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Quantitative trait loci mapping for fatty acid composition traits in perirenal and back fat using a Japanese wild boar × Large White intercross

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Summary

Here, we analysed quantitative trait loci (QTL) for fatty acid composition, one of the factors affecting fat quality, in a Japanese wild boar × Large White cross. We found 25 significant effects for 17 traits at 13 positions at the 5% genome-wise level, of which 16 effects for 12 traits at 10 positions were significant at the 1% level. QTL for saturated fatty acids (SFA) in back fat were mapped to swine (*Sus scrofa*) chromosomes (SSC) 1p, 9 and 15. QTL for unsaturated fatty acids in back fat were mapped to SSC1p, 1q, 4, 5, 9, 15 and 17. Using a regression model that fits back fat thickness as a covariate, two of the QTL for linoleic acid content on SSC4 and SSC17 were not significant, but one QTL for total SFA composition was detected on SSC5 with correction for back fat thickness. Wild boar alleles at six of seven QTL tended to increase SFAs and to decrease unsaturated fatty acids. QTL for fatty acid composition in perirenal fat were mapped on SSC2, 3, 4, 5, 6, 14, 16 and X. QTL for melting point (in back fat samples) were mapped on SSC1, 2 and 15. Wild boar alleles in QTL on SSC1 and SSC15 were associated with elevated melting points whereas those on SSC2 were associated with lower melting point measurements.

Keywords fatty acid composition, meat quality, pigs, quantitative trait loci, wild boar.

Introduction

The Japanese wild boar has not been domesticated, and its productivity is generally low. It is genetically distinct from the European wild boar (Okumura *et al.* 2001) and is thus expected to possess unique genetic characteristics. In Japan, its meat is prized for its rich taste, juiciness and high water-holding capacity (Murakami *et al.* 2001). In a previous study (Nii *et al.* 2005), we analysed quantitative trait loci (QTL) for muscle fibre characteristics thought to be associated with meat quality in a Japanese wild boar × Large White intercross. We detected QTL for which wild boar alleles had favourable effects, including increasing types I and IIA muscle fibres and decreasing type IIB muscle fibres.

The major fatty acid in pig back fat is oleic acid (C18:1), and it makes up approximately 40% of all fatty acids present. Total saturated fatty acids (SFA), consisting mainly of palmitic (C16:0) and stearic (C18:0) acids, also comprise about 40% of the total fatty acid content. Linoleic acid (C18:2), which is not synthesized in mammals but is obtained from feed, comprises approximately 10% (Irie & Sakimoto 1992). The ratio of these saturated and unsaturated fatty acids affects the melting point of fat. Lawrence & Fowler (1997) reported that high linoleic acid content in meat is associated with low juiciness and low consumer acceptance. One of the reasons may be lipid degradation caused by the oxidation of free unsaturated fatty acids, producing off-flavours and rancidity in meat. In this study, we analysed QTL for fatty acid composition of back fat and perirenal fat in a Japanese wild boar × Large White cross. Mapping of these QTL will lead to better

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understanding of the Japanese wild boar and will be useful for the breeding of domestic pigs.

Materials and methods

Resource population

A Japanese wild boar was mated to three female Large White pigs that had been maintained in a closed breeding scheme for seven generations at the Tokushima Prefectural Livestock Research Institute. One F_1 male from each of the three Large White females was mated to two or three full-sib F_1 females (a total of seven sows) to produce 353 F_2 animals. All piglets were weaned at 28 days of age, and males were castrated. Piglets were given an *ad libitum* diet containing 14% crude protein, 2.0% crude fat, 5.0% crude fibre, 6.0% crude ash and 74.5% total digestible nutrition during the testing period from 120 days of age to slaughter, which occurred at an average age of 219.6 ± 9.0 days. The F_2 pigs were slaughtered in 44 batches between May 1999 and March 2002, and the average carcass weight was 51.20 ± 8.32 kg.

Measurement of phenotypic traits

The phenotypic traits measured are listed in Table S1. Fat samples were taken from subcutaneous inner and outer layer back fat between the sixth and seventh ribs and from perirenal fat. Fatty acids in each sample were methylated with boron trifluoride-methanol and quantified by gas chromatography (GC14A, Shimadzu, Kyoto, Japan) as described by Ramsay *et al.* (2001). The melting points of inner and outer layer back fat and perirenal fat were measured using the rising melting point method (Suzuki *et al.* 2003).

