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Quantitative trait locus mapping in an F_2 Duroc × Pietrain resource population: II. Carcass and meat quality traits[1]

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ABSTRACT: Pigs from the F_2 generation of a Duroc × Pietrain resource population were evaluated to discover QTL affecting carcass composition and meat quality traits. Carcass composition phenotypes included primal cut weights, skeletal characteristics, backfat thickness, and LM area. Meat quality data included LM pH, temperature, objective and subjective color information, marbling and firmness scores, and drip loss. Additionally, chops were analyzed for moisture, protein, and fat composition as well as cook yield and Warner-Bratzler shear force measurements. Palatability of chops was determined by a trained sensory panel. A total of 510 F_2 animals were genotyped for 124 microsatellite markers evenly spaced across the genome. Data were analyzed with line cross, least squares regression interval, mapping methods using sex and litter as fixed effects and carcass weight or slaughter age as covariates. Significance thresholds of the *F*-statistic for single QTL with additive, dominance, or imprinted effects were determined on chromosome- and genome-wise levels by permutation tests. A total of 94 QTL for 35 of the 38 traits analyzed were found to be significant at the 5% chromosome-wise level. Of these 94 QTL, 44 were significant at the 1% chromosome-wise, 28 of these 44 were also significant at the 5% genome-wise, and 14 of these 28 were also significant at the 1% genome-wise significance thresholds. Putative QTL were discovered for 45-min pH and pH decline from 45 min to 24 h on SSC 3, marbling score and carcass backfat on SSC 6, carcass length and number of ribs on SSC 7, marbling score on SSC 12, and color measurements and tenderness score on SSC 15. These results will facilitate fine mapping efforts to identify genes controlling carcass composition and meat quality traits that can be incorporated into marker-assisted selection programs to accelerate genetic improvement in pig populations.

Key words: carcass composition, meat quality, pig, quantitative trait loci

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INTRODUCTION

Enhancement of production efficiency and improvement of product quality are major concerns for producers of food animals. Swine have been selected for increased lean growth, but the antagonistic relationship with meat quality, with genetic correlations of carcass leanness with ultimate pH (–0.13), reflectance (0.16), and drip loss (0.05) as reported in a literature review by Sellier (1998), has caused a decrease in meat quality. Additionally, Wood (1985) reported increased occurrence of less juicy pork products with leaner pigs. Locating QTL for meat quality and using these in genetic improvement programs will help overcome this relationship and allow improvement in both efficient production and product quality.

The Duroc and Pietrain breeds are utilized worldwide as sire breeds, and these breeds differ in carcass and meat quality phenotypes. Quiniou and Noblet (1995) used Pietrain boars in their study because of the breed's propensity toward leanness. Affentranger et al. (1996) compared Duroc and Pietrain pigs and reported more backfat for Duroc animals as compared with Pietrain animals. In a study of Duroc- vs. Pietrain-sired pigs that were all homozygous normal for the RYR1 gene (Edwards et al., 2003), Duroc-sired pigs had longer carcasses than Pietrain-sired pigs, whereas Pietrain-sired pigs had less backfat at the 10th rib and larger LM area at slaughter than Duroc-sired pigs. Meat quality was more favorable for Duroc- vs. Pietrain-sired pigs in Affentranger et al. (1996) and Edwards et al. (2003). In general, Duroc and Duroc-sired pigs have favorable

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meat quality (Langlois and Minvielle, 1989; Jeremiah et al., 1999), whereas Pietrain and Pietrain-sired animals are leaner with average meat quality (Edwards et al., 2003).

The objective of this study was to conduct a full genome scan using microsatellite markers to search for QTL affecting carcass and meat quality traits in an F_2 Duroc × Pietrain resource population.

MATERIALS AND METHODS

Experimental procedures were approved by the All University Committee on Animal Use and Care at Michigan State University.

Population Development

A 3-generation resource population was developed from 4 F_0 Duroc sires and 16 F_0 Pietrain dams at Michigan State University to study traits of growth, body composition, and meat quality. All grandparents were confirmed to be homozygous normal for the RYR1 gene by a DNA test (Fujii et al., 1991). Further details of population development and animal management are found in Edwards et al. (2008).

Phenotype Collection

At slaughter, pigs were transported to 1 of 2 abattoirs. A total of 176 pigs were slaughtered at the Michigan State University Meat Laboratory (East Lansing, MI) to facilitate tissue collection for future studies, and the remaining pigs were transported to a small federally inspected plant in western Michigan (DeVries Meats, Coopersville, MI). Slaughter age was 165.8 ± 9.2 d. All groups were fasted and allowed to rest overnight with access to water. Ear tag and tattoo numbers were recorded at slaughter to maintain identity of each carcass. Carcass traits collected included HCW and LM pH and temperature at 45 min and 24 h postmortem. Dressing percent was calculated by dividing HCW weight by live slaughter weight. After overnight chilling, midline first-rib backfat, last-rib backfat, last-lumbar backfat, number of ribs, and carcass length measurements were taken according to National Pork Producers Council guidelines (NPPC, 2000). Weights of primal cuts of ham, closely trimmed loin, picnic shoulder, Boston shoulder, belly, and spareribs were recorded. During carcass fabrication, measurements of 10th-rib backfat and LM area were also recorded (NPPC, 2000). A section of loin from the 10th-rib to the last rib was further evaluated for meat quality traits at Michigan State University. All measurements were taken from the left side of each carcass.

