Quantitative trait loci analysis for growth and carcass traits in a Meishan × Duroc F2 resource population

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ABSTRACT: We constructed a pig F2 resource population by crossing a Meishan sow and a Duroc boar to locate economically important trait loci. The F2 generation was composed of 865 animals (450 males and 415 females) from four F1 males and 24 F1 females and was genotyped for 180 informative microsatellite markers spanning 2,263.6 cM of the whole pig genome. Results of the genome scan showed evidence for significant quantitative trait loci (<1% genomewise error rate) affecting weight at 30 d and average daily gain on *Sus scrofa* chromosome (SSC) 6, carcass yield on SSC 7, backfat thickness on SSC 7 and SSC X, vertebra number on SSC 1 and SSC 7, loin muscle area on SSC 1 and SSC 7, moisture on SSC 13, intramuscular fat content on SSC 7, and testicular weight on SSC 3 and SSC X. Moreover, 5% genomewise significant QTL were found for birth weight on SSC 7, average daily gain on SSC 4, carcass length on SSC 6, SSC 7, and SSC X and lightness (L value) on SSC 3. We identified 38 QTL for 28 traits at the 5% genomewise level. Of the 38 QTL, 24 QTL for 17 traits were significant at the 1% genomewise level. Analysis of marker genotypes supported the breed of origin results and provided further evidence that a suggestive QTL for circumference of cannon bone also was segregating within the Meishan parent. We identified genomic regions related with growth and meat quality traits. Fine mapping will be required for their application in introgression programs and gene cloning.

Key Words: Growth, Linkage Analysis, Meat Quality, Pigs, Quantitative Trait Loci

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Introduction

Quantitative trait loci affecting economically important traits of livestock are of great interest. Several recent studies reported the location of QTL regions on a variety of pig chromosomes. Andersson et al. (1994) first reported a cluster of loci affecting growth and fatness on *Sus scrofa* chromosome (SSC) 4 in wild boar and Large White pigs. A more detailed whole-genome scan of the same population identified more QTL (Knott et al., 1998). Marklund et al. (1999) confirmed the presence of QTL with major effects on growth and fatness on SSC 4 by backcrossing.

We generated an F2 resource population from a cross between a Meishan female and a Duroc male in order to map loci affecting economically important traits. Duroc boars are extensively used in terminal crosses as sires for the production of pork meat with improved meat quality in Japan because the Duroc breed is characterized by high meat quality and large muscle mass. Meishan, characterized by large litter size, differ from commercial breeds in many respects, including genetic characters. These two breeds exhibit large differences not only in growth performance, carcass composition, and meat quality, but also in reproductive traits. Therefore, we selected Meishan and Duroc breeds as parents for a resource population to detect QTL affecting growth, carcass and reproductive traits in pig and to obtain information and tools for breeding programs, such as marker-assisted introgression. We report porcine QTL results for 48 traits, including carcass traits and meat quality.

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Table 1. Performance, growth, carcass composition, and meat quality traits of F2 animals from an intercross of F1 derived from a Meishan sow and Duroc boar

Trait	n	Avg	SD	Minimum	Maximum
Testicular wt					
Right, g	449	9.10	3.31	1.57	23.32
Left, g	449	9.54	3.32	1.62	24.01
Total, g	449	18.64	6.51	3.19	46.31
Growth					
Birth wt, kg	864	1.07	0.17	0.50	1.65
Weight at 3 wk, kg	859	4.51	0.89	1.62	8.00
Weight at 30 d, kg	859	6.90	1.50	1.14	10.90
Weight at 60 d, kg	292	18.40	3.28	7.00	27.70
Day at 30 kg body wt, d	165	80.42	5.71	65	107
Day at 90 kg body wt, d	165	164.10	16.29	133	226
Days from 30 to 90 kg body wt, d	165	83.67	14.18	57	146
Daily gain from 30 to 90 kg body wt, g/d	165	734.4	106.7	421.2	1,026.3
Slaughter wt, kg	165	86.36	1.83	82.0	91.2
Body length at slaughter, cm	165	108.00	4.97	95.0	122.7
Body size					
Circumference of chest, cm	165	100.91	3.06	93.5	112.0
Circumference of cannon bone, cm	165	15.30	0.89	13.8	18.0
Height at withers, cm	165	61.09	2.95	52.2	70.8
Chest depth, cm	165	34.27	1.53	25.7	37.8
Chest width, cm	165	27.43	1.84	22.0	38.0
Carcass measurements					
Carcass wt, kg	165	64.54	1.93	60.0	69.3
Carcass yield, %	165	74.74	1.59	69.2	78.3
Carcass length					
I, cm	165	86.46	4.22	74.0	98.5
II, cm	165	72.28	3.24	65.8	82.0
III, cm	165	62.52	3.20	55.3	72.0
Carcass thickness, cm	165	34.08	1.22	31.1	38.0
Vertebra number					
Thoracic	165	14.84	0.62	14	16
Lumbar	165	5.68	0.54	5	7
Total	165	20.52	0.70	19	22
Subcutaneous fat thickness					
Shoulder, cm	165	5.57	0.78	3.0	7.5
Back, cm	165	3.15	0.67	1.6	5.2
Loin, cm	165	4.33	0.72	2.3	6.8
Avg, cm	165	4.35	0.65	2.63	5.87
Forebelly, cm	165	2.87	0.56	1.3	4.5
Middle belly, cm	165	2.20	0.49	1.0	3.4
Hind belly, cm	165	3.57	0.61	1.8	4.8
Avg, cm	165	2.88	0.40	1.93	3.80
Longissimus muscle					
Length, cm	165	52.30	2.91	45.0	60.5
Loin muscle area					
at 4–5 rib, cm^2	165	10.65	1.79	6.6	16.4
at the middle, cm^2	165	17.68	2.68	11.7	27.0
Wholesale cuts					
Shoulder and picnic, %	165	31.53	1.63	27.00	35.51
Loin and belly, %	165	42.68	2.07	36.30	48.18
Ham, %	165	25.78	1.29	22.27	29.20
Meat quality					
Redness (a value)	165	9.57	1.14	6.10	12.60
Yellowness (b value)	165	8.73	1.54	6.28	16.09
Lightness (L value)	165	44.25	3.72	29.14	51.57
Cooking loss, %	165	31.09	2.70	22.08	41.39
Shear force value, kg/cm^2	165	41.44	9.94	21.15	71.70
Moisture, %	165	72.16	1.72	61.25	74.89
Intramuscular fat, %	165	5.45	1.95	2.01	11.94

Table 2. Summary of QTL location, genomewise probability, additive and dominance effects