Genotyped markers and linkage map

We used 220 markers in the USDA linkage map (Rohrer *et al.* 1996) to genotype the four parents, 10 F_1 pigs and 353 F_2 pigs. Amplified polymerase chain reaction (PCR) fragments were electrophoresed through an ABI PRISM 377 sequencer, and their genotypes were analysed with GENESCAN ANALYSIS 2.0 software and GENOTYPER 2.0 software (Applied Biosystems, Foster City, CA, USA). A sex-averaged linkage map for the resource family was constructed for the 18 autosomes and the sex chromosomes (Table S2) with CRI-MAP software (Green *et al.* 1990). The total length was 2098.8 cM, and the average marker interval was 10.2 cM. We did not include markers around *Sus scrofa* chromosome (SSC)5p because all available markers were non-informative.

QTL analysis

A QTL analysis for each trait was performed using the method developed by Haley *et al.* (1994). The analysis assumed that the parental breeds were fixed for alternative alleles at a given QTL. The statistical model was based on a linear regression of phenotypes on probabilities of QTL genotypes at a given location. In the analysis of back fat, carcass weight and back fat thickness were incorporated into the linear model as covariates. In the analysis of perirenal fat, carcass weight was incorporated as a covariate.

The linear model was expressed as:

$$y = \mathbf{X}b + \mathbf{V}c + \mathbf{U}g + e,$$

where $\boldsymbol{y}$ is a vector of phenotypic observations of a trait for all F_2 individuals; $\boldsymbol{b}$ is a vector of non-genetic fixed effects consisting of mean and effects of sex and parity; $\boldsymbol{c}$ is a coefficient vector for covariates incorporated in the model; $\boldsymbol{g}$ is a vector of additive effect a and dominance effect d at a QTL [i.e. $\boldsymbol{g} = (a,d)'$]; $\mathbf{X}$ and $\mathbf{U}$ are incidence matrices relating y to fixed effects $\boldsymbol{b}$ and genetic effects $\boldsymbol{g}$, respectively; $\mathbf{V}$ is a matrix of phenotypic values of all F_2 individuals for the covariate traits and $\boldsymbol{e}$ contains residuals. The ith row of $\mathbf{U}$ is obtained by the probability of QTL genotype for the ith F_2 individual and is written as [prob(QQ) − prob(qq), prob(Qq)], where prob(XX) is the probability of an individual being genotype XX, and Q and q indicate alleles inherited from the wild boar sire and Large White dams respectively. The ith row of $\mathbf{V}$ is the phenotypic values of covariate traits for the ith F_2 individual. The least-squares method was used to detect a QTL. We calculated F-ratios from residual sums of squares under the null model assuming no QTL [$\boldsymbol{g} = (0, 0)'$], and under the full model, including parameters for QTL effects for every 1 cM on our linkage map as well as the information content described by Knott *et al.* (1998).

Sex chromosomes were analysed following the method of Knott *et al.* (1998). The pseudoautosomal section of the sex chromosomes was analysed using the model described above. The QTL genotypes of the sex-specific genomic sections of the wild boar sire and Large White dams were denoted as QY and qq, respectively, where Y indicates the Y chromosome. The possible QTL genotypes were, therefore, QY and qY for F_2 males and QQ and Qq for F_2 females. Thus, one effect corresponding to the difference between the two possible genotypes of a QTL, instead of additive and dominance effects, was fitted separately for each sex in the analyses of the sex chromosomes. Genome-wise significant thresholds were obtained with 1000 repetitions of the permutation test, where the rows of $\boldsymbol{y}$ and $\mathbf{V}$ were simultaneously permuted. Threshold values were almost the same in the model corrected only for carcass weight and in the model that was corrected for both carcass weight and back fat thickness (results not shown). Threshold values for the model corrected only for carcass weight are listed in Table 1 for each trait.

To evaluate the risk of detecting spurious QTL effects because of multiple analyses for a total of 27 traits (Table S1), we calculated the false discovery rate (FDR) for significant QTL detected in the analyses corrected for

Table 1 Summary of QTL for fatty acid composition in fat tissues.

