Detection of Mendelian and Parent-of-origin Quantitative Trait Loci in a Cross between Korean Native Pig and Landrace I. Growth and Body Composition Traits

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ABSTRACT : This study was conducted to detect quantitative trait loci (QTL) affecting growth and body composition in an F_2 reference population of Korean native pig and Landrace crossbreds. The three-generation mapping population was generated with 411 progeny from 38 F_2 full-sib families, and 133 genetic markers were used to produce a sex-average map of the 18 autosomes. The data set was analyzed using least squares Mendelian and parent-of-origin interval-mapping models. Lack-of-fit tests between the models were used to characterize QTL for mode of expressions. A total of 8 (39) QTL were detected at the 5% genome (chromosome)-wise level for the 17 analyzed traits. Of the 47 QTL detected, 21 QTL were classified as Mendelian expressed, 13 QTL as paternally expressed, 6 QTL as maternally expressed, and 7 QTL as partially expressed. Of the detected QTL at 5% genome-wise level, two QTL had Mendelian mode of inheritance on SSC6 and SSC9 for backfat thickness and bone weight, respectively, two QTL were maternally expressed for leather weight and front leg weight on SSC6 and SSC12, respectively, one QTL was paternally expressed for birth weight on SSC4, and three QTL were partially expressed for hot carcass weight and rear leg weight on SSC6, and bone weight on SSC13. Many of the Mendelian QTL had a dominant (complete or overdominant) mode of gene action, and only a few of the QTL were primarily additive, which reflects that heterosis for growth is appreciable in a cross between Korean native pig and Landrace. Our results indicate that alternate breed alleles of growth and body composition QTL are segregating between the two breeds, which could be utilized for genetic improvement of growth via marker-assisted selection. (**Key Words :** Quantitative Trait Loci, Swine, Growth, Korean Native Pig, Landrace)

INTRODUCTION

Most traits that are of economic importance in livestock production are multi-factorial, i.e. phenotypic variation is influenced by the effect of many genes along with interactions with environmental factors. With the development of genome-wide maps and molecular tools, it has been enabled to identify chromosomal regions that harbor genes responsible for production traits in farm

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animals (http://www.animalgenome.org/). In swine, most experimental populations to detect quantitative trait loci (QTL) were generated by crossing two breeds with different characteristics on reproduction, growth or carcass traits in order to exploit the benefits of heterosis and breed complementarity (Bidanel and Rothschild, 2002).

Korean native pigs have good meat qualities such as high glucose content, low fat and cholesterol, and high unsaturated/saturated fatty acid ratio as well as good indigenous adaptability compared to western breeds. However, the Korean native pigs have unfavorable characteristics for economically important traits, i.e. small birth weight, slow growth, late maturity and small body size. On the other hand, Landrace has good complementary characteristics, i.e. fast growth, high feed efficiency, moderate meat qualities, and excellent reproductive performance and mothering ability.

Genomic imprinting, or parent-of-origin effects is due to non-Mendelian expression for which the alleles that descended from only one of the two parents contributed to

Table 1. Means and standard deviations for growth and body composition measured on F_2 animals

Trait	Number of observation	Mean	Standard deviation
Birth weight (kg)	311	1.26	0.195
21-d weight (kg)	300	4.96	1.043
Average daily gain at weaning (kg/day)	300	0.19	0.049
Average daily gain on test (kg/day)	307	0.53	0.553
Live weight (kg)	307	89.73	15.499
Hot carcass weight (kg)	318	71.20	12.183
Loin eye area (cm^2)	143	29.29	6.460
Back fat thickness (mm)	318	24.08	8.142
Bone (kg)	318	9.72	2.549
Leather (kg)	316	5.75	1.311
Front leg (kg)	318	7.59	1.228
Rear leg (kg)	318	12.59	1.962
Loin weight (kg)	318	3.63	1.015
Sirloin weight (kg)	318	0.94	0.278
Kalbi area (kg)	318	3.51	0.609
Galmegi (kg)	318	0.29	0.098
Samgyup (kg)	318	9.60	2.073

offspring phenotypes. Characterization of the detected QTL for their mode of gene expression provides valuable information for subsequent QTL analyses and marker-assisted selection. There are several reports on detection of parent-of-origin QTL in swine (de Koning et al., 2000; Thomsen et al., 2003; Kim et al., 2005a) and for a QTL near IFG2 gene on chromosome 2, a causal mutation was identified (van Laere et al., 2003).

