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Identification of Quantitative Trait Loci Affecting Carcass Composition in Swine: II. Muscling and Wholesale Product Yield Traits

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ABSTRACT: A genomic scan was conducted on 540 reciprocal backcross Meishan \times White composite pigs for hot carcass weight (HCWT); loin eye area (LOIN); carcass length (CRCL); belly weight (BELLY); and weight of trimmed ham, loin, picnic, and Boston butt adjusted to a constant live (TWPLWT) or carcass (TWPCWT) weight. Genetic markers spanned the entire porcine linkage map and were spaced at approximately 20-cM intervals. Grandparental breed of origin for all chromosomal segments was determined using multipoint linkage procedures, and a least squares regression analysis was conducted. Nominal *P*-values were converted to a genome-wide level of significance to adjust for the number of tests actually conducted. Seven associations were significant at the genome-wide level relating to chromosomes 1 (SSC 1), 7 (SSC 7), and X (SSC X). The SSC 1 region affected LOIN, TWPLWT, and TWPCWT; SSC

7 affected HWCT and CRCL; and SSC X affected TWPLWT and TWPCWT. Twelve associations relating to seven chromosomal regions (including SSC 1 and X) presented suggestive evidence for quantitative trait loci (QTL), and many of these regions are likely to contain QTL. Chromosomes 8 and 14 had two and three traits with suggestive evidence for QTL, respectively. Many pleiotropic effects were detected for regions on SSC 1, 7, 14, and X in this study and a companion study looking for fat deposition QTL in the same population. In addition, SSC 4 was nearly significant for CRCL in the same region identified as affecting backfat in a wild boar \times Large White population. These results expand our knowledge of the inheritance of quantitative traits and are directly relevant to composite populations containing Meishan germplasm.

Key Words: Pigs, Quantitative Traits, Muscles, Genomes, Mapping

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Introduction

To date, there are no reports of genomic scans for quantitative trait loci (QTL) in swine for measures of muscling, percentage lean, or carcass length. Considerable differences have been reported for these traits between swine of Chinese origin and typical commercial swine in the United States (Young, 1992). In our companion article, we detected QTL for fat deposition in a reciprocal backcross Meishan \times White composite population (Rohrer and Keele, 1998). Three genomic regions were detected that significantly affect backfat thickness in this population on chromosomes 1, 7, and X. Additional regions were detected that suggested a QTL may be present based on the criteria of Lander and Kruglyak (1995). However, pleiotropic effects on other carcass traits for the identified regions were not tested. The objectives of this study were to identify QTL that affect musculature, carcass length,

and wholesale product yield, and to evaluate pleiotropic effects of the identified loci. We report the detection of QTL for hot carcass weight, loin eye area, carcass length, and measures of trimmed wholesale product yield in the population previously studied, which contained 540 backcross Meishan \times White composite pigs genotyped for 156 markers spaced at approximately 20-cM intervals. We describe the pleiotropic effects of the detected QTL and discuss their utility for commercial production.

Materials and Methods

The three-generation resource population and genotypic data are described in the companion paper (Rohrer and Keele, 1998). Genetic markers that spanned the genome covered by the current linkage map (Rohrer et al., 1996) with intervals of approximately 20 cM were selected. The animals studied ($n = 540$) were either $\frac{3}{4}$ Meishan- $\frac{1}{4}$ White composite or $\frac{1}{4}$ Meishan- $\frac{3}{4}$ White composite. Males were castrated.

All the male pigs and approximately half of the female pigs (randomly selected) were slaughtered

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Table 1. Phenotypic means for dependent variables and covariates

Trait	$\frac{3}{4}$ Meishan- $\frac{1}{4}$ White composite	$\frac{1}{4}$ Meishan- $\frac{3}{4}$ White composite
Live weight, kg	98.6	99.6
Hot carcass weight, kg	57.5	63.3
Loin eye area, cm ²	20.1	28.3
Carcass length, cm	126.7	139.6
Belly weight, kg	7.1	7.4
Trimmed wholesale product, kg	13.9	16.9

when they weighed approximately 100 kg. Live weight before slaughter was recorded. Carcasses were skinned, rather than scalded and dehaired, so dressing percentage was lower than what is typically observed in the industry. Hot carcass weights were recorded, and carcasses were chilled overnight. Twenty-four hours after death, the carcasses were weighed (chilled carcass weight) and then processed. Carcass length was measured from the anterior edge of the first rib to the anterior edge of the aitch bone. One side of the carcass was split between the 10th and 11th ribs, 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: ham, loin, picnic, Boston butt, and belly. Weight of each wholesale cut was recorded. The ham, loin, picnic, and Boston butt were then trimmed to less than 6 mm of subcutaneous fat, and weight of each trimmed wholesale cut was recorded.