			Corrected for carcass weight						Corrected for carcass weight and back fat thickness					
	Genome-wise F^1		Map position			Effect[2]			Map position			Effect[2]		
Trait	5%	1%	SSC	cM	*F*-ratio	a	d	PVE	SSC	cM	*F*-ratio	a	d	PVE
Inner layer back fat														
C16:1 (%)	8.65	10.64	1	20.1	12.69	−0.10	−0.02	0.06	1	21.1	13.48	−0.11	−0.02	0.07
			9	64.6	9.24	−0.06	0.08	0.05	9	64.6	9.72	−0.07	0.08	0.05
C18:0 (%)	8.67	10.88	1	16.1	12.76	0.60	−0.06	0.06	1	17.1	13.50	0.61	−0.04	0.06
			9	67.6	15.18	0.48	−0.57	0.07	9	66.6	15.85	0.50	−0.56	0.07
C18:2 (%)	8.73	10.15	4	69.7	10.83	−0.44	0.03	0.04			ns			
Other PUFAs (%)	8.44	9.95	5	48.0	10.22	0.05	−0.05	0.05	5	48.0	10.05	0.05	−0.05	0.05
SFA (%)	8.55	10.32			ns				5	33.8	8.82	−0.62	0.29	0.04
			9	78.6	9.52	0.56	−0.57	0.04	9	76.6	10.25	0.63	−0.42	0.04
Melting point (°C)	8.76	10.45	2	53.4	10.92	−0.82	0.00	0.04	2	53.4	11.54	−0.84	−0.04	0.05
Outer layer back fat														
C16:0 (%)	8.50	9.98	15	35.9	15.41	0.50	−0.05	0.07	15	36.9	14.00	0.47	0.01	0.06
C16:1 (%)	8.59	10.24	1	22.8	13.02	−0.13	−0.07	0.07	1	22.8	12.95	−0.13	−0.07	0.07
			1	84.4	13.60	−0.15	0.04	0.07	1	84.4	13.62	−0.15	0.04	0.07
C18:0 (%)	8.80	11.01	1	23.8	10.64	0.39	0.24	0.05	1	23.8	11.85	0.41	0.23	0.05
			9	67.6	9.75	0.39	−0.19	0.04	9	67.6	11.40	0.14	−0.17	0.05
C18:1 (%)	8.73	10.49	15	57.0	10.14	−0.56	−0.21	0.04	15	57.0	10.10	−0.55	−0.21	0.04
C18:2 (%)	8.53	9.83	17	62.3	10.24	−0.51	0.38	0.04			ns			
SFA (%)	8.52	10.40	15	45.3	14.23	0.67	0.38	0.05	15	56.6	14.79	0.72	0.21	0.05
Melting point (°C)	8.67	10.30	1	21.1	8.93	0.73	0.92	0.04	1	21.1	9.65	0.75	0.91	0.04
			15	57.7	8.89	0.86	−0.48	0.04	15	57.7	8.74	0.84	−0.44	0.04
Perirenal fat														
C14:0 (%)	8.77	10.62	16	0.0	8.99	0.03	0.04	0.04						
C16:0 (%)	8.74	10.58	3	87.8	10.57	−0.40	−0.25	0.05						
			6	73.2	11.81	−0.44	0.07	0.05						
			14	17.2	12.56	0.50	−0.09	0.06						
C18:0 (%)	8.70	10.53	X	24.0	9.04	−0.63	nd	0.04						
C18:1 (%)	8.50	10.40	2	63.2	13.85	0.99	0.05	0.06						
			4	71.6	11.33	0.99	0.03	0.06						
C18:2 (%)	8.87	10.75	4	65.5	11.36	−0.46	0.21	0.05						
Other PUFAs (%)	8.83	10.82	5	49.9	11.50	0.04	−0.04	0.05						
Melting point (°C)	8.55	10.11	X	68.7	8.89	−0.36	nd	0.04						

[1]Genome-wise *F*-ratio thresholds at the 5% and 1% levels determined by permutation test of 1000 repetitions in the model corrected for carcass weight.