Trait	Genomewise[a] 5%	Genomewise[a] 1%	Location SSC	Location cM	*F*-ratio	Additive[c] effect	Dominance[c] effect	Variance explained
Testicular wt								
Right, g	8.6	10.4	3	47.3	10.57**	–1.01	0.56	0.05
			X	77.7	20.26**	–1.02		0.09
Left, g	8.6	10.5	3	47.3	10.53**	–0.99	0.61	0.05
			X	77.7	15.99**	–0.92		0.07
Total, g	8.5	10.4	3	47.3	11.62**	–2.05	1.23	0.05
			X	77.7	19.36**	–1.96		0.09
Growth								
Birth wt, kg	8.6	10.2	7	84.7	10.97*	–0.04	–0.02	0.03
Weight at 30 d, kg	8.5	10.2	6	102.7	16.16**	0.36	–0.20	0.04
Day at 30 kg body wt, d	8.7	10.7	7	70.2	9.27*	2.54	–1.83	0.10
Days from 30 to 90 kg body wt, d	8.9	11.1	6	126.2	9.93*	–6.72	2.61	0.11
Daily gain from 30 to 90 kg body wt, g/d	8.9	10.8	4	81.1	9.62*	3.18	62.66	0.11
			6	116.7	12.65**	49.95	–7.89	0.14
Carcass measurements								
Carcass yield, %	8.8	10.7	7	63.2	13.00**	0.95	–0.07	0.14
Carcass length								
I, cm	8.9	10.8	6	138.2	9.37*	–1.98	1.36	0.10
II, cm	8.9	10.9	X	76.7	10.64*	1.03		0.12
III, cm	8.8	10.8	7	113.3	10.24*	1.51	–0.72	0.11
Vertebra number								
Thoracic	8.8	10.7	7	98.1	70.77**	0.64	0.10	0.47
Lumbar	8.9	10.9	1	132.9	12.54**	0.29	0.04	0.13
Total	8.9	10.8	1	130.9	25.94**	0.48	–0.22	0.24
			7	100.1	35.93**	0.60	–0.02	0.31
Subcutaneous fat thickness								
Shoulder, cm	8.8	10.7	7	56.2	11.45**	0.35	0.24	0.12
Back, cm	8.8	10.9	X	74.6	15.79**	–0.29		0.16
Loin, cm	9.0	11.0	X	73.6	11.54**	–0.27		0.12
Avg, cm	8.9	11.0	7	56.2	11.11**	0.28	0.20	0.12
			X	73.6	14.67**	–0.28		0.15
Middle belly, cm	8.9	10.7	4	30.7	9.35*	–0.16	0.26	0.10
Avg, cm	8.8	10.8	1	63.7	9.38*	0.15	0.15	0.10
Longissimus muscle								
Length, cm	8.9	10.8	1	130.9	14.42**	1.51	–0.50	0.15
			7	111.3	11.20**	1.43	–0.53	0.12
Loin muscle area								
at 4–5 rib, cm^2	8.8	10.7	1	137.9	10.75**	0.93	–0.53	0.12
			7	59.2	15.54**	1.01	–0.46	0.16
at the middle, cm^2	8.8	10.8	7	63.2	9.19*	1.23	–0.61	0.10
Wholesale cuts								
Loin and belly, %	8.8	10.9	8	6.0	9.37*	–0.91	0.89	0.10
Meat quality								
Lightness (L value)	8.8	10.8	3	37.6	10.14*	–0.41	2.43	0.11
Moisture, %	8.5	10.5	7	114.3	10.48*	–0.73	0.68	0.11
			13	112.6	11.04**	–0.74	0.54	0.12
Intramuscular fat, %	8.9	11.0	7	113.3	13.60**	0.95	–0.88	0.14
			9	0	10.75*	0.61	–0.94	0.12

[a]Genomewise *F*-statistic thresholds at the 1 and 5% levels determined by permutation test.
[b]* and ** = 5 and 1% genomewise significance levels, respectively.
[c]Additive (a) and dominance (d) QTL effects correspond to genotype values of +a, d, and –a for, respectively, individuals having inherited two Durocs alleles, heterozygous, and individuals with two Meishan alleles. Positive additive effects indicate that Duroc alleles increased the trait and negative, that Duroc alleles decreased it. Dominance effects are relative to the mean of two homozygous.

Materials and Methods

Phenotype Measurement

Population. Construction of an F2 resource family and measurement of phenotypes were performed in the Ibaraki Branch of the National Livestock Breeding Center. An F1 generation (27 males, 25 females) was produced from a Meishan sow and a Duroc boar. A total of 865 progeny (450 males, 415 female) was produced with six farrowings from 4 F1 males and 24 F1 females. The same sows were always mated to the same boars.

Coat Color. Coat color was recorded from six angled photographs taken of each animal, and scored as follows: Class 1 score = gray coat color; Class 2 score = brown coat color; Class 3 score = black; Class a score =