Traits that were included as dependent variables were hot carcass weight (**HCWT**), carcass length (**CRCL**), loin eye area (**LOIN**), belly weight (**BELLY**), and summed weight of the trimmed wholesale product, adjusted to a constant live weight (**TWPLWT**) or carcass weight (**TWPCWT**). Fixed effects fitted were sex, contemporary group, and breed composition. The covariate fitted for HCWT and TWPLWT was live weight, and CRCL, LOIN, BELLY, and TWPCWT were regressed to a constant hot carcass weight. Analysis of TWPCWT was conducted because it is an estimate of the percentage of muscle and bone in the carcass, and TWPLWT reflects the percentage of bone and muscle in the live animal. Phenotypic means for all dependent variables and covariates by breed type are presented in Table 1.

Genotypic effects were parameterized as described (Rohrer and Keele, 1998), which was a modification of Haley et al. (1994) by including the CHROMPIC option of CRI-MAP (Green et al., 1990). Linear contrasts were designed to estimate a and d , where the genotypic value for individuals homozygous for Meishan alleles vs White composite alleles was a and $-a$, respectively. Nominal significance values were

converted to genome-wide significance (Lander and Kruglyak, 1995), as described (Rohrer and Keele, 1998). Critical F-ratio values were approximately 6.6 and 10.15 for suggestive and significant linkages, respectively. Analyses for QTL on chromosome X were conducted with two methods. One test fit a single degree of freedom contrast estimating a and the other estimating a within males and females separately and d within females (3 df). Significance tests were similar for both analyses. Estimates of a in males and females were similar in the second model, and all estimates of d were virtually null; therefore, the single degree of freedom model, estimating a across sexes, has been reported.

Results

Graphical representations of the F-ratio curves are plotted in Figures 1 and 2. Significance levels along with estimates of a and d are presented in Table 2 for all associations with at least a suggestive level of significance. Only seven significant associations were detected, and 12 associations presented suggestive evidence for QTL (Table 2). The only dependent variable without a significant association was BELLY, and only one region with suggestive evidence for a QTL was detected for this trait. The seven significant associations were located in three chromosomal regions (SSC1, 7, and X). The SSC 1 region affected LOIN and both measures of trimmed wholesale product yield (TWPLWT and TWPCWT) and may influence CRCL, SSC 7 affected HCWT and CRCL, and SSC X affected trimmed wholesale product yield (TWPLWT and TWPCWT) along with suggestive associations for LOIN and CRCL. The White composite alleles for the SSC 1 and X regions produced carcasses with more trimmed wholesale product, as would be expected based on differences between the parental breeds and phenotypic averages of the backcross animals (Table 1). However, White composite alleles at SSC 7 yielded shorter and heavier carcasses, even though $\frac{1}{4}$ Meishan- $\frac{3}{4}$ White composite pigs were considerably longer than $\frac{3}{4}$ Meishan- $\frac{1}{4}$ White composite pigs in this study.

Five other chromosomes presented suggestive evidence of a significant association for at least one of the dependent variables. Most convincing were the findings on SSC 8 and 14. A region on SSC 8 displayed evidence for QTL that affect LOIN and TWPCWT in practically the same region of the chromosome. The F-ratio curves for SSC 14 also resembled each other with the strongest evidence of a QTL for LOIN, followed by TWPLWT and TWPCWT. The SSC 11 region had extremely similar results for LOIN and BELLY with peaks at 16 and 15 cM, respectively, and displayed transgressive variation as the Meishan allele produced heavier muscled pigs. The peak on SSC 4 for CRCL