[2]a and d, additive and dominance effects respectively of wild boar alleles compared with Large White alleles.

nd, not done; ns, no significant effect was detected; PVE, proportion of phenotypic variance explained by QTL; PUFA, polyunsaturated fatty acids; SFA, total saturated fatty acids.

carcass weight following Weller *et al.* (1998). In brief, *F*-ratios obtained at the marker points across the analyses of all traits, which totalled 5940 *F*-ratios (220 markers and 27 traits), were collected and ranked by ascending order with respect to the comparison-wise error rate (CWER). Denoting the CWER of the *i*th ordered *F*-ratio as $P_{(i)}$ and the null hypothesis corresponding to $P_{(i)}$ as $H_{(i)}$ ($i = 1, 2,\ldots, 5940$), we calculated the FDR as $5940P_{(m)}/m$ when m hypotheses, $H_{(1)}$ $H_{(2)}$ …, $H_{(m)}$, were rejected.

Results

Statistics on traits are listed in Table S1. Oleic + vaccenic acids (C18:1) were the most abundant, followed by palmitic (C16:0) and stearic (C18:0) acids, in all three sampling positions. The content of total SFAs was the highest in the perirenal fat, followed by inner and outer layer back fat respectively. Melting point was also the highest in perirenal fat, followed by inner and outer layer back fat respectively.

The results of QTL mapping are summarized in Table 1. For fatty acid composition, we analysed 24 traits (eight types of fatty acids in three fat tissues) and detected 25 significant effects for 17 traits at 13 positions at the 5% genome-wise level (Table 1), of which 16 effects for 12 traits at 10 positions were significant at the 1% level. The FDR for the analyses of 27 traits (containing three traits for melting point) for 220 markers was calculated as shown in Table S3. Assuming that all of the null hypotheses corresponding to CWERs of *F*-ratios for the QTL declared as significant in the interval mapping were rejected, the FDR was calculated as 0.046 (Table S3). Therefore, we confirmed that the possibility for inclusion of spurious QTL was negligible.

In outer layer back fat, wild boar alleles increased SFA composition or decreased unsaturated fatty acid composition at all QTL detected. In inner layer back fat, wild boar alleles in three of the four QTL increased SFA composition or decreased unsaturated fatty acid composition, but no such tendency was seen in perirenal fat. Quantitative trait loci for melting point were mapped at four positions. In outer layer back fat, QTL for melting point were mapped on SSC1 (between *SW1824* and *SWR485*) and SSC15 (between *SWR1945* and *SW2083*), where QTL for fatty acid compositions were also mapped. Wild boar alleles in these QTL elevated the melting point of fat. In inner layer back fat, a QTL was mapped on SSC2 (between *FSHB* and *SW942*), where QTL for fatty acid composition were not mapped in back fat, and wild boar alleles lowered the melting point. In perirenal fat, a QTL for melting point was mapped on SSCX (between *SW1861* and *SW1943*) and wild boar alleles lowered the melting point. A QTL for C18:0 was also mapped on SSCX (between *SW949* and *SW980*).

When we used a regression model that fits the back fat thickness as a covariate adding to carcass weight, two QTL for linoleic acid (C18:2) content (outer layer back fat on SSC17 and inner layer back fat on SSC4) were not significant. On the other hand, one QTL for total SFA composition of inner layer back fat was detected on SSC5 (between *SW963* and *SW904*) at 5% genome-wise significance after correction for back fat thickness. Quantitative trait loci detected on SSC1, 4, 9 and 15 in inner and outer layer back fat are illustrated in Fig. 1.

Discussion

We detected genome-wise significant QTL affecting subcutaneous back fat and perirenal fatty acid composition on SSC1, 2, 3, 4, 5, 6, 9, 14, 15, 16, 17 and X. Clop *et al.* (2003) scanned the whole genome for subcutaneous back fat fatty acid composition using a cross of Iberian × Landrace pigs and mapped significant QTL on SSC4, 6, 8, 10 and 12. There are two common chromosomes in these studies. Clop *et al.* (2003) mapped QTL for C18:2, double bond index and unsaturated index on SSC4 (between *SW839* and *DECR*), and we mapped QTL for C18:2 of inner layer back fat between *SW839* and *SW1089* when correcting only for carcass weight. In both studies, effects were not significant when correction for back fat thickness was added to that for carcass weight. Interestingly, the other QTL for C18:2 that we detected on SSC17 was also not significant when correction for back fat thickness was added. C18:2 is not synthesized in mammals, so its content is affected by feed and is associated with the amount of fat deposit. Clop *et al.* (2003) mapped a QTL for double bond index and unsaturated index on SSC6, but we did not detect any QTL for back fat.