The purpose of this study was to detect Mendelian and parent-of-origin QTL for growth and body composition traits in a QTL mapping population by crossing Korean native boars and Landrace sows.

MATERIALS AND METHODS

Animals, phenotypes and genetic map construction

A three-generation resource population was generated at National Livestock Research Institute (NLRI), Songhwan, Korea by crossing five Korean native (domesticated wild) sires and ten Landrace dams. Ten F_1 boars were randomly chosen and each was *inter se* mated up to six F_1 sows to produce 38 full-sib F_2 families. A total of 411 F_2 progeny were produced at the first and the second (N = 130) parities, among which 318 individuals were available in this study.

Among the traits analyzed were birth weight, 21-d weight, average daily gain at weaning and on test, live weight, hot carcass weight, loin eye area, back fat thickness, bone weight, leather weight, front leg (picnic) weight, rear leg (ham) weight, loin weight, sirloin weight, Kalbi (spare rib) weight, Galmegi (skirt meat) weight, and Samgyup (single ribbed belly) weight. Details about raising and

management of the population and trait measurements were described in Choy et al. (2002a) and Choy et al. (2002b). Table 1 contains means and standard deviations for the 17 growth and body composition traits.

A total of 133 genetic markers, mainly microsatellites, were used to generate linkage maps and to perform QTL analyses. Details on DNA isolation, marker selection, and genotyping are described in Choi et al. (2006). Linkage maps were constructed using Cri-map version 2.4 (Green et al., 1996) by using the flips and all options to get the best order.

QTL analysis

Least squares interval mapping models were used for Mendelian and parent-of-origin QTL detection on the autosomal chromosomes. The base model was the Mendelian line-cross model (Mend), which assumes that alternate breed alleles are fixed in grand-parental breeds (Haley et al., 1994):

Mend model: $Y = Xb + aP_a + dP_d + e$

where Y is a vector of phenotypes of F_2 individuals; X is a design matrix; b is a vector of fixed and covariate effects; a is the additive QTL effect, modeled as half of the difference between Korean native pig and Landrace homozygotes; d is the dominance effect, modeled as the difference between the average of Korean native pig and Landrace heterozygotes and the homozygote midpoint; P_a and P_d are vectors containing functions of genotype probabilities for each animal at the chromosomal position of the putative QTL conditional on flanking marker genotypes. The second model was the full (partial) expression model (Full):

Full model: $Y = Xb + a_{pat}P_{pat} + a_{mat}P_{mat} + dP_d + e$

where Y, X, b, and e are as defined previously, and a_{pat}, a_{mat}, and d are the paternally inherited, maternally inherited, and dominance QTL coefficients, respectively. Vector P_{pat} contains probabilities of inheriting a Korean native pig allele, Q vs. Landrace allele, q from its sire, P_{mat} probabilities of inheriting a Korean native pig allele, Q vs. Landrace allele, q from its dam, and P_d probabilities of being heterozygous. All of the Mendelian and parent-of-origin genotype probabilities were calculated by using QTLexpress (http://qtl.cap.ed.ac.uk/).

The next models are the paternal (Pat) and maternal (Mat) expression models, and the null model:

paternal expression model: $Y = Xb + a_{pat}P_{pat} + e$,

maternal expression model: $Y = Xb + a_{mat}P_{mat} + e$,

Table 2. Markers used in the QTL study, their relative map positions to the first marker on each chromosome, and average information content based on linked markers