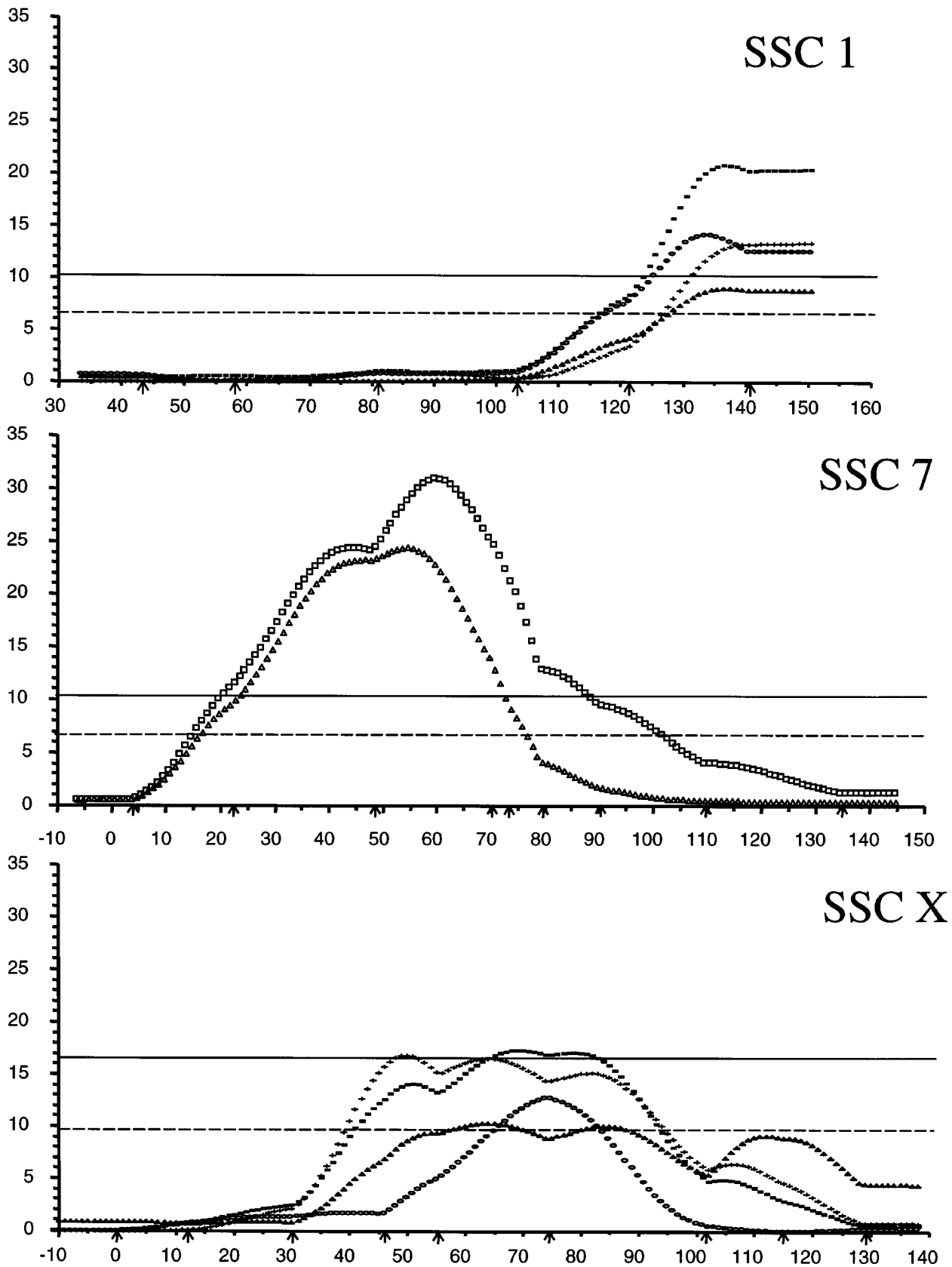


Figure 1. F-ratio curves for analyses with at least one significant association to a trait. Numerator degrees of freedom was two for chromosomes 1 and 7 and only one for the X chromosome. The x-axis indicates the relative position in the linkage map based on Rohrer et al. (1996). The y-axis represents the F-ratio. Arrows on the x-axis indicate a marker position. Horizontal lines indicate threshold values for significant (solid line) and suggestive (dashed line) genome-wide significance. ■ = trimmed product/carcass weight, ○ = loin eye area, + = trimmed product/live weight, △ = carcass length, □ = carcass weight.