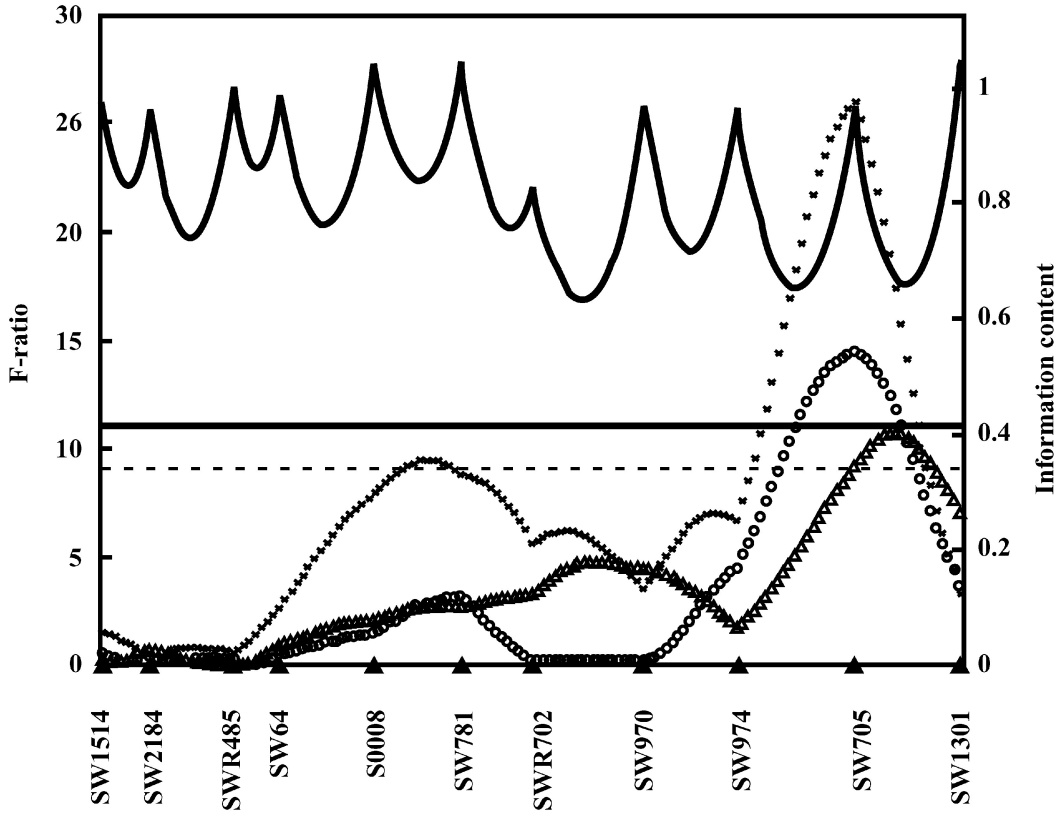

Figure 1. SSC 1. Plot of the *F*-ratio from multilocus least squares analysis (Haley et al. 1994). The x-axis indicates the relative position in the linkage map. The y-axis represents the *F*-ratio. Triangles on the x-axis indicate a marker position. Horizontal lines indicate threshold values for genomewise 5% level (dashed line) and genomewise 1% level (solid line). These levels were different for each trait but, for simplicity, values of 9.00 and 11.00, respectively, are indicated. The specific thresholds are in Table 2. Curved lines indicate information content, △ = loin muscle area 4th to 5th rib, ○ = loin length, and × = vertebra number.

spotting; Class b score = no spotting. Although coat color is a qualitative trait, we treated it as a quantitative trait for analysis.

Data Collection. Pigs were weighed at birth and at 21, and 30 d of age. From these pigs, 292 were weighed at 60 d of age. Testicular weights were recorded from F2 males that were castrated at 2 mo of age. Among the castrated males, 165 were raised until they obtained a body weight of 90 kg. Average daily gain was calculated between 30-kg and 90-kg body weights. These males were slaughtered at a live weight of approximately 90 kg. At slaughter, these males were recorded for body weight, size, and length, including the circumference of the chest and cannon bone, the height at the withers, and the chest depth and width. Carcasses were scalded and dehaired, and chilled overnight. Then carcass measurements were recorded for weight; lengths I, II, and III; thickness; and vertebra number. Carcass lengths I, II, and III refer to the lengths from the first cervical to the pubic bone, from the first rib to the pubic bone, and from the first rib to last lumbar vertebra, respectively. Depth of backfat over the midline was recorded at the first rib (shoulder), the thinnest depth at ribs (back), and the first lumbar vertebra (loin) with a ruler. Depth of belly over the midline was recorded at the last rib (forebelly), at the diaphragm (middle belly), and at the last lumbar vertebra (hind belly). One side of the carcass was split between the 4th and 5th ribs, last rib, and the first lumbar vertebra (at the middle); the longissimus muscle was traced on acetate paper; and the area was determined using computerized morphometric planimetry. The remaining side was then weighed and cut into the major wholesale cuts. The weight of each wholesale cut was recorded. Intramuscular fat (**IMF**) content was measured as described by Gerbens et al. (1999). After minced meat was dried by heating to 102°C for 24 h in a drying oven, moisture was calculated from weights taken before and after drying and was expressed as a percentage. Objective measurements of meat color were taken with a color meter, model ZE 2000 (Nippon Denshoku Industries Co., Tokyo, Japan); L values measure light reflectance, a values represent the degree of redness, and b values represent the degree of yellowness. Cooking loss and shear force were measured as described by Hovenier et al. (1992).

Table 1 summarizes the data of 48 traits, including ADG, vertebra number, backfat thickness (**BFT**), and

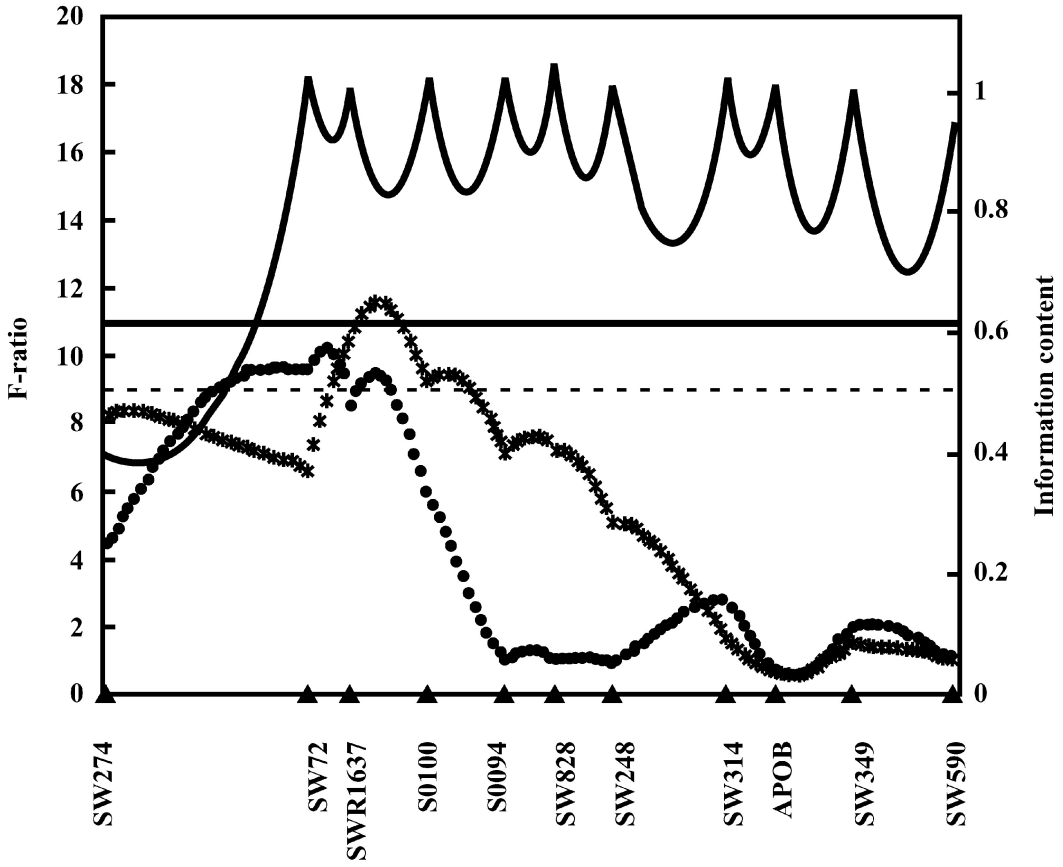

Figure 2. SSC 3. Plot of the *F*-ratio from multilocus least squares analysis (Haley et al. 1994). The x-axis indicates the relative position in the linkage map. The y-axis represents the *F*-ratio. Triangles on the x-axis indicate a marker position. Horizontal lines indicate threshold values for genomewise 5% level (dashed line) and genomewise 1% level (solid line). These levels were different for each trait but, for simplicity, values of 9.00 and 11.00, respectively, are indicated. The specific thresholds are in Table 2. Curved lines indicate information content, ● = lightness (L value) and * = testicular weight.