SSC	Marker	Position (cM)	Number of alleles	Information content[a]	SSC	Marker	Position (cM)	Number of alleles	Information content[a]
1	SW1514	0	5	0.45	8	S0144	103.3	5	0.73
1	SW1515	27.2	5	0.75	8	SW61	130.3	6	0.68
1	S0008	62.6	4	0.61	8	S0178	173.8	6	0.62
1	SW2185	89.4	3	0.53	9	SW983	0	6	0.37
1	SW1970	129.5	2	0.34	9	S0024	34.5	4	0.55
1	SW974	164.1	6	0.77	9	SWR1848	49.3	5	0.65
3	SW274	0	5	0.32	9	SW2074	72.0	5	0.79
3	SW72	29.9	5	0.80	9	S0019	98.2	4	0.84
3	SW1443	54.3	4	0.61	9	S0295	109.5	4	0.80
3	SW902	73.8	6	0.87	9	SW174	137.6	3	0.46
3	S0167	106.0	4	0.44	9	SW749	167.7	2	0.49
3	S0002	128.1	4	0.38	10	SW830	0	5	0.76
4	SW2404	0	8	0.59	10	SW249	31.0	6	0.70
4	SW489	9	3	0.65	10	S0351	60.7	3	0.57
4	S0301	23.9	4	0.72	10	S0070	89.4	5	0.80
4	SW2409	48.8	4	0.73	10	SW2043	118.4	4	0.55
4	SW1678	59.2	4	0.69	10	SW1626	143.2	9	0.70
4	SW35	73.6	4	0.75	10	SW2067	165.3	6	0.34
4	S0214	93.6	4	0.47	11	S0385	0	6	0.70
4	SW445	119.2	6	0.59	11	SW1632	20.3	5	0.56
4	S0097	139.8	5	0.46	11	S0182	35.6	3	0.49
4	SWR153	159.3	4	0.27	11	SW1684	53.7	6	0.80
5	SW413	0	6	0.60	11	SW486	81.0	4	0.69
5	SWR453	45.4	3	0.49	11	SW1377	120.7	2	0.42
5	SW2	74.1	6	0.80	11	SW903	139.7	4	0.54
5	SW963	96.1	6	0.81	11	SW2413	155.8	4	0.61
5	S0018	120.7	6	0.74	12	SW2490	0	4	0.48
5	SW995	142.1	6	0.83	12	SW2494	11.8	2	0.46
5	SW378	165.7	2	0.49	12	S0229	25.7	4	0.56
6	S0035	0	6	0.52	12	S0083	47.5	6	0.43
6	SW1057	27.2	8	0.63	12	SW1553	68.0	3	0.43
6	SW1067	54.0	7	0.52	12	ALOX12	108.4	4	0.52
6	SW71	76.0	6	0.78	12	SWR1021	118.3	5	0.67
6	S0003	98.5	5	0.77	13	S0219	0	4	0.36
6	S0228	109.0	6	0.82	13	SW1378	23.9	3	0.62
6	SW824	115.3	4	0.72	13	SW344	47.2	9	0.65
6	S0121	121.0	5	0.59	13	S0222	65.2	8	0.86
6	SW1881	129.3	6	0.48	13	S0068	81.2	9	0.86
6	SW1328	160.8	6	0.57	13	SW398	101.7	6	0.74
6	SW2415	179.7	2	0.34	13	SW2440	125.8	5	0.70
7	SW2564	0	3	0.40	13	S0289	137.7	5	0.79
7	SWR1343	27.2	8	0.52	13	S0291	151.9	5	0.79
7	SW2155	50.1	3	0.57	14	SW857	0	5	0.76
7	SW1369	68.5	5	0.75	14	SW210	45.4	5	0.78
7	SW1856	76.3	6	0.88	14	S0007	71.4	7	0.61
7	SWR2036	94.6	6	0.87	14	SW1557	104.5	3	0.50
7	SW252	121.1	4	0.69	14	SWC27	133.1	7	0.76
7	SW632	131.2	6	0.75	15	SW2072	0	5	0.48
7	S0101	165.7	4	0.51	15	S0004	18.3	4	0.47
8	S0098	0	7	0.44	15	SW1989	52.6	7	0.78
8	SW268	21.0	7	0.42	15	SW1316	74.0	3	0.56
8	SW205	57.8	5	0.58	15	SW936	92.4	3	0.65
8	S0086	71.3	5	0.70	15	SW1983	110.6	6	0.73
8	S0225	89.2	4	0.51	15	SWR2121	149.0	8	0.43

[a] Information content was obtained by averaging information content values of Mendelian (additive and dominance) and imprinting effects by using multiple linked markers.

null model: $Y = Xb + e$,

where all terms are defined previously. All models were tested at each 1 cM position along the chromosomes.