The inner and outer subcutaneous back fat layers of pigs are separated by scarious connective tissue, and their fatty acid compositions are different (Villegas *et al.* 1973). In the F_2 population in this study, total SFA content (%) of outer layer back fat was lower than inner layer back fat (41.07 ± 2.25 and 44.62 ± 2.28 respectively), while C18:1 content (%) of outer layer back fat was higher than inner layer back fat (44.72 ± 2.00 and 42.49 ± 2.06 respectively; Table S1). However, QTL detected in this study showed similar effects in both layers. Wild boar alleles of QTL on SSC1 increased C18:0 and decreased C16:1 in both layers. Endogenous C16:1 and C18:0 are synthesized from C16:0, so the QTL may affect the oxidation or elongation of carbon chains of fatty acids. Wild boar alleles of QTL on SSC9 increased C18:0 in both layers and increased SFA and decreased C16:1 in the inner layer. Wild boar alleles of QTL on SSC15 increased C16:0 and SFA in the outer layer. Thus, wild boar alleles tended to increase SFAs in back fat. At only one QTL on SSC5, wild boar alleles decreased SFA and increased the content of other polyunsaturated fatty acids (PUFAs).

We also analysed the fatty acid composition of perirenal fat, which has a different fatty acid composition from that of back fat. The SFA content was highest in the perirenal fat in our study, which is similar to Wood *et al.* (1985). We