Boneless LM were removed from loin sections and external fat was trimmed. A small portion of LM was diced and frozen for proximate analysis. Two 2.54-cm-thick chops were cut from the anterior end of the LM for fresh meat quality analysis. The 2 chops were allowed to bloom for a minimum of 10 min and evaluated for subjective scores of color and marbling (NPPC, 2000) and firmness (NPPC, 1991). The color score scale ranged from 1 (pale pinkish gray) to 6 (dark purplish red). The marbling score scale was 1 to 10 (closely approximating fat percentage). The firmness score scale was 1 (very soft and watery) to 5 (very firm and dry). A single trained evaluator was used for subjective scoring across all slaughter dates. Additionally, objective color scores of CIE L* (lightness), a* (redness), and b* (yellowness) were obtained using a Minolta CR-310 colorimeter (Ramsey, NJ) with a D_{65} illuminant and a 2-degree standard observer. Chops were weighed, hung in sealed plastic bags for 24 h at 4°C, and then weighed again for drip loss measurement. The remaining section of the LM was vacuum-packaged, aged at 4°C until 7 d postmortem, and frozen for further meat quality tests of cook yield, shear force, and sensory panel analysis.

From frozen loin sections, chops were cut for cook yield, Warner-Bratzler shear force (**WBS**), and sensory analysis. Frozen chops for these analyses were thawed for 24 h at 2.6°C and then cooked on a Taylor clamshell grill (Model QS24, Taylor Co., Rockton, IL). The upper plate was set to 104.4°C and the bottom plate was set to 102.8°C with a 2.16-cm gap between plates. Temperature was monitored by inserting a copper constantan thermocouple (0.051-cm diam., 15.2-cm length, Omega Engineering Inc., Stamford, CT) into the geometric center of the pork chop. Chops were cooked to a final internal temperature of 71°C. For cook yield measurements, each thawed chop was weighed, cooked, cooled to room temperature, and weighed again. From these chops, six 1.27-cm-diam. cores (3 cores from each chop) were taken parallel to the muscle fiber direction using a drill press-mounted corer. Cores were sheared perpendicular to muscle fibers using a Warner-Bratzler head on a TA-HDi texture analyzer (Texture Technologies Corp., Scarsdale, NY) with a crosshead speed of 3.30 mm/s. Samples for proximate composition were ground using dry ice and measured for moisture (oven drying), fat (soxhlet ether extraction), and protein (nitrogen combustion, Model FP-2000, Leco Inc., St. Joseph, MI) following AOAC procedures (2000).

Trained Sensory Panel Evaluation

A trained panel of 7 healthy adults (ages 20 to 65) was utilized to determine specific sensory attributes of each top loin (LM) chop. The sensory panel was trained according to Meilgaard et al. (1991) and AMSA (1995). All panelists had experience in sensory evaluation and were previously trained to evaluate various meat products. Each sample was evaluated for juiciness, muscle fiber and overall tenderness, connective tissue, and off-flavor using an 8-point hedonic scale. Greater scores in each of the first 4 categories were more favorable and indicated extremely juicy, extremely tender, or no connective tissue for each of these attributes, respectively,

whereas lower scores for off-flavor were indicative of less off-flavor.

Cooked chops were prepared as described previously. Sample preparation included cutting 1.27-cm cubes from the center portion of each chop, placing 2 cubes each into soufflé cups, and covering them with a lid. Soufflé cups were placed in a Pyrex bowl with a lid, and the bowl was covered with warm towels to keep the samples warm. The insulated bowl was placed in an insulated container and transferred to the sensory evaluation room.

Testing took place in a climate-controlled room with partitioned booths and cool incandescent light. The order of sample preparation was randomized within each session to minimize positional bias and a 3-digit random code was used to label the samples. The samples were picked up with a toothpick, chewed with the molars, and evaluated. Expectorant cups were provided to prevent taste fatigue, and distilled deionized water was used to clean the palate between samples. The panelists were standardized each day by evaluating a warm-up sample and discussing the results. A total of 18 to 24 samples were evaluated each day, and the days were divided into 3 sessions each with a 15-min break between each session.

Genotype Collection

Carcass and meat quality trait measurements were obtained on 958 F_2 pigs, of which 510 were used for this study. Genotypes for 124 dinucleotide microsatellite genetic markers were determined for the 510 F_2 animals, their parents, and their grandparents at a commercial laboratory (GeneSeek Inc., Lincoln, NE). These 510 animals were sampled across all farrowing groups from 61 entire litters and represented all F_1 sires with at least 100 grand progeny from each F_0 sire. Fifteen of the 16 F_0 dams had a son or daughter as a parent that produced multiple litters of the selected F_2 pigs, with the remaining F_0 dam represented by a single F_1 daughter with 1 litter in this group. Details regarding genotyping and the markers used in this genome scan were reported in Edwards et al. (2008).

QTL Analysis

Genetic linkage maps were constructed for all 18 autosomes and the X chromosome using Crimap version 2.4 software (Green et al., 1990) and are reported in Edwards et al. (2008). These maps were used in an F_2, least squares interval mapping framework for QTL analysis (Haley et al., 1994), similar to that described in Edwards et al. (2008). The F_2 analysis option of the QTL Express software (Seaton et al., 2002) was used to search for single QTL with additive, dominance, or imprinting effects on the 18 autosomes and additive effects on the X chromosome for the carcass and meat quality traits, with the fixed effects of sex of the animal and slaughter date along with the covariates listed in Table 1. The terms that were included in each model were those that were found to be important to the model ($P < 0.20$) when each trait was analyzed by ordinary least squares analysis of variance without QTL effects. Fixed effects of sex of the animal and slaughter date were included in every model. Some models contained the covariates of carcass weight or slaughter age, whereas others had neither covariate (Table 1).