To define a QTL as a Mendelian, paternal, maternal, or partial expression QTL, the following decision tree was used based on the trees in Thomsen et al. (2004), Kim et al. (2005a) and McElroy et al. (2006), with some minor modifications for the specific tests:

If the Mend model vs. the null model was significant :

i) The Full model was tested against the Mend model at the most likely position under the full model around the region where QTL was detected in the Mend model. If this *F*-test was not significant, then the QTL was classified as a Mend QTL.

ii) If the Full model vs. the Mend model was significant, then the Full model was tested against the Pat and Mat models.

• If the Full model vs. the Pat model was not significant and the Full model vs. the Mat model was significant at the most likely position under the Pat model, then the QTL was classified as a paternally expressed QTL.

• If the Full model vs. the Pat model was significant and the Full model vs. the Mat model was not significant at the most likely position under the Mat model, then the QTL was classified as a maternally expressed QTL.

• If the Full model vs. the Pat model and the Full model vs. the Mat model were both significant or both not significant, then the QTL was classified as a partially expressed QTL.

If the Mend model vs. the null model was not significant :

i) The Full model was tested against the null model. If this test was significant, then the Full model was tested against the Mat model and Pat model as described in step 2 above.

ii) If the Full model vs. the null model was not significant, then the Pat model and Mat model was tested against the null model. If the Pat model vs. the null model was significant, then the QTL is classified as a paternally expressed QTL. If the Mat model vs. the null model was significant, then the QTL is classified as a maternally expressed QTL.

A paternally (maternally) expressed QTL is one that shows a significant allelic effect when inherited from the sires (dams) of progeny without showing a significant allelic effect when inherited from the dams (sires) of progeny. A partially expressed QTL is one that shows an allelic effect when inherited from the sires and dams of progeny, but the effect is different depending on the sex of the parents from which it was inherited.

For all models, the estimated proportion of phenotypic variance explained by a detected QTL was calculated by comparing the reduction of the residual sum of squares with and without fitting the QTL in the model. For all models, fixed effects were included for parity, gender, F_1 sire. Covariates were litter size for birth weight, 21-day weight and average daily gain at weaning, age at slaughter for live weight and average daily gain on test, and age at slaughter and live weight for post-slaughter measures.

Significance thresholds to determine presence of QTL, i.e. Full, Mend, Pat, or Mat model vs. null model were based on single-trait analysis under one QTL model. Permutation tests were performed with 10,000 replicates to empirically determine p values at the chromosome-wise (CW) significance level. For a QTL detected at 5% CW significance level, the p value for a genome-wise (GW) significance level was then obtained based on size of the chromosome relative to the whole chromosome (Kim et al., 2005a). Significance thresholds to determine type of QTL, i.e. Full model vs. Mend, Pat or Mat model were determined at the 5% comparison-wise level. The overall significance level reached by a QTL was determined using the model that corresponded to the classification of the QTL, i.e. Mend, Full (partial), Pat, or Mat. Multiple QTL were declared on a chromosome if significant effects were separated by at least 40 cM for QTL significant at the 5% CW level.

RESULTS

Marker linkage maps

Marker orders and relative locations were obtained for all autosomes except porcine chromosomes (SSC) 2, 17 and 18. Table 2 presents markers, their estimated positions, and information contents. In general, marker orders were in good agreement with the USDA-MARC swine genome map (http://www.marc.usda.gov/genome/genome.html). However, for most chromosomes, map lengths were larger than the distances between corresponding markers in the USDA maps. Estimates of average information contents over Mendelian and parent-of-origin effects on marker positions ranged between 0.27 and 0.88 with the average value of 0.62±0.15 (Table 2). These values were lower than expected, partly due to many missing genotypes and large marker intervals.