IMF. Because the 165 F2 males were produced in three independent groups and in different parities, possible phenotypic differences derived from groups and parities were corrected for using the mixed-model least squares, maximum-likelihood computer program described by Harvey (1977).

Genotyping

The DNA was extracted from blood using an automatic extraction machine (Kurabo, Osaka, Japan), and the DNA concentration was adjusted to 20 ng/μL. Polymerase chain reaction primers for microsatellite markers were labeled with fluorescent dyes: 6-FAM, HEX, and TET (Perkin-Elmer, Foster City, CA). The PCR was performed in a total volume of 15 μL containing 20 ng of genomic DNA, 6.25 pmol of each primer, 0.2 m*M* each dNTP, 10 m*M* tris·HCl (pH 8.3), 50 m*M* KCl, 1.5 m*M* $MgCl_2$, and 0.375 U of recombinant Taq polymerase (Takara, Kyoto, Japan). Reaction mixtures were denatured at 94°C for 4 min, cycled 30 times (94°C for 30 s, 55°C or 60°C for 30 s, and 72°C for 30 s), and incubated at 72°C for 5 min. The PCR product sizes were measured using an ABI 377 sequencer and analyzed by Genescan software and Genotyper software (Perkin-Elmer).

Linkage Analysis

Linkage maps were constructed using CRI-MAP (Green et al., 1990) for 18 autosomes and the sex chromosome. The sex-averaged map was used for the whole-genome scan of QTL. The information content was calculated using the method described by Knott et al. (1998). When a given location belonged to a pseudoautosomal region of a sex chromosome, analyses were performed using the same method as for autosomes. For testing QTL in sex-specific regions of the sex chromosome, the analysis model was modified as described by Knott et al. (1998). We assumed that the Y chromosome contained no loci. A test statistic for detecting QTL and the threshold was constructed as for autosomes.

A QTL analysis for each trait was performed using the method developed by Haley et al. (1994). The statistical model in the method is based on a linear regression of phenotypes on the probabilities of QTL genotypes at

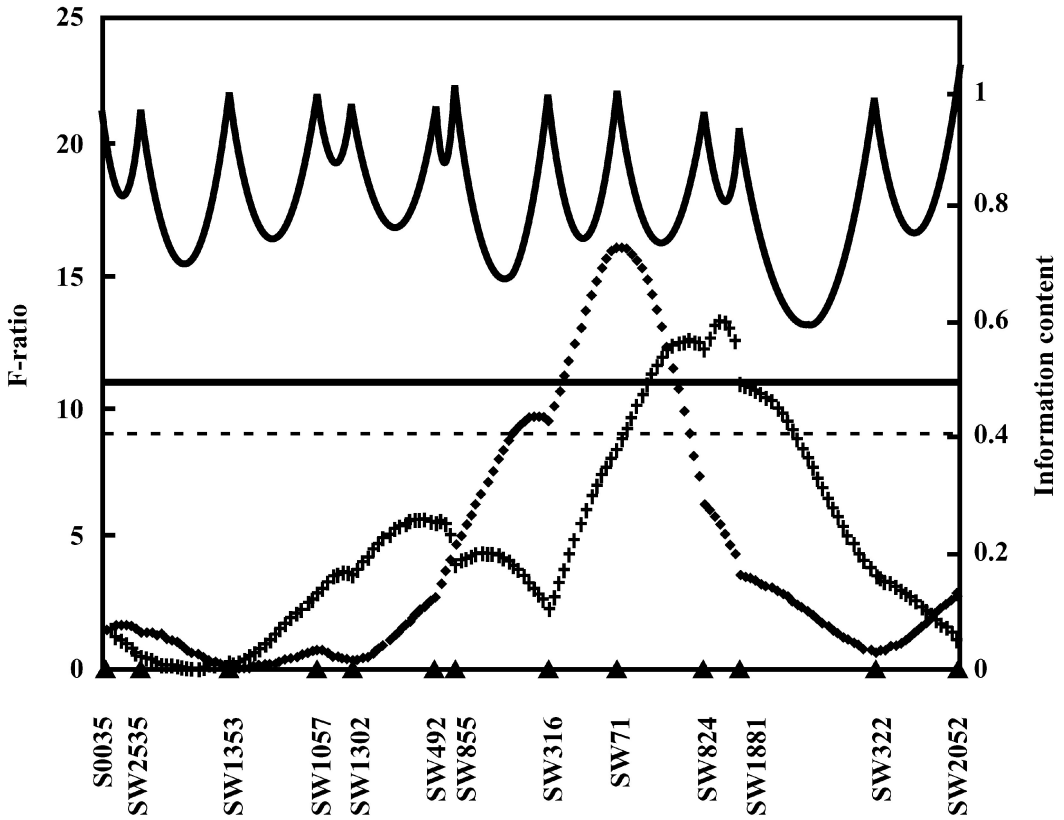

Figure 3. SSC 6. Plot of the *F*-ratio from multilocus least squares analysis (Haley et al. 1994). The x-axis indicates the relative position in the linkage map. The y-axis represents the *F*-ratio. Triangles on the x-axis indicate a marker position. Horizontal lines indicate threshold values for genomewise 5% level (dashed line) and genomewise 1% level (solid line). These levels were different for each trait but, for simplicity, values of 9.00 and 11.00, respectively, are indicated. The specific thresholds are in Table 2. Curved lines indicate information content, ♦ = 30-d weight and + = ADG.

a given location. We assumed that the grandparental breeds were fixed for alternative alleles at a QTL. Two alleles at a putative QTL at a given location were denoted by Q and q. Probabilities of QTL genotypes, denoted by Prob(QQ), Prob(Qq), and Prob(qq), were calculated from the observed genotypes of markers linked to the QTL. The calculation was described by Haley et al. (1994). In the analyses of real data, sex difference was taken into account.