Tests of the full model including additive, dominance, and imprinting effects vs. the reduced model without

Table 1. Statistical model terms for carcass and meat quality trait QTL analyses[1]

	Covariate[2]	
Trait	Carcass weight	Slaughter age
Carcass measure		
Off-farm BW	—	X
Hot carcass weight	—	X
Dressing percent	—	—
45-min carcass temperature	X	—
24-h carcass temperature	X	—
45-min pH	X	—
24-h pH	X	—
45-min to 24-h pH decline	X	—
Carcass length	X	—
Number of ribs	—	—
First-rib backfat	X	—
Last-rib backfat	X	—
Last-lumbar vertebra backfat	X	—
Tenth-rib backfat	X	—
LM area	X	—
Primal cut weight		
Ham weight	X	—
Loin weight	X	—
Boston shoulder weight	X	—
Picnic shoulder weight	X	—
Belly weight	X	—
Spareribs weight	X	—
Meat quality evaluation		
Color	—	—
Marbling	—	X
Firmness	—	X
L*	—	—
a*	—	—
b*	—	—
Proximate analysis		
Moisture	X	—
Fat	X	—
Protein	X	—
Laboratory analyses		
Drip loss	—	X
Cook yield	—	—
Warner-Bratzler shear force	—	—
Sensory panel analyses		
Juiciness	—	—
Tenderness	—	—
Overall tenderness	—	—
Connective tissue	—	—
Off-flavor	—	—

[1]All models included sex of the animal and slaughter date as fixed effects.
[2]X = used in model, and — = not used in model.

these effects were carried out to determine *F*-ratios at 1-cM intervals across the genome. Significance thresholds of 5 and 1% at the chromosome-wise and 5 and 1% at the genome-wise levels were determined through the use of permutation tests (Churchill and Doerge, 1994) in QTL Express using 30,000 permutations. For each QTL determined to be significant at the 5% genome-wise level, confidence intervals of the QTL position were determined using a bootstrap method, with 5,000 permutations in QTL Express (Visscher et al., 1996).

RESULTS AND DISCUSSION

QTL Analysis

Trait means and standard deviations for genotyped animals with measured phenotypes are reported in Table 2. These means and standard deviations are similar to those measured in other resource populations reporting similar traits (e.g., Malek et al., 2001a; Stearns et al., 2005). The permutation test results of F-ratio calculations to determine significance thresholds for the model testing additive, dominance, and imprinting effects ranged from 3.44 to 4.35 across different chromosomes for the 5% chromosome-wise levels and from 4.71 to 5.64 for the 1% chromosome-wise levels. Genome-wise *F*-ratio threshold levels were 6.34 and 7.63 for 5% and 1% levels, respectively. Significance levels of the *F*-statistic for the additive effect only model for SSC X were 6.68 and 9.93 for 5% and 1% chromosome-wise levels, respectively, whereas the significant F-ratios were 12.86 and 16.05 for 5% and 1% genome-wise levels, respectively.

Estimates of position and F-ratio for carcass and meat quality QTL significant at the 5% chromosome-wise level are listed in Table 3. The table is sorted by chromosome and position within each chromosome. Additionally, the additive, dominance, and imprinting effect of each QTL along with the standard errors are listed in Table 3. A total of 94 QTL for 35 of the 38 traits were found to be significant at 5% chromosome-wise levels. Of these 94 QTL, 44 were significant at the 1% chromosome-wise, 28 of these 44 were also significant at the 5% genome-wise, and 14 of these 28 were also significant at the 1% genome-wise significance thresholds. No significant QTL were detected in this population for subjective firmness, Boston shoulder weight, or picnic shoulder weight.

All chromosomes, except 13, contained at least 1 QTL for these 38 traits. Although the 2 breeds used to create this resource population are used in similar capacities in many pork production chains, many important QTL that impact phenotypic differences between the breeds still exist and are possible candidates to explore more thoroughly for identifying genes controlling these traits. Differences in carcass and meat quality traits between animals sired by Duroc or Pietrain boars in a crossbred progeny study (Edwards et al., 2003) have been previously reported. Some of the breed allelic QTL effects in the current study had effects in the same direction as breed effects reported in Edwards et al. (2003), but a few cryptic alleles were also detected that acted in an opposite direction to the general trend for the overall breed effects.

Carcass Traits

The carcass traits included many of the classically measured carcass traits that affect prices paid for market pigs. Measures of off-farm BW and HCW are related, and QTL for these 2 traits appeared in similar positions. Two significant QTL were identified. One on SSC 4 expressed an additive effect, where Pietrain alleles increased these weights, and one on SSC 10 indicated the largest effect for imprinting, where alleles from Pietrain dams increased these weights. These QTL were significant at the 5% genome-wise and 1% chromosome-wise levels, respectively. Whereas other studies have reported QTL for live weight at slaughter on SSC 4 (Marklund et al., 1998; Cepica et al., 2003), the position of these QTL was more distal from the origin of the map than the 12-cM distance observed in this study. By utilizing the population of Cepica et al. (2003), a subsequent analysis by Dragos-Wendrich et al. (2003) identified a QTL for live weight at slaughter on SSC 10 but, again, not in the same position as reported here. Several studies have reported QTL for carcass weight on SSC 4 (Pérez-Enciso et al., 2000; Malek et al., 2001b; Cepica et al., 2003), but all of these studies reported positions more distal (85 to 121 cM from the first marker) than was discovered in this population.