Overall QTL results

A total of 47 QTL were detected, i.e. 8 QTL at the 5% GW level and 39 QTL at the 5% CW level. Two of the GW-QTL had Mendelian mode of inheritance on SSC6 and SSC9 for backfat thickness and bone weight, and two were maternally expressed for leather weight and front leg weight on SSC6 and SSC12, respectively (Table 3). One GW QTL was paternally expressed for birth weight on SSC4, and three GW QTL were partially expressed for hot carcass

Table 3. Quantitative trait loci for growth and body composition that were detected with at least the 5% chromosome-wise evidence for linkage

SSC	Trait	cM[a]	-logP[b]	%σ_p^{2c}	QTL type[d]	QTL effect (standard errors)[e]		
1	Birth weight (kg)	0	2.20	4.1	Partial	-0.028 (0.015)	0.041 (0.015)	-0.058 (0.015)
1	Average daily gain at weaning (kg/d)	89	2.68	4.1	Mend	0.137 (0.055)	-0.197 (0.086)	
4	Birth weight (kg)	108	2.95**	3.6	Pat	-0.049 (0.015)		
4	Front leg weight (kg)	55	3.14	4.7	Mend	-0.076 (0.078)	0.451 (0.120)	
4	Rear leg weight (kg)	56	2.93	4.4	Mend	-0.098 (0.126)	0.702 (0.192)	
5	Birth weight (kg)	126	2.38	2.7	Pat	-0.036 (0.013)		
5	Average daily gain at weaning (kg/d)	96	2.80	3.4	Pat	-0.010 (0.003)		
5	21-d weight (kg)	94	2.79	3.4	Pat	-0.214 (0.067)		
6	Loin eye area (cm²)	153	3.56	12.6	Mend	3.456 (1.160)	5.238 (1.942)	
6	Back fat thickness (mm)	106	4.35**	6.5	Mend	-1.457 (0.497)	2.576 (0.691)	
6	Hot carcass weight (kg)	54	5.29***	8.8	Partial	-0.702 (0.421)	0.839 (0.421)	4.393 (0.421)
6	Loin weight (kg)	179	2.67	3.1	Pat	0.250 (0.081)		
6	Rear leg weight (kg)	54	6.44***	10.4	Partial	-0.226 (0.093)	0.231 (0.093)	0.994 (0.093)
6	Leather weight (kg)	175	4.11**	5.1	Mat	-0.402 (0.100)		
7	Birth weight (kg)	86	2.61	4.0	Mend	-0.033 (0.017)	0.079 (0.027)	
7	Average daily gain at weaning (kg/d)	115	2.88	4.5	Mend	-0.011 (0.005)	0.022 (0.008)	
7	Average daily gain at weaning (kg/d)	77	2.76	4.5	Mend	-0.011 (0.005)	0.022 (0.008)	
7	21-d weight (kg)	80	3.42*	5.4	Mend	-0.319 (0.093)	0.308 (0.137)	
7	Live weight (kg)	102	2.67	4.1	Mend	-1.962 (1.143)	5.585 (1.861)	
9	Bone weight (kg)	0	4.10**	6.1	Mend	-1.004 (0.277)	-1.343 (0.424)	
9	Hot carcass weight (kg)	9	2.25	2.5	Pat	-1.700 (0.609)		
9	Galmegi weight (kg)	0	2.40	3.6	Mend	1.747 (0.011)	-0.016 (0.017)	
9	Loin weight (kg)	0	2.57	3.8	Mend	-0.305 (0.100)	-0.340 (0.153)	
10	Birth weight (kg)	13	2.43	3.7	Mend	0.057 (0.019)	-0.032 (0.033)	
10	Average daily gain at weaning (kg/d)	158	2.60	4.9	Partial	-0.009 (0.005)	0.009 (0.005)	0.029 (0.005)
10	Average daily gain at weaning (kg/d)	81	2.62	3.2	Pat	-0.011 (0.004)		
10	21-d weight (kg)	162	2.34	4.5	Partial	-0.230 (0.102)	0.177 (0.102)	0.521 (0.102)
10	21-d weight (kg)	81	2.75	2.3	Pat	-0.230 (0.073)		
11	Front leg weight (kg)	121	2.90	4.3	Mend	-0.001 (0.089)	-0.579 (0.158)	
12	Average daily gain at weaning (kg/d)	26	2.81	3.4	Pat	-0.012 (0.004)		
12	21-d weight (kg)	28	2.66	3.2	Pat	-0.243 (0.078)		
12	Average daily gain on test (kg/d)	112	2.34	2.7	Pat	0.123 (0.043)		
12	Loin eye area (cm²)	111	2.83	10.1	Mend	-3.594 (0997)	0.871 (1.634)	
12	Hot carcass weight (kg)	0	2.63	4.7	Partial	-1.560 (0.556)	2.025 (0.556)	-0.190 (0.556)
12	Hot carcass weight (kg)	50	2.64	3.0	Mat	1.543 (0.502)		
12	Front leg weight (kg)	47	3.65***	4.4	Mat	0.246 (0.066)		
12	Kalbi weight (kg)	41	2.36	2.6	Mat	0.097 (0.034)		
12	Rear leg weight (kg)	118	3.21	4.8	Mend	-0.419 (0.114)	-0.234 (0.175)	
13	Birth weight (kg)	96	3.15	3.8	Mat	0.018 (0.016)		
13	Average daily gain at weaning (kg/d)	47	2.32	3.7	Mend	-0.013 (0.006)	0.016 (0.008)	
13	21-d weight (kg)	75	2.82	4.4	Mend	-0.279 (0.117)	0.306 (0.169)	
13	Bone weight (kg)	40	3.28***	5.7	Partial	-0.339 (0.198)	-0.168 (0.198)	-0.686 (0.198)
13	Galmegi weight (kg)	22	2.47	3.7	Mend	0.007 (0.009)	0.038 (0.016)	
13	Loin weight (kg)	47	2.78	3.2	Pat	-0.159 (0.069)		
14	Live weight (kg)	83	3.15*	4.8	Mend	-0.966 (1.330)	9.244 (2.488)	
14	Kalbi weight (kg)	104	2.43	2.7	Mat	0.091 (0.031)		
15	Galmegi weight (kg)	149	2.03	2.2	Pat	0.014 (0.008)		