There are three possible genotypes, QQ, Qq, and qq, for a QTL at the given location on an autosome. Let the effects of genotypes QQ, Qq, and qq be denoted by a, d, and $-a$. We assume that phenotypic value of a trait is written for the ith individual in F2 as follows:

$$y_i = \mu + s_i h + c_{ai} a + c_{di} d + e_i$$

where μ is the mean; s_i is the indicator of the sex of individual i, which is equal to 1 or −1 for male or female, respectively; h is a sex effect; c_{ai} is the coefficient for the additive component for individual i at the given location that is calculated from the probability of QTL genotypes, and equal to Prob(QQ) − Prob(qq); c_{di} is the coefficient for the dominance component for individual i at the given location, which is equal to Prob(Qq); and e_i is the residual error. Model parameters, μ, h, a, and d, are estimated by a least squares method. That is, estimators of the parameters are obtained such that a sum of squares,

$$S = \sum_{i=1}^{n} (y_i - \mu - s_i h - c_{ai} a - c_{di} d)^2$$

is minimized, where n is the number of individuals of F2. Denoting least squares estimators of μ, h, a, and d, by the terms $\hat{\mu}$, $\hat{h}$, $\hat{a}$, and $\hat{d}$, the minimum sum of squares is obtained as

$$S_1 = \sum_{i=1}^{n} (y_i - \hat{\mu} - s_i \hat{h} - c_{ai} \hat{a} - c_{di} \hat{d})^2$$

Under the null model corresponding to no QTL, where $a = d = 0$ is assumed, the minimum sum of squares is denoted by S_0. Significance detection of QTL is declared based on the ratio of S_1 and S_0. In this report, we used *F*-ratio, $[(S_0 - S_1)/2]/[S_1/(n-2)]$, as a statistic for detecting QTL. Significance thresholds were obtained with 10,000 repeated permutation test cycles for each trait.

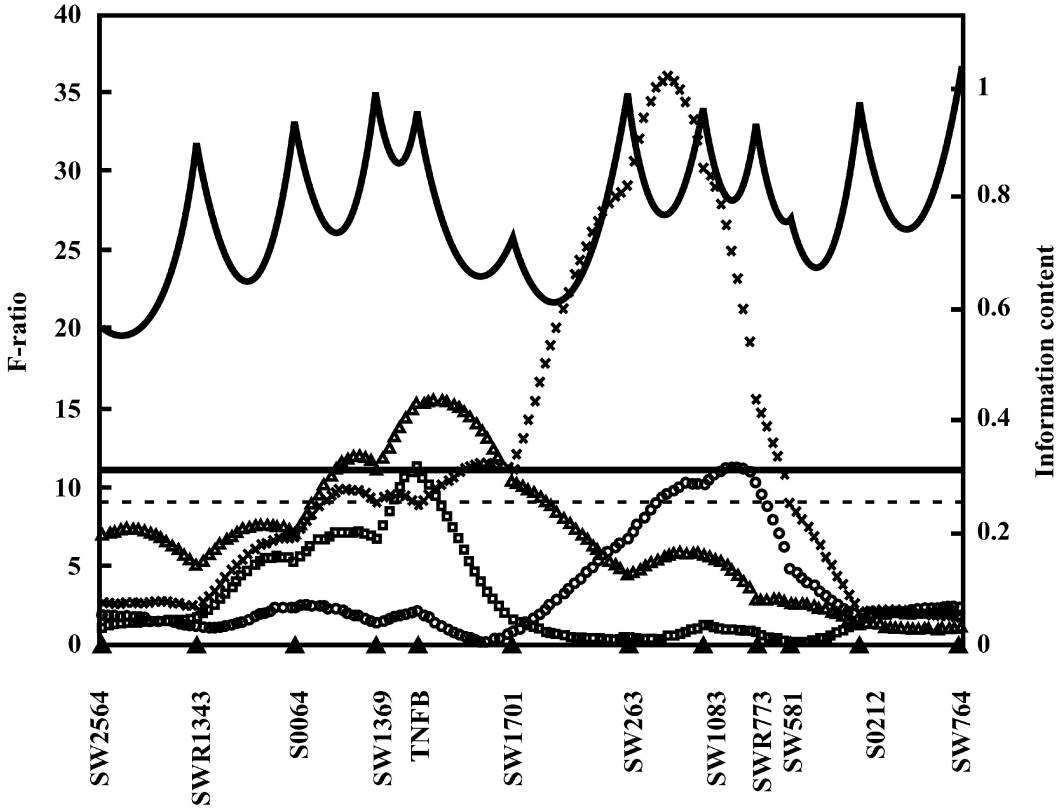

Figure 4. SSC 7. Plot of the *F*-ratio from multilocus least squares analysis (Haley et al. 1994). The x-axis indicates the relative position in the linkage map. The y-axis represents the *F*-ratio. Triangles on the x-axis indicate a marker position. Horizontal lines indicate threshold values for genomewise 5% level (dashed line) and genomewise 1% level (solid line). These levels were different for each trait but, for simplicity, values of 9.00 and 11.00, respectively, are indicated. The specific thresholds are in Table 2. Curved lines indicate information content, □ = backfat thickness, △ = loin muscle area 4th to 5th rib, ○ = loin length, and × = vertebra number.

In chromosomal regions exceeding the suggestive and significance level on some QTL, *P*-values of the nearby markers were computed by SAS-GLM (SAS Inst. Inc., Cary, NC). When two parents have more than two marker alleles, an analysis of the individual marker genotypes will efficiently detect the associations of the different alleles in one or both breeds with specific traits. Phenotypic difference among genotypes of nearby markers was estimated with SAS-GLM. The number of marker genotypes was different depending on the genotypes of the parents. This analysis of variance supported results of QTL analysis and estimated within-breed allele effects rather than between-breed allele effects.

Linkage Map

We searched for informative microsatellites from the USDA-MARC linkage map (Rohrer et al., 1996) and selected 180 microsatellites at approximately 20-cM intervals in the whole pig genome. The 180 microsatellites were genotyped across parents, 28 F1, and 865 F2 animals. A sex-averaged linkage map was constructed with multipoint analysis. The order of the markers was the same as in the USDA-MARC linkage map (Rohrer et al., 1996). The average interval was 12.6 cM, and the total length was 2,263.6 cM, which was comparable to that of the USDA-MARC linkage map (Rohrer et al., 1996). Two large gaps existed between SW274 and SW72 on SSC 3 (34.6 cM) and SW949 and SW980 on SSC X (40.7 cM). The average information content was 0.80.

As this F2 population consisted of only full-sib families, each genotype was checked for segregation distortion. To confirm the presence of a lethal allele, we examined whether the segregation ratio at each marker fit with mendelian ratios 1:2:1, Duroc homozygous, heterozygous, and Meishan homozygous, respectively, by chi-squared test.