Carcass temperature and pH at 45 min and 24 h postmortem are important early indicators of meat quality. The pH decline between these 2 time points is a rarely studied trait, but is indicative of changes in meat properties that affect further quality parameters. Figure 1 shows the F-ratio curves plotted vs. relative marker positions on SSC 3 and illustrates the similar shapes of F-ratios for 45-min pH and pH decline from 45 min to 24 h postmortem. A QTL that was significant at the 1% chromosome-wise level was discovered in this population that was additive and increased 45-min pH when Pietrain alleles were present. In addition, a QTL in this position also caused a smaller decrease in pH from 45 min to 24 h with Pietrain alleles. The Pietrain alleles caused favorable changes for these 2 traits, which should improve meat quality. These can be considered cryptic alleles because previous studies reported lower pH values for Pietrain or Pietrain-cross pigs compared with animals from other breeds (Affentranger et al., 1996; Garcia-Macias et al., 1996; Edwards et al., 2003). This QTL region affecting pH on SSC 3 was in a similar location to a pH QTL reported by Beeckmann et al. (2003) in a population that contained Pietrain germplasm. Additional QTL significant at the 5% genome-wise level were found for 24-h carcass temperature on SSC 5, which was estimated to have a dominance effect with a large magnitude, and another

Table 2. Number of records, means, and SD for carcass and meat quality traits measured

Trait	n	Mean	SD
Carcass measure			
Off-farm BW, kg	504	111.89	9.12
Hot carcass weight, kg	504	81.35	7.19
Dressing percent, %	504	72.69	2.12
45-min carcass temperature, °C	503	39.20	2.26
24-h carcass temperature, °C	502	2.74	1.19
45-min pH	497	6.38	0.23
24-h pH	484	5.53	0.15
45-min to 24-h pH decline	478	0.84	0.23
Carcass length, cm	503	78.92	2.59
Number of ribs	357	14.84	0.86
First-rib backfat, mm	417	40.67	7.19
Last-rib backfat, mm	503	28.65	6.29
Last-lumbar vertebra backfat, mm	502	22.29	6.59
Tenth-rib backfat, mm	499	24.15	7.25
LM area, cm^2	500	40.94	4.60
Primal cut weight			
Ham weight, kg	503	9.56	0.81
Loin weight, kg	503	8.17	0.86
Boston shoulder weight, kg	503	3.72	0.63
Picnic shoulder weight, kg	503	3.89	0.65
Belly weight, kg	503	4.94	0.69
Spareribs weight, kg	502	1.48	0.20
Meat quality evaluation			
Color, 1 to 6	502	3.21	0.82
Marbling, 1 to 10	503	2.88	0.80
Firmness, 1 to 5	489	2.86	0.81
L*	487	53.63	2.21
a*	487	17.26	1.91
b*	487	9.10	1.61
Proximate analysis			
Moisture, %	494	73.88	1.50
Fat, %	494	3.27	1.33
Protein, %	493	23.39	1.09
Laboratory analyses			
Drip loss, %	503	1.71	1.18
Cook yield, %	498	77.46	2.94
Warner-Bratzler shear force, kg	497	3.19	0.69
Sensory panel analyses			
Juiciness, 1 to 8	501	5.28	0.58
Tenderness, 1 to 8	501	5.59	0.61
Overall tenderness, 1 to 8	501	5.65	0.55
Connective tissue, 1 to 8	501	6.39	0.38
Off-flavor, 1 to 8	501	1.14	0.21

on SSC 6, which was additive in its effect and indicated animals with Duroc alleles increased 24-h carcass temperature. On SSC 9, QTL for 45-min temperature and 24-h temperature were found, but these were in separate regions of the chromosome. No other QTL studies have reported carcass temperature measurements, but our work indicates that significant QTL controlling carcass temperature at 45 min and 24 h after slaughter are present and warrant further study.

Measurements of skeletal characteristics of a carcass are important in determining size and ability to grow to heavier weights while maintaining leanness. Carcass length QTL were present on SSC 6 and 7 with both significant at the 1% genome-wise level. The QTL on SSC 6 showed a positive value for the dominance effect, whereas the one on SSC 7 affected both carcass length and dressing percent in an additive manner (Figure 2). Duroc alleles caused a lengthening of the carcass and decreased dressing percent. A similar dominance effect QTL was reported on SSC 6 by Malek et al. (2001b), while the QTL on SSC 7 was in a similar position to one reported by Rohrer and Keele (1998). Two putative QTL were detected for the number of ribs in each carcass with one on SSC 7 and one on SSC 18. Our QTL on SSC 7 was estimated to have a positive value for the imprinting effect, whereas animals that received a Duroc allele from the sire had an increase of 0.34 ribs. The QTL for number of ribs on SSC 7 was found in the same location as one detected in several populations by Mikawa et al. (2005). Of 9 families reported in their

Table 3. Position and significance level of carcass and meat quality QTL significant at the 5% chromosome-wise level, with additive, dominance, and imprinting effects and SE