[a] Position at which the test-statistic value was maximized for the inferred QTL model.
[b] Negative logarithm of the comparison-wise p-value of the test statistic against the null hypothesis of no QTL at the most likely position for the inferred QTL model. * Significant at the 0.1 genome-wise level. ** Significant at the 0.05 genome-wise level. *** Significant at the 0.01 genome-wise level.
[c] Proportion (%) of phenotypic variance explained by QTL ((RSS_{noQTL}-RSS_{QTL})/RSS_{noQTL}), where RSS is residual sum of squares for the model with or without QTL.
[d] Declared QTL type: Mend = Mendelian expressed QTL; Pat = QTL with paternal expression; Mat = QTL with maternal expression; Partial = parent-of-origin QTL with expression of both parental alleles.
[e] Estimates of additive and dominance effects for Mend QTL; paternal, maternal and dominance effects for Partial QTL; paternal effect for Pat QTL; Maternal effects for Mat QTL.

weight and rear leg weight on SSC6, and bone weight on SSC13, respectively (Table 3). In all, 21 QTL were classified as Mendelian expressed, 13 QTL as paternally expressed, 6 QTL as maternally expressed, and 7 QTL as partially expressed. All detected QTL explained small to moderate portions (2.2%-12.6%) with an average 4.6±2.2% of the phenotypic variance among the traits (Table 3).

