTL was between *S0113-SW1957* and the other on distal SSC1. When fitting model 2 in the current study, the test of two QTL vs. no QTL reached the 1% genome-wide significance threshold (F_{4df} ratio: 9.48***) and the test of two QTL vs. one QTL reached the suggestive significance threshold (F_{2df} ratio: 6.05*). Heterozygotes for the QTL under the single- and two-QTL models showed a lower rate of growth. Duroc alleles were associated with a faster growth rate than Pietrain alleles. The QTL for live weight was located on distal SSC1 and had similar position and mode to the ADG4 QTL.

Multiple QTL analyses with imprinting effect

Mendelian QTL were obtained on SSC2 for F1314 in the interval between *S0141-S0226* under model 1 (Table 1). This result was similar to the reported QTL for backfat in a resource population based on Meishan and commercial Dutch pig lines (de Koning *et al.* 1999; Rattink *et al.* 2000).

The position of the QTL was the same under model 3 as model 1 and the effect was also Mendelian (Table 2), but the profiles of the QTL showed a second peak at 11 cM rather than 55 cM under model 1 (Fig. 3). After performing the cofactor analyses under model 3 and testing the parent-of-origin effect (imprinting vs. Mendelian), an imprinted QTL in the *IGF2* domain was uncovered for F1314. Using a *t*-test, the parent-of-origin effect showed significant paternal expression (Table 3). The parent-of-origin effect on this chromosome confirmed the results of Jeon *et al.* (1999); Nezer *et al.* (1999); de Koning *et al.* (2000) and Thomsen *et al.* (2004). Furthermore, we fitted model 4, revealing two linked QTL segregation for F1314 (Fig. 3). One QTL indicated significant paternal expression in the *IGF2* region, whereas the second QTL was in the middle region and had Mendelian expression in the middle region. The results were consistent with the cofactor analysis under model 3.

A maternal expressed QTL for cooking loss was found at 4 cM on SSC18 near the marker *SW1808*. de Koning *et al.* (2001) also found a maternally expressed QTL for cooking loss on SSC18 but the QTL mapped to the middle of this chromosome.

Multiple QTL on SSC1

Prominent effects were found for growth, fatness, leanness and meat quality on SSC1 in the Duroc-Pietrain resource

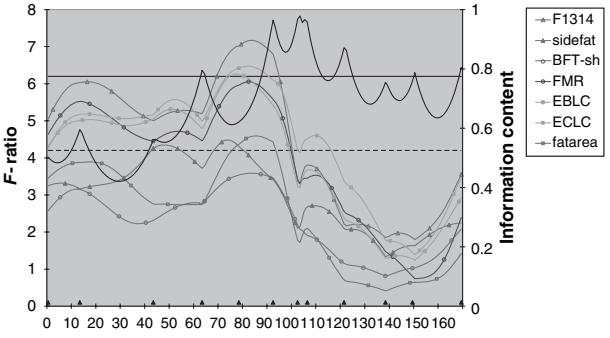

Figure 3 QTL results on SSC2 by model 3. Two threshold levels are shown: the dashed line is the suggestive significance ($F = 4.20$*) and the thick solid line is the genome-wide significance ($P < 0.05$, $F = 6.22$**). Genetic distances in Haldane cM are given on the *x*-axis where black triangles indicate marker positions: *SW2443, SW2623, S0141, SW240, SW1564, SW834, S0226, SW1517, SWR2157, SW1879, SW1844* and *SWR308* respectively. The thin solid black curve represents the information content of multiple markers. Trait abbreviations are given in Table 1.

Table 3 Test of imprinting and parental effects.

SSC[1]	Trait[2]	Position (cM)[3]	Additive (SE)[4]	Dominance (SE)[5]	Imprinting (SE)[6]	*T*-test[7]	Paternal (SE)[8]	Maternal (SE)[9]	*T*-test[10]
2	F1314	11	−0.0442 (0.0176)	−0.0307 (0.0310)	−0.0667 (0.0172)	−3.89***	−0.1129 (0.0285)	−0.0262 (0.0202)	−3.97***
18	Cook	4.0	0.3670 (0.1934)	−0.2623 (0.3150)	−0.6216 (0.1864)	−3.33**	−0.3056 (0.2801)	0.9996 (0.2617)	−3.82**

[1]*Sus scrofa* chromosome.
[2]Trait abbreviations are given in Table 1.
[3]Position in Haldane cM.
[4]Additive effects.
[5]Dominance effects.
[6]Imprinting effects.
[7]*T*-test of imprinting effects.
[8]Paternal effects.
[9]Maternal effects.
[10]*T*-test of parental effects. SSC2, paternal effect; SSC18, maternal effect.
***$P < 0.0001$; ** $P < 0.001$

population. Chromosome 1 had the largest number of QTL (19), of which 15 QTL exceeded genome-wide threshold.