Chr[1]	Trait	Pos,[2] cM	Additive effect	SE	Dominance effect	SE	Imprinting effect	SE	*F*-ratio[3]
1	LM area, cm^2	10	–1.23	0.31	0.44	0.56	0.13	0.30	5.47
1	Dressing percent, %	71	–0.42	0.12	0.05	0.20	–0.38	0.13	6.03*
1	Spareribs wt, kg	172	0.02	0.01	–0.11	0.02	–0.04	0.01	11.24***
2	Juiciness, 1 to 8	54	–0.10	0.04	–0.16	0.07	–0.08	0.04	4.64
2	Off-flavor, 1 to 8	70	–0.05	0.01	0.01	0.02	–0.02	0.02	4.70
3	45-min to 24-h pH decline	86	–0.05	0.02	–0.03	0.02	0.04	0.02	5.70*
3	45-min pH	91	–0.06	0.02	–0.02	0.02	0.03	0.02	6.49**
3	Loin wt, kg	114	0.06	0.04	–0.21	0.06	–0.08	0.04	6.60**
3	LM area, cm^2	155	0.16	0.27	–1.37	0.41	–0.27	0.27	4.29
4	LM area, cm^2	0	–0.33	0.26	–1.09	0.35	0.35	0.24	4.71
4	HCW, kg	12	–2.18	0.50	0.94	0.83	–0.47	0.47	7.14**
4	Off-farm BW, kg	13	–2.70	0.65	0.76	1.08	–0.71	0.61	6.56**
4	Color, 1 to 6	45	0.02	0.06	0.35	0.10	0.04	0.06	4.21
4	Spareribs wt, kg	53	0.02	0.01	–0.03	0.01	0.00	0.01	4.31
5	First-rib backfat, mm	86	0.64	0.47	1.16	0.74	1.79	0.47	6.28*
5	24-h carcass temperature, °C	117	0.02	0.03	0.20	0.05	0.09	0.03	7.13**
5	Cook yield, %	159	–0.28	0.20	0.37	0.32	0.82	0.22	5.52*
6	a*	24	0.24	0.07	0.15	0.11	–0.14	0.08	6.49**
6	Color, 1 to 6	92	0.17	0.06	0.04	0.10	–0.15	0.06	4.77
6	Warner-Bratzler shear force, kg	101	–0.14	0.05	–0.14	0.07	0.05	0.05	4.64
6	Marbling, 1 to 10	116	0.43	0.06	–0.15	0.11	0.04	0.06	18.41***
6	Fat, %	117	0.71	0.10	–0.37	0.17	0.14	0.10	20.01***
6	Ham wt, kg	121	–0.17	0.03	0.18	0.06	–0.04	0.03	11.79***
6	Tenth-rib backfat, mm	125	3.66	0.39	–2.09	0.70	0.42	0.42	32.18***
6	Last lumbar vertebra backfat, mm	129	2.11	0.42	–2.31	0.70	0.03	0.46	11.87***
6	Carcass length, cm	139	–0.57	0.13	1.02	0.20	0.16	0.14	14.57***
6	Loin wt, kg	141	–0.18	0.03	0.17	0.06	0.04	0.04	12.25***
6	Last-rib backfat, mm	144	1.04	0.38	–2.19	0.65	–0.17	0.41	6.10*
6	Protein, %	150	–0.39	0.08	0.24	0.14	–0.17	0.09	10.06***
6	Spareribs wt, kg	154	–0.03	0.01	0.04	0.02	–0.01	0.01	4.84
6	LM area, cm^2	156	–1.27	0.28	–0.69	0.48	0.06	0.30	7.40**
6	24-h carcass temperature, °C	176	0.14	0.03	–0.04	0.05	0.01	0.04	6.70**
6	Moisture, %	181	–0.19	0.09	–0.34	0.17	–0.34	0.10	6.21*
7	L*	1	0.23	0.14	0.24	0.21	–0.50	0.16	4.32
7	Color, 1 to 6	2	–0.05	0.05	–0.07	0.08	0.21	0.06	4.52
7	Protein, %	6	–0.24	0.07	–0.21	0.13	0.02	0.08	4.48
7	Carcass length, cm	67	0.81	0.17	0.40	0.34	0.19	0.18	9.01***
7	Dressing percent, %	70	–0.73	0.15	–0.65	0.31	–0.05	0.16	10.13***
7	LM area, cm^2	108	–1.28	0.36	–1.61	0.72	0.17	0.37	6.28*
7	Number of ribs	124	0.19	0.06	0.10	0.11	0.34	0.06	15.13***
7	Spareribs wt, kg	135	0.01	0.01	–0.01	0.01	0.03	0.01	4.93
7	Warner-Bratzler shear force, kg	158	0.19	0.05	0.05	0.08	0.07	0.05	5.74*
7	Overall tenderness, 1 to 8	159	–0.15	0.04	0.00	0.06	–0.01	0.04	4.72
7	Tenderness, 1 to 8	160	–0.16	0.04	–0.01	0.07	–0.01	0.04	4.75
7	45-min to 24-h pH decline	164	0.04	0.02	0.01	0.02	0.04	0.02	4.35
8	Spareribs wt, kg	62	0.03	0.01	0.02	0.02	–0.01	0.01	4.41
8	LM area, cm^2	96	–0.82	0.24	–0.38	0.36	–0.15	0.26	4.68
8	Moisture,%	152	–0.35	0.12	0.45	0.21	–0.03	0.12	4.19
9	Drip loss,%	1	–0.04	0.07	0.36	0.10	–0.05	0.07	4.75
9	Off-farm BW, kg	3	–0.37	0.56	2.89	0.83	0.77	0.59	4.39
9	HCW, kg	3	–0.40	0.44	2.38	0.65	0.76	0.46	5.25
9	Overall tenderness, 1 to 8	5	0.00	0.04	0.04	0.06	0.14	0.04	4.42
9	Ham wt, kg	8	–0.11	0.03	0.01	0.05	–0.04	0.03	5.09
9	24-h carcass temperature, °C	13	0.09	0.03	–0.02	0.04	–0.06	0.03	4.08
9	Warner-Bratzler shear force, kg	17	–0.01	0.04	–0.09	0.07	–0.18	0.05	4.77
9	Tenderness, 1 to 8	28	–0.02	0.05	0.07	0.09	0.19	0.05	4.85
9	Fat, %	62	–0.14	0.10	–0.11	0.16	0.35	0.10	4.66
9	Moisture, %	64	0.21	0.10	–0.01	0.17	–0.34	0.11	4.14
9	45-min carcass temperature, °C	108	0.06	0.10	0.67	0.19	0.03	0.11	4.27
9	b*	127	–0.13	0.05	0.14	0.07	0.01	0.07	4.25
10	Tenderness, 1 to 8	0	0.06	0.04	0.19	0.06	0.01	0.04	4.08
10	Overall tenderness, 1 to 8	0	0.05	0.04	0.19	0.05	–0.02	0.04	4.65
10	Connective tissue, 1 to 8	61	0.08	0.04	0.15	0.07	–0.05	0.03	5.36*