Results and Discussion

Population

Although we constructed a pig F2 resource population by crossing only a Meishan sow and a Duroc boar, the genotypes (Duroc homozygous, heterozygous, and Meishan homozygous) segregated in a ratio of 1:2:1 at 159 markers on autosomes. Another 11 markers had segregation distortion ($P < 0.05$). However, adjacent marker

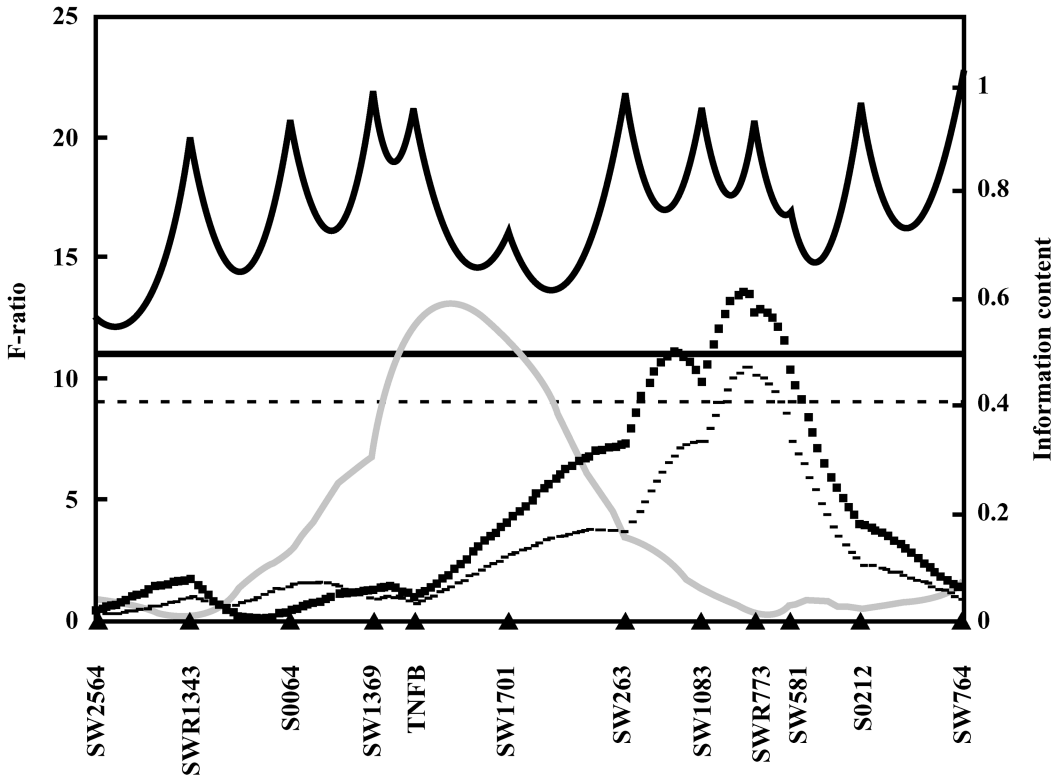

Figure 5. SSC 7. Plot of the *F*-ratio from multilocus least squares analysis (Haley et al. 1994). The x-axis indicates the relative position in the linkage map. The y-axis represents the *F*-ratio. Triangles on the x-axis indicate a marker position. Horizontal lines indicate threshold values for genomewise 5% level (dashed line) and genomewise 1% level (solid line). These levels were different for each trait but, for simplicity, values of 9.00 and 11.00, respectively, are indicated. The specific thresholds are in Table 2. Curved lines indicate information content, ■ = IMF %, — = moisture%, and bold line = carcass yield.

information indicated that this F2 population did not have lethal alleles. This mating made linkage analysis simple and results easily understood.

Mapping of Coat Color Traits

The F2 animals exhibited coat colors of black (n = 373), brown (n = 383), and gray (n = 109). Several brown and gray pigs had black spotting (spotting, n = 289; no spotting, n = 576). The regions associated with coat color were mapped on SSC 1 (107.7 cM) at an *F*-ratio of 28.2 and SSC 6 (1 cM) at an *F*-ratio of 122.0. The spotting region was also mapped on SSC 6 (2 cM) with an *F* ratio of 111.7. The locus on SSC 1 was not previously reported. On SSC 6, the genotypes of marker S0035 at the coat color and the spotting loci were tightly linked to black and brown coat color and spotting. Because the *melanocortin-1 receptor* (*MC1R*) gene was mapped on the SSC 6 telomeric region (Mariani et al., 1996) and the mutations were associated with pig coat color and spotting (Kijas et al., 1998, 2001), partial *MC1R* was amplified by PCR using genomic DNA from F1 and F2 pigs, and sequenced. We confirmed a previous report that Duroc and Meishan pigs are homozygous for *MC1R**4 and heterozygous for *MC1R**2/3 (Kijas et al., 1998), respectively, suggesting that the *MC1R* gene is responsible for coat color and spotting on SSC 6.

QTL Mapping Results

The QTL mapping results are summarized in Table 2. We identified 38 QTL for 28 traits at the 5% genomewise level. Of the 38 QTL, 24 QTL for 17 traits were significant at the 1% genomewise level. The significant QTL are presented in Figures 1 through 7 in detail. Some of the detected QTL replicated previous findings.

We mapped significant QTL for 2-mo testicular weight on SSC 3 (Figure 2) and SSC X (Figure 7). Our results show that males with Meishan alleles at each QTL had larger testicular weight than males with Duroc alleles. The onset of sperm production occurs at a much younger age (56 to 84 d) in Meishans than in conventional boars (120 to 180 d; Lunstra et al., 1997). Ford et al. (2001) have reported mapping a QTL for 220-d testicular size on SSC X using a Meishan × White composite crossbred population. Boars with Meishan alleles at SSC X QTL had smaller testicles than boars with White composite alleles. Therefore, our results for testicular weight at 2 mo of age support the Lunstra et al. (1997) report and are not inconsistent with the