QTL analyses for growth and body composition traits

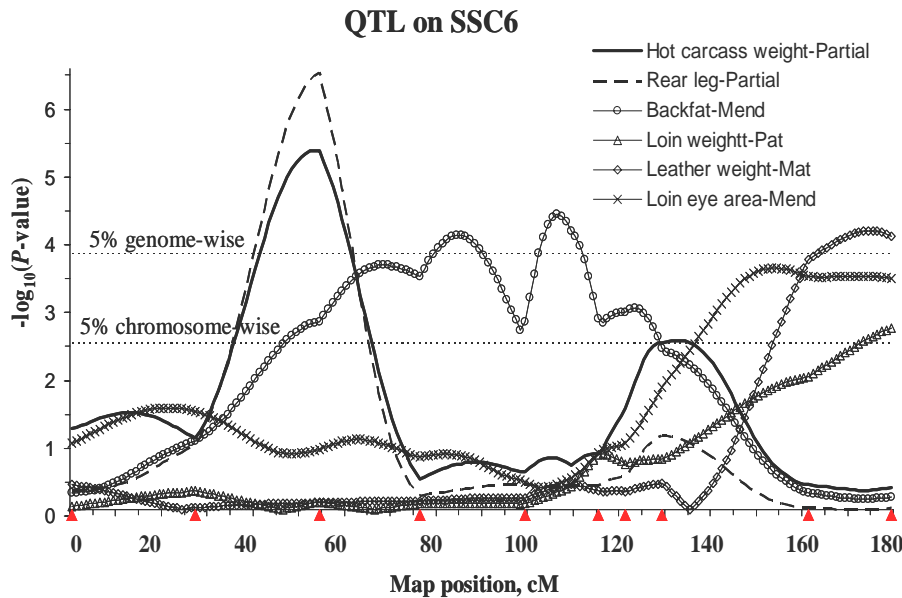Six QTL for birth weight were detected on SSCs 1, 4, 5,

Figure 1. Profiles for QTL on SSC6 using data from a Korean native pigs and Landrace cross. Shown is the negative of the logarithm of the comparison-wise significance value for the inferred QTL models against position on the linkage map. Also, shown are profiles for the inferred models; the partial expressed model for hot carcass weight and rear leg weight, the Mendelian model for backfat thickness and loin eye area, the paternal expression model for loin weight, and the maternal expression model for leather weight. The average 5% genome-wise (3.76) and chromosome-wise threshold values (2.44) were obtained by 10,000 permutations for the inferred QTL models on SSC6. Filled triangles below X-axis indicate marker positions.

8, 10 and 13. One QTL that was detected at 108 cM of SSC4 at the 5% GW level was paternally expressed with increasing Landrace allele of 0.05 kg effect (Table 3). In the similar interstitial region, two QTL for birth weight were detected in Walling et al. (2000) and Bidanel et al. (2001), respectively. However, they did not test for imprinting. In the similar region where the Mendelian QTL for birth weight were detected on SSC7, Bidanel et al. (2001) and Sato et al. (2003) reported evidence of Mendelian birth weight QTL in F$_2$ reference populations by crossing Meishan and Large White, and Meishan and Duroc, respectively. One maternally expressed QTL for birth weight were detected at 96 cM of SSC13. Knott et al. (1998) detected one birth weight QTL in the similar region, but did not find evidence of parent-of-origin effects.

Several QTL for 21-d weight and average daily gain at weaning were detected; Mendelian expressed QTL on SSCs 1, 7 and 13, paternally expressed QTL on SSCs 5, 10 and 12, and partially expressed QTL on SSC10. Most of the QTL had increasing Landrace allele effects in their corresponding expression types (Table 3).

For the back fat thickness QTL that was detected on SSC6 at the 5% GW level, the Landrace allele conferred additive thickness 1.46 mm higher than the Korean native allele (Table 3). Ovilo et al. (2002) detected a Mendelian QTL for backfat thickness in an Iberian and Landrace cross in the similar QTL region of this study. Yue et al. (2003) also detected a Mendelian expressed backfat thickness QTL

in a population with founder breeds from Meishan, Pietrain and European wild boars, whose location was similar to the backfat QTL in this study. Kim et al. (2005a) detected a Mendelian QTL and a maternally expressed QTL for the same trait in crosses between Berkshire and Yorkshire, and between Berkshire and Duroc, respectively in the similar chromosomal region where the backfat QTL was detected in this study. In conclusion, these studies clearly demonstrate the presence of backfat thickness QTL on the interstitial region of SSC6.