Continued

Table 3 (Continued). Position and significance level of carcass and meat quality QTL significant at the 5% chromosome-wise level, with additive, dominance, and imprinting effects and SE

Chr[1]	Trait	Pos,[2] cM	Additive effect	SE	Dominance effect	SE	Imprinting effect	SE	*F*-ratio[3]
10	Off-farm BW, kg	74	–0.59	0.82	2.22	1.35	–2.72	0.77	5.62*
10	HCW, kg	75	–0.37	0.63	0.93	1.03	–2.38	0.60	5.93*
10	Marbling, 1 to 10	79	–0.12	0.08	0.30	0.11	–0.14	0.07	4.22
11	45-min to 24-h pH decline	107	0.07	0.02	–0.08	0.06	0.03	0.03	3.80
11	Fat, %	119	0.28	0.12	–0.43	0.25	0.36	0.13	4.78
11	Moisture, %	119	–0.40	0.13	0.30	0.27	–0.28	0.14	4.69
12	Belly wt, kg	53	0.11	0.03	0.01	0.04	0.01	0.03	6.04*
12	Moisture, %	54	–0.37	0.10	0.31	0.16	–0.11	0.10	7.26**
12	Fat, %	57	0.30	0.09	–0.32	0.15	0.11	0.09	6.99**
12	24-h pH	61	–0.02	0.01	–0.04	0.01	0.01	0.01	4.23
12	Marbling, 1 to 10	67	0.21	0.06	–0.24	0.10	0.02	0.06	7.04**
14	a*	51	–0.28	0.07	0.05	0.12	0.01	0.07	5.05
14	Belly wt, kg	114	0.06	0.03	–0.24	0.06	–0.05	0.03	7.53**
15	Protein, %	57	0.38	0.08	–0.01	0.14	0.41	0.08	14.89***
15	L*	60	0.70	0.17	–0.70	0.29	0.18	0.17	8.03***
15	a*	64	–0.25	0.07	0.15	0.11	–0.13	0.07	5.60*
15	Color, 1 to 6	64	–0.16	0.06	0.16	0.09	–0.13	0.06	5.03*
15	Tenderness, 1 to 8	65	–0.12	0.04	0.00	0.07	–0.17	0.04	7.57**
15	Overall tenderness, 1 to 8	65	–0.10	0.04	0.00	0.06	–0.15	0.04	7.25**
15	Warner-Bratzler shear force, kg	70	0.08	0.05	0.04	0.08	0.18	0.05	5.02*
15	Cook yield, %	75	0.55	0.21	–0.15	0.34	0.42	0.21	3.86
16	24-h pH	81	0.02	0.01	–0.04	0.02	0.03	0.01	4.90
17	Protein, %	23	–0.03	0.07	0.38	0.11	0.04	0.07	3.98
17	45-min to 24-h pH decline	51	–0.06	0.02	–0.14	0.06	–0.01	0.03	3.94
18	Last-rib backfat, mm	0	1.33	0.54	1.45	0.78	1.36	0.56	4.10
18	24-h pH	0	–0.01	0.01	0.07	0.02	–0.01	0.01	4.60
18	Tenth-rib backfat, mm	5	0.21	0.59	3.46	0.97	1.06	0.63	4.77*
18	Spareribs wt, kg	19	–0.02	0.01	0.01	0.03	–0.05	0.01	3.83
18	Number of ribs	48	–0.11	0.05	0.15	0.08	0.06	0.06	3.45
X	Moisture, %	14	–0.36	0.13	NA		NA		8.02
X	Fat, %	169	0.31	0.11	NA		NA		7.68

[1]Chr = chromosome.
[2]Pos = position.
[3]Significant at *1% chromosome-wise, **5% genome-wise, or ***1% genome-wise levels.

study, the one that contained Duroc germplasm had the highest *F*-ratio corresponding to a significant QTL on SSC 7. Their study reported an additive effect for this QTL, but they did not test for imprinting effects.

Carcass backfat thickness and LM area are predictive of body composition and have been used to determine pricing structure at packing plants. Traditionally, carcass measurements of backfat have been taken along the midline at the first rib, last rib, and last lumbar vertebra in pigs, whereas measurements of backfat and LM area at the 10th rib have been taken on a ribbed carcass. These measures can be used to estimate body composition. A region of SSC 6 (Figure 3) contained a significant QTL that affected many of these related backfat traits as well as carcass LM area. This was an additive QTL in which Duroc alleles increased backfat and reduced LM area. These results were consistent with overall breed results reported in Edwards et al. (2003), whereas Duroc germplasm contributed to an increase in backfat compared with Pietrain-sired pigs. The region of SSC 6 that affected 10th-rib backfat was also found to be significant by Malek et al. (2001b). A QTL for LM area was found by Ovilo et al. (2002b) in the same region of SSC 6 as the one reported here. An additional QTL on SSC 18 that had a large dominance effect and increased last-rib and 10th-rib backfat when Duroc alleles were present was discovered in this analysis. Finally, a QTL significant at the 1% chromosome-wise level was found for first-rib backfat on SSC 5. No previous pig QTL studies have reported a first-rib backfat QTL in this region (Hu et al., 2005), although Rohrer et al. (2005) recently identified a QTL in this region for 10th-rib backfat in a Duroc × Landrace F_2 population. Su et al. (2004) reported a QTL for carcass LM area on SSC 7 in a similar region to the QTL significant at the 1% chromosome-wise level discovered in this study. Sato et al. (2003) also discovered a QTL for LM area on SSC 7 in a population with a Duroc founder boar, but their QTL was located in a more proximal position relative to the origin of the map than the QTL reported here.