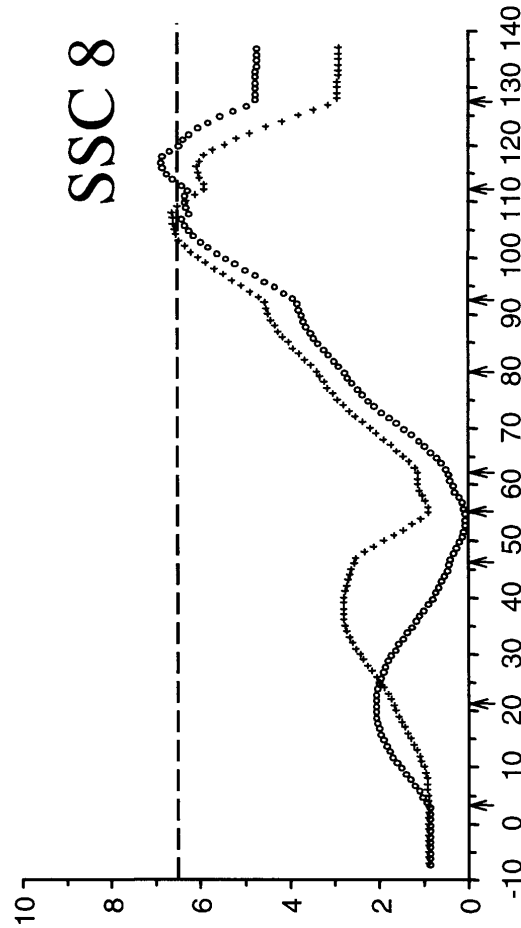
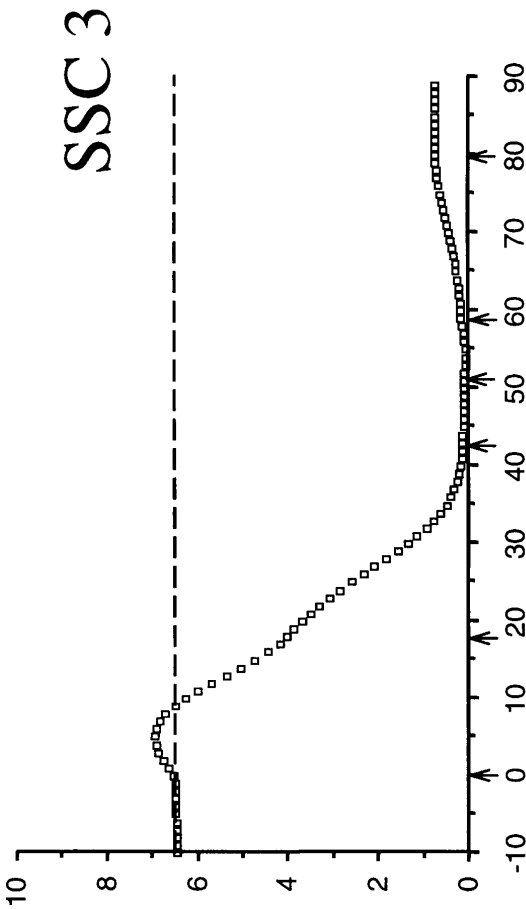
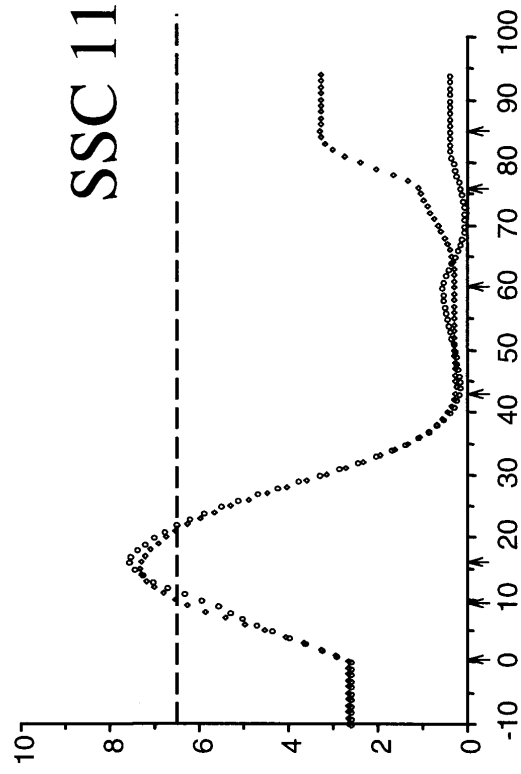