On the same chromosome, two QTL for hot carcass weight and rear leg weight were detected at 54 cM at the 1% GW level (Table 3; Figure 1). Yue et al. (2003) detected QTL for cold carcass weight and ham weight in an F$_2$ population derived from Meishan, Pietrain and European wild boars, whose location was distal to the QTL in this study. One QTL for leather weight was detected on SSC6 at the 5% GW level in our study. Su et al. (2004) detected one QTL for skin weight in a F$_2$ cross between Dabai and Meishan, whose location is distal to the detected QTL in this study.

Two QTL for bone weight were detected on SSC9 and SSC13 at the 5% GW level with Mendelian and partial expression, respectively, and Landrace alleles had increasing effects for the corresponding inheritance modes (Table 3). However, there was no confirming evidence of the QTL in other reports, partly due to limited number of QTL studies for the trait.

The weight QTL for hot carcass, front leg and Kalbi were localized around 50 cM of SSC12, among which the front leg QTL was detected at the 5% GW level. All of the QTL had maternal expression inheritance mode with increasing Korean native alleles (Table 3).

DISCUSSION

A comprehensive set of Mendelian and parent-of-origin models were used, which was based on the least squares framework and the assumption that alternate breed alleles were fixed in each grand parental breeds. Application of the set of QTL models showed robustness in detection and characterization of QTL type as well as ease of implementation in previous reports (Thomsen at al., 2004; Kim et al., 2005a). Detection of the 47 QTL in this study indicates that alleles are segregating between Korean native pig and Landrace in many chromosomal regions where genes responsible for growth and carcass composition reside. Selection for fast growth and correspondingly low backfat thickness has been consistently implemented in the Landrace breed for the last several decades (Cameron, 1994). Therefore, it is likely that favorable alleles for growth have increased in frequency at QTL within Landrace, while implementation of selection program for growth in Korean native pig has been limited due to priority for breed restoration program (Kim et al., 2005c). Consequently, it is likely that there are many growth genes with different genotype or allele frequencies between the two breeds, for which some of the chromosomal regions harboring those genes were localized in this study (Table 3).

Only a few of the QTL that were classified as Mendelian expressed had primarily additive effects (i.e. three QTL for Galmegi weight on SSC9, and loin eye area and rear leg weight on SSC12), and 18 of the 21 Mendelian expressed QTL had a complete or over-dominance mode of gene action (Table 3). Heterosis has been utilized to improve growth and carcass composition by crossing between pig breeds with divergent characteristics for growth and carcass measures (McLaren et al., 1987; Edwards et al., 2003). This heterosis may be due in large part to the dominant QTL influencing the growth traits that were detected in this study.

Selection for fast growth and correspondingly low backfat thickness has been consistently implemented in the Landrace breed for the last several decades (Cameron, 1994). However, for several of Mendelian QTL, the favorable allele originated from the Korean native pigs, e.g. the QTL for average daily gain at weaning on SSC1, for loin eye area on SSC6, and for birth weight on SSC10, which had Korean native pig allele with increasing effects (Table 3). The parent-of-origin effects on the growth and fat deposition in mammalian species support the hypothesis of an intergenomic conflict, wherein the paternally derived genome enhances pre- and postnatal growth, while the maternally derived genome suppresses nutritional demands on the mother (Moore and Haig, 1991), thereby causes Landrace allele to increase growth for paternally expressed QTL. However, the paternally expressed QTL that were detected for loin weight on SSC6, average daily gain on test on SSC12, and Galmegi weight on SSC15 had increasing Korean native pig alleles (Table 3). The finding of such cryptic alleles, which has also been reported in other pig studies (Rohrer and Keele, 1998; de Koning et al., 1999; Kim et al., 2005b), indicates that opportunities to select genes for increased performance in breed crosses exist.

Our results confirmed evidence of several QTL that were detected for growth and body composition in previous studies, and would provide a basis for further studies, i.e. performing fine mapping, marker-assisted selection, and characterizing causal mutation for the QTL for traits of interest, especially those that have favorable alleles in Korean native pigs. QTL results on meat quality traits are described in a companion paper. Also, additional analyses to detect QTL that are segregating within breeds are in progress.

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