Primal Cut Weights

Because primal cut weights were adjusted for carcass weight in the model to determine significance of QTL,

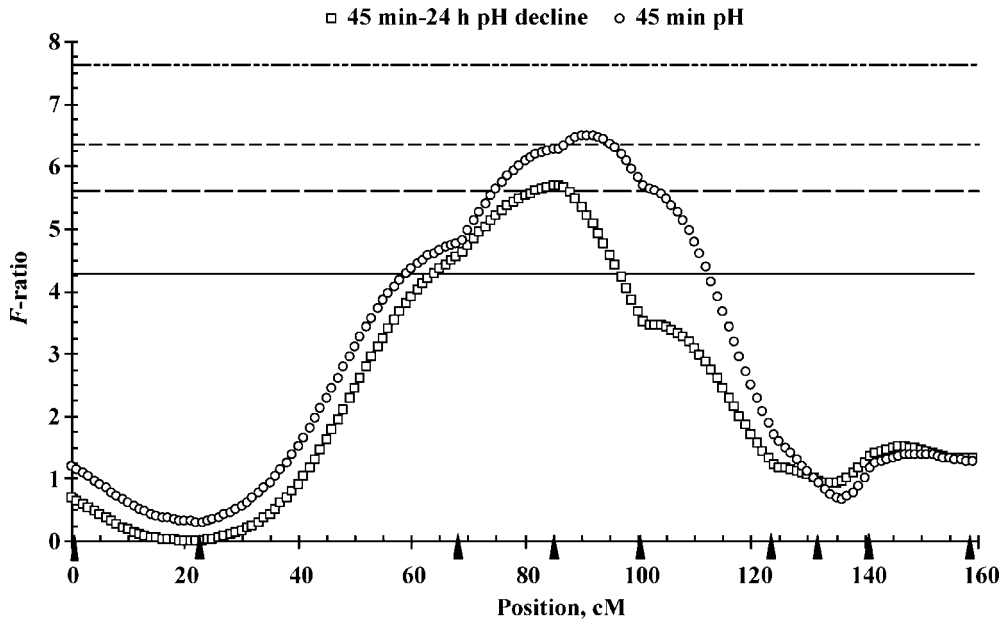

Figure 1. *F*-ratio plots vs. relative positions on SSC 3. Arrows on the x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for the 5% chromosome-wise (—), 1% chromosome-wise (– –), 5% genome-wise (- - -), and 1% genome-wise (— –) significance levels.

these adjusted primal weights have a similar interpretation to primal cut weights as a percentage of carcass weight. Although QTL were not found in this study for Boston shoulder and picnic shoulder weights, these primal cut weights were highly dependent on where they were separated from one another and had higher standard deviations than other primal cuts compared with their mean weights (Table 2). Therefore, larger environmental variation may have prevented discovery of significant QTL. Other primal cuts had several putative QTL in this study. Again, SSC 6 contained a QTL that indicated more muscling in the ham and loin for animals with Pietrain alleles, which paralleled results of Edwards et al. (2003), who reported Pietrain-sired

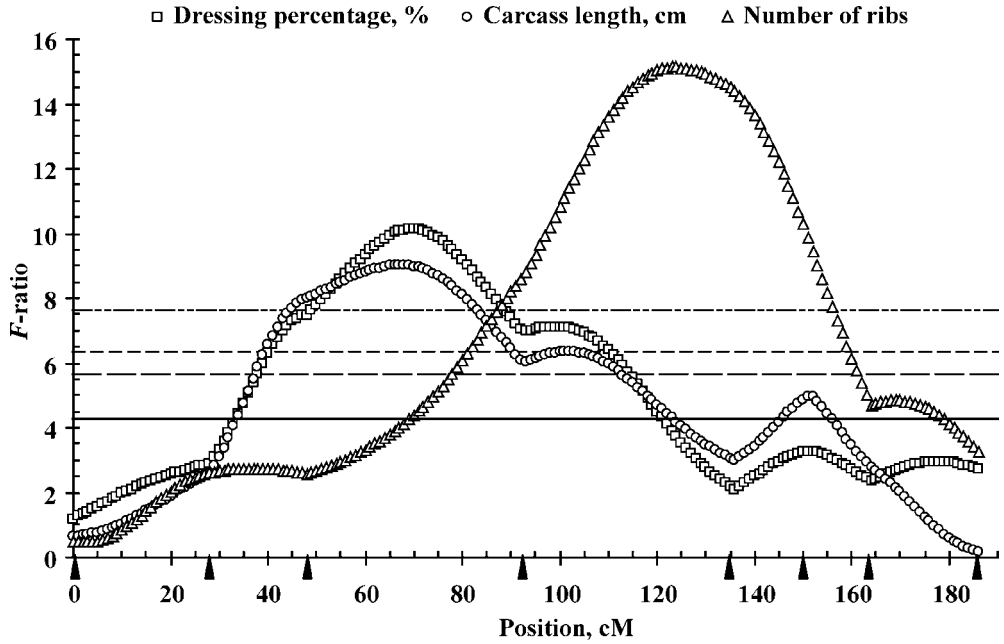

Figure 2. *F*-ratio plots vs. relative positions on SSC 7. Arrows on the x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for the 5% chromosome-wise (—), 1% chromosome-wise (– –), 5% genome-wise (- - -), and 1% genome-wise (— –) significance levels.