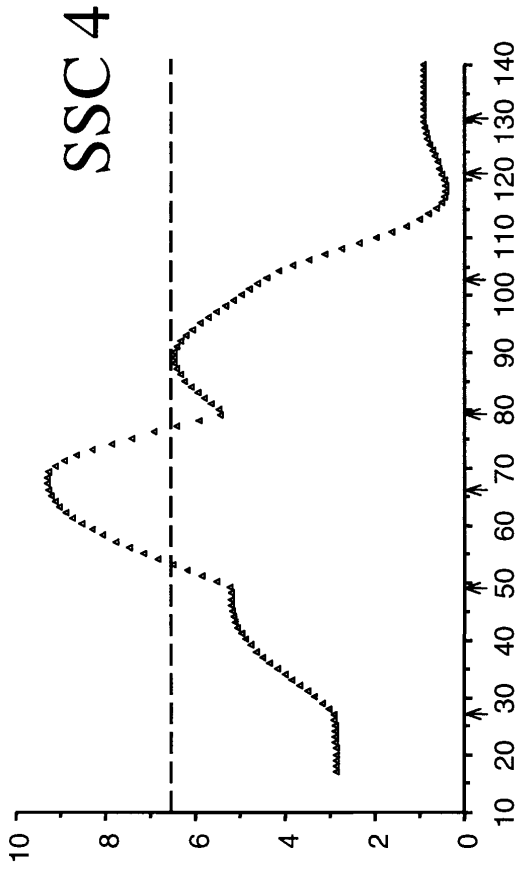
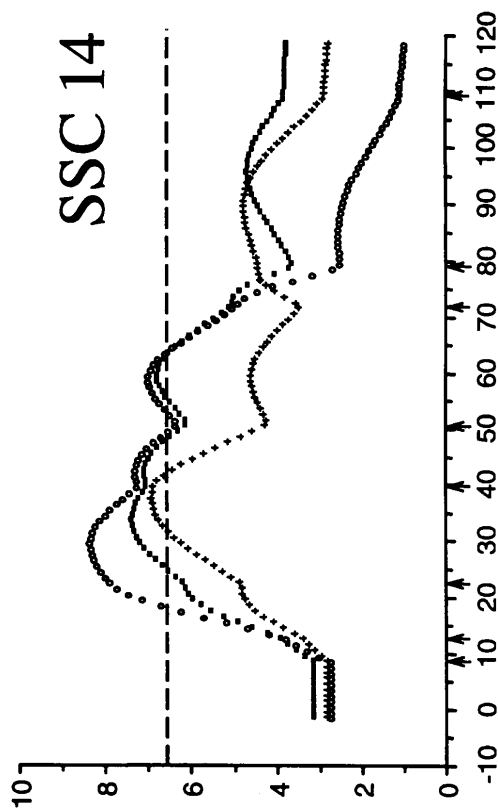