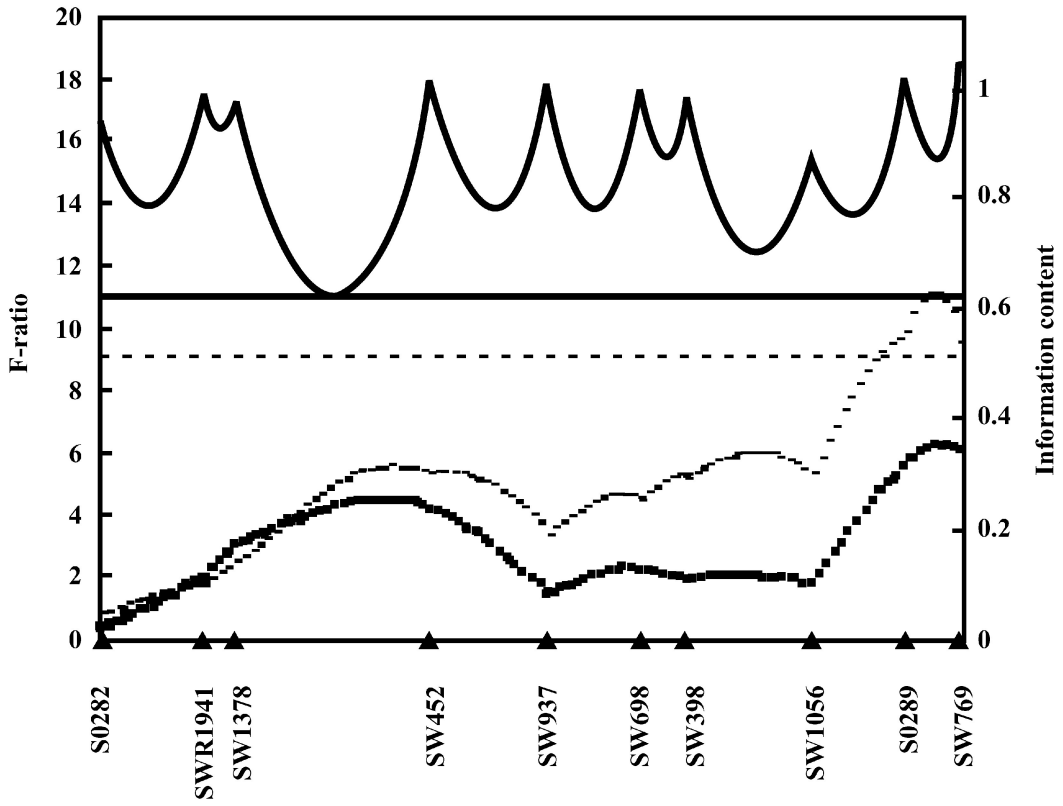

Figure 6. SSC 13. Plot of the *F*-ratio from multilocus least squares analysis (Haley et al. 1994). The x-axis indicates the relative position in the linkage map. The y-axis represents the *F*-ratio. Triangles on the x-axis indicate a marker position. Horizontal lines indicate threshold values for genomewise 5% level (dashed line) and genomewise 1% level (solid line). These levels were different for each trait but, for simplicity, values of 9.00 and 11.00, respectively, are indicated. The specific thresholds are in Table 2. Curved lines indicate information content, ■ = IMF % and — = moisture%.

result of Ford et al. (2001). The *androgen receptor* (*AR*) gene was mapped to the same region of SSC X (Seifert et al., 1999), and testicular weight in *AR*-knockout mice was 80% smaller than wild type mice (Yeh et al., 2002). The location of the QTL on SSC X corresponds to human chromosome Xp11.23-21 and the distal end of mouse chromosome Xp, where mouse *Ihtw1* (*Interspecific hybrid testis weight 1*), one of the loci responsible for testicular weight, was mapped (Elliott et al., 2001). Although the two genes were located near the testicular weight QTL, there could be additional genes affecting testicular weight on SSC X.

We located a significant QTL for birth weight on SSC 7 (Figure 4) and QTL for 30-d weight and ADG (from 30 to 90 kg) on SSC 6 (Figure 3). A potential QTL for ADG was detected on SSC 4, and almost the same region was previously characterized as a QTL affecting growth rates between weaning and 70 kg (Knott et al., 1998) and between weaning and 35 to 56 kg (Paszek et al., 1999). Growth-related QTL other than on SSC 4 that were reported previously, however, were not detected in the present study. On SSC 4, large overdominance effects detected in this study may be due to two QTL linked in repulsion or the negative effect of homozygotes at this QTL. The unique effect at this QTL in our family will provide good information on the role of genes responsible for growth traits. The overdominance effect at this QTL needs to be investigated further. Understanding this QTL based on molecular genetics may aid our understanding of the heterosis effect.

For carcass traits, significant QTL affecting vertebra number were located on SSC 1 and SSC 7 as shown in Figures 1 and 4. At the same regions on SSC 1, we detected QTL for loin length and loin area (Figure 1). Rohrer and Keele (1998a) and Wada et al. (2000) reported QTL for carcass length and vertebra number on the corresponding region of SSC 1, suggesting that a vertebra number QTL could be important for carcass length. A potential QTL was mapped on SSC 6 for carcass length (Table 2) and probably replicated the carcass length QTL on SSC 6 (P-value < 0.01) reported by Paszek et al. (2001). We confirmed the presence of a BFT QTL reported previously on SSC 7 (Rohrer and Keele, 1998a; de Koning et al., 1999; Wada et al., 2000; Malek et al., 2001b) and on SSC X (Knott et al., 1998; Rohrer and Keele, 1998a). Near the BFT QTL on SSC 7, we located a significant QTL for carcass yield and loin muscle area.

For meat quality, we located a significant QTL for IMF on SSC 7, where a potential QTL for muscle mois-