The greatest impact of QTL on meat pH value in loin ($P < 3.0 \times 10^{-14}$) was in the *S0312-S0113* interval, with positive alleles contributed by the Duroc breed. Within the same CI, genome-wide significant QTL for meat colour and meat conductivity were mapped. Genome-wide significant QTL for fatness, meat content traits and ADG were also identified on SSC1 in the *SWR2300* and *SW2512* interval, which encompassed the region responsible for meat quality. There was strong suggestion of multiple QTL for carcass composition and ADG on SSC1: the shape of the *F*-value plots implied two QTL regions in the *SWR2300-SW2166* interval and the *SW2166-SW373* interval respectively. The intervals were proximal and distal respectively of the QTL region for meat pH value (*S0312-S0113*). The *SWR2300-SW2166* interval exhibited QTL for average BFT, shoulder BFT and fat area; the *SW2166-SW373* interval had QTL for F1314, BFT at loin, ratio of fat area to LEA, leanness content, LEA and ADG4. These QTL confirmed results from other populations as described above. Although both regions commonly affected fat deposition, the QTL within the *SW2166-SW373* interval had stronger impact on meat content than fatness. Multiple QTL analysis for these traits showed more than two peaks after fitting model 2. The distal region of SSC1 between *SW373-SW2512* had QTL for ADG. Further investigation of SSC1 is warranted but unfortunately, the public comparative map for SSC1 is not well defined, because pig chromosome 1 includes equivalent regions of several human chromosomes with relatively complicated rearrangement (Goureau *et al.* 2000; Rink *et al.* 2002; Demeure *et al.* 2005). The chromosome breakpoints during mammalian evolution are marked by high gene density, accumulation of segmental duplications in humans and footprints of telomeres and centromeres (Murphy *et al.* 2005). Comparative mapping studies like those of Meyers *et al.* (2005) will facilitate uncovering biologically significant sites and positional cloning of genes influencing complex traits of both agricultural and biomedical interest. Further insight into non-coding but potentially regulating DNA sequences will also enhance the identification of functional positional candidate genes by integrating map-based, positional approaches and function-driven expression analyses.

Karlskov-Mortensen *et al.* (2006) demonstrated that SSC1 contained two QTL in a Hampshire-Landrace population after detailed dissections of measurements of single muscles. In the centre of the QTL the *melanocortin 4 receptor* (*MC4R*) gene is an obvious candidate gene for fatness traits, playing a major role in energy balance. Bidanel & Rothschild (2002) found that *MC4R* was significantly associated with 5–8% differences in backfat, relating to a QTL for BFT on SSC1. Following Kim *et al.* (2000), an association between a mutation in the *MC4R* gene and fatness in several pig lines has been reported (Hernandez-Sanchez *et al.* 2003; Houston *et al.* 2004; Kim *et al.* 2004a,b; Jokubka *et al.* 2006; Meidtner *et al.* 2006; Stachowiak *et al.* 2006). The *MC4R* gene is located in the QTL affecting meat quality in our DuPi population and its effects on meat quality should be further explored.

Vidal *et al.* (2006) reported that the *malic enzyme 1* (*ME1*) gene was significantly associated with backfat thickness and muscular pH in a Landrace population. The *ME1* locus has been mapped on SSC1p1.2, and two transcript forms have been described (Nunes *et al.* 1996). Malic enzyme activity has a strong influence on intramuscular fat content (Mourot & Kouba 1999). Large differences in malic enzymatic activity have been found between Landrace and Iberian pigs, two breeds which also have major differences in fatness traits (Morales *et al.* 2002). Meat yellowness has also been associated with *ME1* genotype (Vidal *et al.* 2006). Therefore, the *ME1* gene is likely one of candidate gene responsible for the greatest association in the present study. The location of the *ME1* gene between *SW1851-S0312*, i.e.

just outside the highest peak in this study (*S0312-S0155* interval), suggests that there could also be another gene(s) in this region that affects the pork quality traits.

It may be inferred from the results that the SSC1 *SWR2300-SW2512* interval can be divided into four functional regions with respect to associations of QTL: the *SWR2300-SW2166* region was mainly associated with fatness traits; the *SW2166-SW373* region was mainly associated with meat content as well as growth rate; the *SW373-SW2512* region was associated with body weight and growth rate; and the central *S0312-S0113* region was mainly associated with meat quality but overlapped with neighbouring regions. In sum, this chromosome harbours regions with significant effects for almost all the traits of economic importance and the regions probably have different roles for genetic variation and network consequence of genes, e.g. pleiotropy, epistasis and co-regulation. The QTL regions contain *ME1* and *MC4R*, which are potential candidate genes for these effects but other genes also reside within these intervals.

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Supplemental Material

The following supplementary material is available for this article online from http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2052.2007.01592.x

Table S1 Characteristics of traits analysed in the study.

Table S2 Markers used in the study.