Figure 2. F-ratio curves for association with suggestive evidence of linkage to a QTL. The x-axis indicates the relative position in the linkage map based on Rohrer et al. (1996). Arrows on the x-axis indicate the position where a marker was present. The y-axis represents the F-ratio. The dashed horizontal line indicates the threshold value for suggestive genome wide significance.



was nearly significant at the genome-wide level and SSC 3 presented evidence of a QTL for HCWT.

Additional associations, not quite at the suggestive level of significance, were detected on SSC 2 for LOIN and TWPCWT, SSC 4 for TWPLWT, SSC 5 for BELLY, and SSC 8 for BELLY and TWPLWT.

Discussion

There have not been any reports of genome scans for measures of musculature or product yield in pigs, even though these are extremely important factors that determine the price of market hogs. The mutation in the ryanodine receptor (**RYR1**) discovered by Fujii et al. (1991) either increases muscle content or is linked to a QTL that enhances muscle accretion because homozygotes (stress-susceptible) tend to have larger loineyes and are leaner than nonstress-susceptible pigs (Christian and Rothschild, 1981). However, RYR1 has been mapped to SSC 6, and no evidence for QTL existed on SSC 6 in this study. This is probably because the recessive mutation for the RYR1 gene was not present in this population (Rohrer et al., 1997). Two different mutations affecting muscling in livestock have been identified. The muscle hypertrophy phenotype in cattle is hypothesized to be caused by a mutation in GDF8 (Grobet et al., 1997; Kambadur et al., 1997), which maps to SSC15 (Sonstegard et al., 1998). In sheep, callipyge causes extreme muscling (Cockett et al., 1994), and its porcine homologue is likely to be located in the interval spanned by SSC 7q2.1–2.6. Neither of these regions coincide with locations of putative QTL from this study.

A comparison of the results from this study and those of our companion article (Rohrer and Keele, 1998) identifies many pleiotropic associations. The QTL identified for body composition possibly affect metabolism or energy partitioning and would imply that pleiotropic effects are likely to exist. Furthermore, phenotypic correlations between some traits were high (Table 3). An understanding of all the pleiotropic effects of a QTL may reveal the biochemical pathway that is affected and provide valuable insight into the selection of positional candidate genes. The QTL on SSC 1 affects backfat accretion and loin eye area, thus producing a very dramatic effect on trimmed wholesale product. Based on the data reported by Goureau et al. (1996), this region should be homologous to human chromosome (HSA) 9, and most likely the human homologue for the QTL lies on HSA 9q (the long arm). Unfortunately, few positional candidate genes lie within this region. The QTL on SSC 7 affects fat deposition, carcass length, and dressing percentage with all of the desirable effects associated with the Meishan allele. Even though a QTL for body mass index has been identified in a

similar region in humans (Norman et al., 1995), the affect of this QTL on body length was not documented. The confidence interval surrounding this QTL covers chromosomal regions homologous to segments of HSA 6 and 15. Refinement of this QTL peak should be conducted to determine positional candidate genes. The significant region for backfat identified on SSC X also presented evidence for a QTL that affects CRCL, LOIN, TWPLWT, and TWPCWT. Currently, too few genes have been mapped in swine within this region to select positional candidate genes from HSA X (Hu et al., 1997).

A similar region on SSC 14 had suggestive evidence for QTL affecting LOIN, TWPCWT, TWPLWT, average backfat, and fat over the first rib and last lumbar vertebra (Rohrer and Keele, 1998). The F-ratio curve for LOIN is shifted to the left of the curves for measures of backfat and may represent two separate loci. Selection of positional candidates for the QTL on SSC 14 will be difficult because the confidence

interval spans a region homologous to segments from four human chromosomes (Goureau et al., 1996). The QTL for backfat and intestinal length identified by Andersson et al. (1994) on SSC 4 is possibly the same region that affects carcass length in this study; even though this region did not seem to affect fat deposition (Rohrer and Keele, 1998).

Caution should be used when evaluating pleiotropic effects because they may be caused by environmental correlations between traits or may be artifacts of the statistical model. In addition, the data are not sufficient to discern between true pleiotropic effects and effects of closely linked nonpleiotropic genes. However, if the observations are due to pleiotropy, multivariate (Zeng, 1997) or infinite-dimensional (Kirkpatrick, 1997) analyses would increase power to localize the region of the chromosome containing the QTL. Collection of genotypes from additional markers in the regions containing putative QTL should create F-ratio curves with sharper peaks (smaller confidence