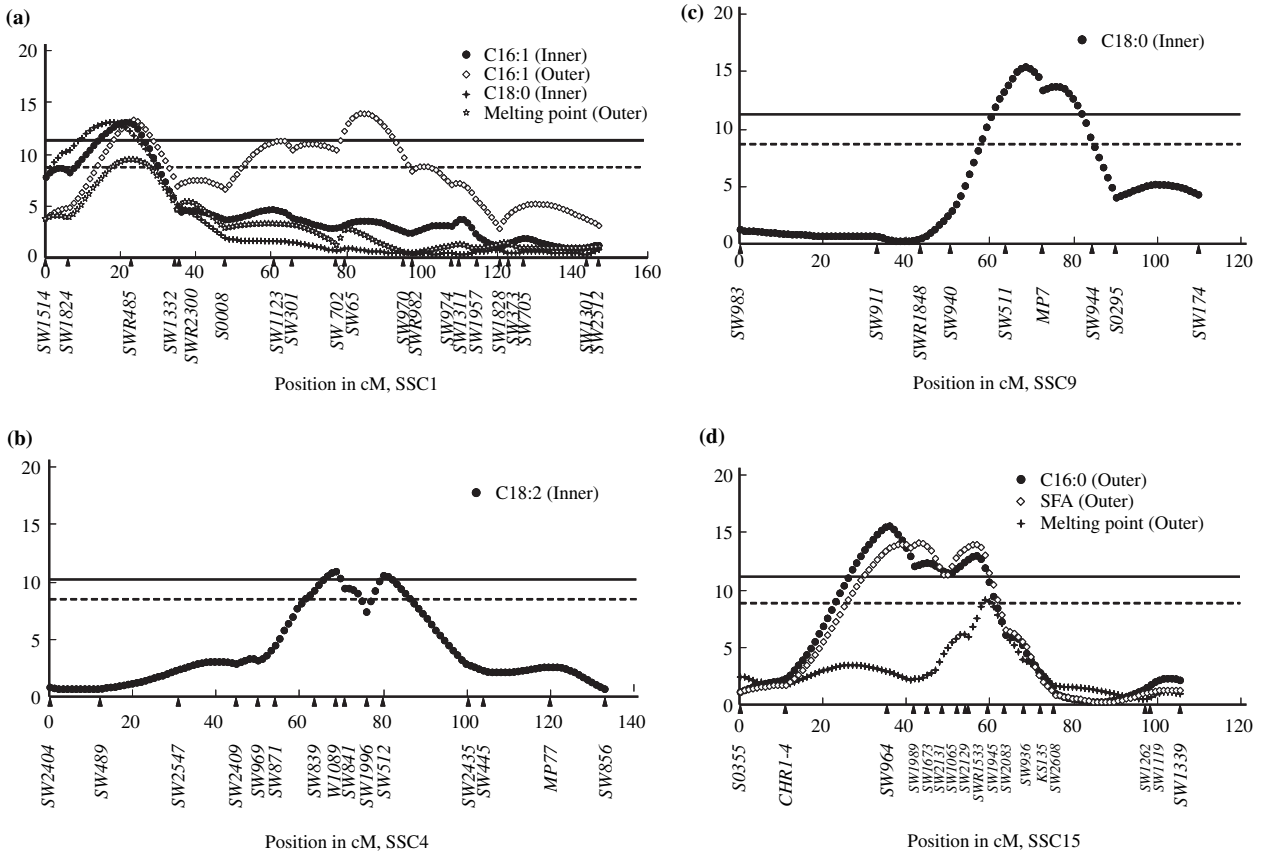

Figure 1 Plots of the *F*-ratio from the least-squares interval mapping analysis (Haley *et al.* 1994). Fatty acid composition quantitative trait loci (QTL) detected in back fat at the 1% genome-wise significance level, as well as melting point QTL in back fat, is shown. The *X*-axes indicate the relative position in the *Sus scrofa* chromosome (SSC) linkage maps. The *Y*-axes represent the value of the *F*-ratio. Arrowheads on the *X*-axes indicate the positions of microsatellite markers. Horizontal lines indicate threshold values for the genome-wise 5% level (dashed line) and the 1% level (solid line). For SSC1 and SSC15, significance levels are shown for C18:0 and saturated fatty acid (SFA) respectively.

detected QTL at eight positions (Table 1), and wild boar alleles in six of them had opposite effects to those seen in back fat – i.e. decreasing SFAs and increasing unsaturated fatty acids. This result suggests that genetic factors affecting fatty acid composition differ between back fat and perirenal fat tissue. In rodent and human, the turnover of lipid metabolism is higher in visceral fat compared with subcutaneous fat. As a result, relative rapid response to the alteration of energy balance occurred in visceral fat (Shimomura *et al.* 1996), but the biological mechanisms explaining the difference are still unclear.

We also detected QTL for melting point of fat. In outer layer back fat, we detected two QTL on SSC1 and SSC15, where QTL for fatty acid composition were also detected. In these regions, wild boar alleles changed fatty acid composition and melting point consistently by increasing SFAs and elevating the melting point. In inner layer back fat, we detected a QTL for melting point on SSC2, but no QTL for fatty acid composition were identified. Furthermore, the wild boar allele lowered the melting point, which is the reverse of the effect of the QTL for fatty acid composition in inner layer back fat. This QTL affected the melting point by an unknown factor different from fatty acid composition. In perirenal fat, QTL for C18:0 and melting point were detected on SSCX, where the wild boar allele decreased C18:0 and lowered the melting point.

A QTL on SSC14 mapped between *S0063* (31.5 cM in the USDA map) and *SW104* (45.2 cM). The *stearoyl-coenzyme A (CoA) desaturase* (*SCD*) gene has been assigned between *SW328* (59.3 cM) and *S0007* (60.0 cM) by Ren *et al.* (2003). SCD is the enzyme responsible for conversion of SFAs into monounsaturated fatty acids in mammalian adipocytes. At a similar position as the QTL on SSC15, Vidal & Amills (2004) assigned the *acyl coenzyme A synthetase long-chain 1* (*ACSL1*) gene. Fatty acyl-CoAs are bioactive fatty acid metabolites that play essential roles in many cellular biochemical processes, such as lipid metabolism, enzyme activation and protein transport. They are used as substrates in the fatty acid β-oxidation pathway and in the synthesis of phospholipids (Weimar *et al.* 2002). *ACSL1* catalyses the formation of these fatty acyl-CoAs.

In this study, we comprehensively analysed QTL for fatty acid composition in three fat tissues using a Japanese wild boar × Large White cross. Wild boar alleles increased SFA

content for most QTL detected in back fat. This result suggests that the fat of wild boar meat (at least back fat) has more SFAs than that of domestic pigs, although other minor QTL may have the opposite effect. The QTL characterizing the properties of wild boar fat may be those on SSC1, SSC9 and SSC15.

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Supplementary Material

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

Table S1 Phenotypic measurements of F_2 individuals.

Table S2 Linkage map information for QTL analysis.

Table S3 Calculation of the false discovery rate (FDR) for QTL detected in the analyses of all traits.