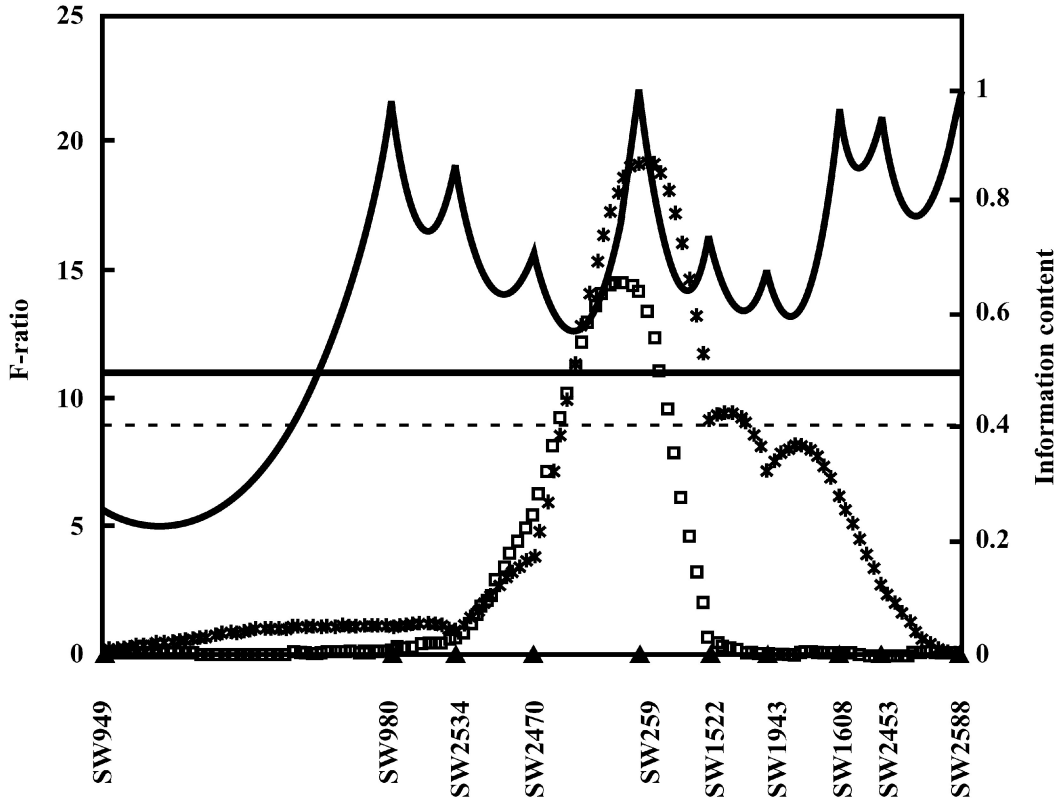

Figure 7. SSC X. Plot of the *F*-ratio from multilocus least squares analysis (Haley et al. 1994). The x-axis indicates the relative position in the linkage map. The y-axis represents the *F*-ratio. Triangles on the x-axis indicate a marker position. Horizontal lines indicate threshold values for genomewise 5% level (dashed line) and genomewise 1% level (solid line). These levels were different for each trait but, for simplicity, values of 9.00 and 11.00, respectively, are indicated. The specific thresholds are in Table 2. Curved lines indicate information content, □ = backfat thickness and * = testicular weight.

ture was detected (Figure 5). In addition, we located both IMF and muscle moisture QTL at the same regions of SSC 9 (near SW983) and SSC 13 (near S0289; Figure 6). On the SSC 9 QTL, the *F*-ratios were 10.75 for IMF and 5.18 for muscle moisture. On the SSC 13 QTL, *F*-ratios were 6.20 for IMF and 11.04 for muscle moisture. Paszek et al. (2001) mapped both QTL on the same region of SSC 6. Whether IMF is directly associated with muscle moisture is not known. *Uncoupling proteins 2* and *3* (*UCP2* and *UCP3*), which are mitochondrial membrane transporters involved in thermogenesis, were mapped to SSC 9p21-p24 (Werner et al., 1999). Because *UCP2* is associated with hyperinsulinemia and obesity in mouse and human (Fleury et al., 1997), *UCP2* and *UCP3* might affect lipid metabolism related to porcine IMF phenotypes.

The results ($P < 0.05$) from analysis of variance based on allele sizes for 22 QTL for 17 traits are shown in Table 3. The genomewise suggestive ($P < 0.10$) QTL for circumference of cannon bone had the highest *P*-value based on analysis of allele sizes. This QTL was mapped at 56.2 cM on SSC 7 with an *F*-ratio of 8.5, and the *P*-value of the nearby marker SW1856 was 9.51×10^{-17} (Table 3). Most of F2 animals that inherited allele 1 from Meishan had larger circumferences of cannon bone. The Meishan population may have genes that affect the circumference of the cannon bone near this marker.

In this study, we detected 24 QTL for 17 traits at the 1% genomewise level. Although crosses with a Meishan breed have been used for detection of QTL by whole-genome scan (de Koning et al., 1999; Paszek et al., 1999; Rohrer and Keele, 1998a,b; Jeon et al., 1999; Wada et al., 2000), we detected more QTL at the 1% genomewise level in this study than previously reported. First, our F2 resource family had a simple structure, with a single boar and sow as founding parents. Second, we genotyped 180 microsatellite markers across 865 F2 offspring, resulting in a high information content of 0.80 in the pig linkage map. These two factors facilitate performing a reliable linkage analysis. Finally, we analyzed a comprehensive set of pig traits, including performance, growth, body size, and carcass and meat quality (Table 1).

Our results identified the presence of several previously identified QTL, such as for testicular weight on SSC X (Ford et al., 2001), growth on SSC 4 (Knott et al., 1998; Paszek et al., 1999), vertebra number on SSC 1 (Wada et al., 2000), and BFT on SSC 7 (Rohrer and Keele, 1998a; de Koning et al., 1999; Wada et al., 2000;

Table 3. Results from analysis of alleles sizes

Trait	SSC	Marker	Alleles[a]	*P*-value
Testicular wt				
Total	3	SWR1637	2/3, 1/3	< 0.001
	3	S0100	2/2, 1/3	< 0.001
Growth				
Birth wt	7	SJ047	1/3, 1/2	0.002
Weight at 30 d	6	SW71	1/1, 2/2	< 0.001
Daily gain from 30 to 90 kg body wt	6	SW1881	2/3, 1/1	< 0.001
Body size				
Circumference of cannon bone	7	SW1856	3/3, 1/2	< 0.001
Carcass measurements				
Carcass yield	7	TNFB	3/4, 1/2	< 0.001
Carcass length III	7	SWR773	1/1, 2/3	0.005
Vertebra number				
Thoracic	7	SW252	1/1, 2/3	< 0.001
Total	1	SW705	1/1, 2/2	< 0.001
Subcutaneous fat thickness				
Shoulder	7	TNFB	3/4, 1/2	< 0.001
Hind belly	6	SW316	1/4, 2/3	0.011
Longissimus muscle				
Length	1	SW705	1/1, 2/2	< 0.001
Loin muscle area at 4–5 rib	7	TNFB	3/4, 1/2	< 0.001
Wholesale cuts				
Loin and belly	8	SW905	1/3, 2/2	0.004
Meat quality				
Lightness (L value)	3	SW72	2/2, 1/3	< 0.001
Moisture	7	SWR773	1/1, 2/3	< 0.001
	9	SW983	1/4, 2/3	0.011
	13	S0289	2/2, 1/3	0.001
Intramuscular fat	7	SWR773	1/1, 2/3	< 0.001
	9	SW983	1/4, 2/3	0.002
	13	SW769	2/2, 1/3	0.003

[a]The value on the left indicates grandparent Duroc alleles, and the value on the right indicates grandparent Meishan alleles. Allele 1 is the smallest-size allele at marker; Allele 4 is the largest-size allele.

Malek et al., 2001b) and on SSC X (Knott et al., 1998; Rohrer and Keele, 1998a). On the other hand, we detected IMF QTL on SSC 7, SSC 9, and possibly SSC 13, although IMF and marbling have also been mapped on SSC 1 (Malek et al., 2001a) and SSC 2, SSC 4, and SSC 5 (de Koning et al., 1999).

Implications

The findings from this study have provided the basic information on the transmission of porcine quantitative traits. Because quantitative trait loci associated with reproduction, growth, and carcass characters were located at the 1% genomewise level in this study, additional markers are necessary to refine the regions. The refined regions should be tested in more commercial populations to estimate their effects. Several quantitative trait loci replicated in this study could be promising targets for marker-assisted selection.

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