Table 2. Putative QTL detected with at least a suggestive level of significance

Trait and chromosome	Position, cM ^a	Genotype value ^b		Significance		
		<i>a</i>	<i>d</i>	F-ratio	nominal ^c	genome ^d
Belly weight						
11	15 (1–30)	–.114	–.040	7.3284	.000725	.54512
Hot carcass weight						
3	5 (–10–25)	–.805	.114	6.8941	.001107	.78407
7	60 (34–75)	–1.833	.168	30.8839	.000000	.00000
Loin eye area						
1	134 (120–150)	–1.525	.183	13.6285	.000002	.00234
8	117 (78–137)	–1.308	–.088	6.8456	.001160	.81641
11	16 (1–30)	1.097	.171	7.5224	.000600	.46301
14	30 (12–77)	–1.308	–.088	8.3226	.000276	.23496
X	74 (52–92)	–1.037	NA ^e	12.6282	.000414	.26912
Carcass length						
1	138 (120–150)	–.944	.058	8.7086	.000190	.16897
4	67 (34–104)	–.943	.020	9.3131	.000106	.10056
7	55 (30–69)	1.560	–.119	24.3642	.000000	.00000
X	64 (36–138)	–.753	NA	10.2373	.001458	.77418
Trimmed wholesale product/live weight						
1	136 (126–150)	–.627	.005	19.9686	.000000	.00001
14	34 (–1–101)	–.372	.005	7.3598	.000703	.53093
X	69 (37–98)	–.392	NA	17.0883	.000041	.03620
Trimmed wholesale product/carcass weight						
1	150 (128–150)	–.580	.013	12.8862	.000003	.00448
8	108 (72–137)	–.354	.000	6.6287	.001434	.97764
14	38 (–1–100)	–.330	.024	6.9292	.001070	.76146
X	50 (36–110)	–.405	NA	16.6996	.000050	.04317

^aRelative position is in centimorgans, based on maps developed in Rohrer et al. (1996), and values in parentheses represent the 95% confidence interval.

^bGenotypic values are as described by Falconer (1981) in units of centimeters for carcass length, square centimeters for loin eye area, and kilograms for the other traits.

^cProbability of a false-positive for a single hypothesis test.

^dExpected number of false-positives per genome-wide scan based on equations from Lander and Kruglyak (1995).

^eNA = not .

Table 3. Phenotypic variances and correlations between all traits analyzed^a

Trait	FRIB	10th	LRIB	LLUM	AVBF	LEAF	HCWT	BELLY	TWP	LOIN	CRCL
1st-rib backfat (FRIB), cm	.92	.65	.58	.59	.86	.47	.19	.32	-.30	-.25	-.30
10th-rib backfat (10th), cm		.87	.70	.73	.80	.56	.18	.33	-.43	-.41	-.36
Last-rib backfat (LRIB), cm			.47	.67	.85	.50	.30	.36	-.23	-.17	-.34
Last lumbar backfat (LLUM), cm				.71	.88	.50	.17	.30	-.37	-.32	-.36
Average backfat (AVBF), cm					.71	.56	.25	.37	-.35	-.29	-.39
Leaf fat (LEAF), kg						.14	.36	.53	-.18	-.15	-.26
Hot carcass weight (HCWT), kg							32.15	.77	.70	.50	.42
Belly weight (BELLY), kg								.76	.29	.18	.17
Trimmed wholesale product (TWP), kg									3.82	.81	.64
Loin eye area (LOIN), cm ²										29.20	.33
Carcass length (CRCL), cm											8.09

^aPhenotypic variances are on the diagonal and phenotypic correlations are on the off-diagonal.

intervals), improve estimates of the QTL effects, and facilitate detection of genotypic errors in the data set.

It is important that future research focuses on characterizing allelic distributions of QTL in target populations. This information is necessary for marker-assisted selection in uncharacterized populations. An analogous problem existed for conventional techniques of genetic improvement before across-herd evaluation systems were in place. Elite swine producers had observed that purchased germplasm tended to be of lower genetic value (contained fewer favorable alleles) than breeding stock available in their own herds despite the magnitude of their predicted breeding values (David et al., 1985). This occurred because the genetic evaluation system was incapable of comparing animals (allelic variation) across herds. In the same way, it is difficult to know whether selection for certain favorable QTL alleles will benefit a population if the current genetic makeup (distribution of QTL alleles) of the population is unknown. The target population may already be fixed for the desirable allele or possess unique alleles superior to those previously characterized for the QTL under consideration.

Implications

This is the first genomic scan conducted in swine for muscle and trimmed product yield traits. These results implicate the importance of pleiotropic effects for QTL that affect quantitative traits. However, before the hypothesis of multiple linked QTL can be ruled out, more markers should be analyzed in the significant regions. The use of multivariate and multiple QTL analyses may help resolve the actual location of QTL. These regions should be tested in other populations to characterize allelic variation prior

to implementation of marker-assisted selection. The QTL on SSC 1, 7, 14, and X warrant further studies and may be useful for marker-assisted selection to improve carcass composition.

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