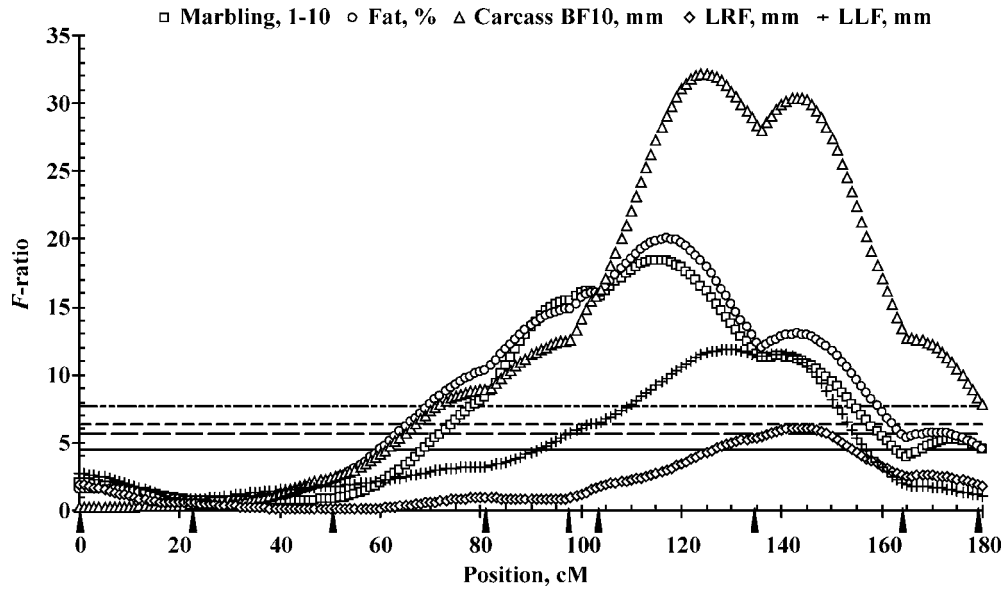

Figure 3. *F*-ratio plots vs. relative positions on SSC 6. Arrows on the x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for the 5% chromosome-wise (—), 1% chromosome-wise (– –), 5% genome-wise (- - -), and 1% genome-wise (— –) significance levels. BF10 = 10th-rib backfat, LRF = last-rib backfat, and LLF = last-lumbar backfat.

pigs had larger ham and loin primal weights than Duroc-sired pigs. Other pig QTL studies that reported loin weight, summarized by Hu et al. (2005), had not found QTL on SSC 6. Geldermann et al. (2003) reported a QTL for ham weight on SSC 6, but it was slightly more proximal to the origin of the map than the QTL reported here. An additional loin weight QTL, significant at the 5% genome-wise level, was found on SSC 3. Two QTL for belly weight were found, one on SSC 12 and one on SSC 14, at the 1% chromosome-wise and 5% genome-wise levels, respectively. The QTL on SSC 12 indicated that Duroc alleles additively increased belly weight, whereas the dominance effect for the QTL on SSC 14 had the largest magnitude. These 2 QTL have not been previously reported (Hu et al., 2005). The analysis for spareribs weight indicated QTL located on SSC 1, 4, 6, 7, 8, and 18 at the 5% chromosome-wise level, although only the QTL on SSC 1 exceeded the 1% chromosome-wise significance threshold.

Meat Quality

Consumer perception of fresh meat products is affected at least in part by color, marbling, and firmness. Evaluation of these variables on chops cut from LM in this study revealed QTL affecting traits of color and marbling, but not firmness. Putative QTL for subjective color were located on SSC 4, 6, 7, and 15. The QTL on SSC 15 was significant at the 1% chromosome-wise level for subjective color as well as for a*, whereas it was significant at the 1% genome-wise level for L* (Figure 4). The additive effects indicate that Duroc alleles lowered the color score and raised the L* value, whereas they lowered the a* value. The population studied by Malek et al. (2001a) also contained a QTL for L* on SSC 15, but it was slightly more distal relative to the origin of the map than the position reported here. A QTL in a similar position to the one reported here for a* was also reported by de Koning et al. (2001). Another QTL for L* was discovered in our study at the same position on SSC 7 as the QTL reported for subjective color score. Although not in the same position on SSC 7 as the QTL reported here, Ovilo et al. (2002a) also reported a QTL for L* on SSC 7. A QTL at the 5% genome-wise level for a* was located on SSC 6 and was additive in its effect, where Duroc alleles increased the a* value. The only QTL for b* found in this study was on SSC 9 and was significant only at the 5% chromosome-wise level.

Another factor that affects a consumer's choice of meat and subsequent eating experience is marbling. The subjective marbling score analysis revealed 3 significant QTL on SSC 6, 10, and 12. The QTL on SSC 6 was additive, indicated that Duroc alleles increased marbling, and was significant at the 1% genome-wise level, whereas the one on SSC 12 was significant at the 5% genome-wise level. Both marbling score and intramuscular fat percentage showed similar *F*-ratio curves when plotted vs. relative marker position on SSC 6 (Figure 3).

Percentage moisture, fat, and protein of LM are highly related as they are derived from percentages of the same whole. As subjective marbling score approximates fat percentage in each chop, 2 significant QTL for fat percentage were found at the same locations as the QTL for marbling score on SSC 6 and 12, again significant at the 1 and 5% genome-wise levels, respectively. Nearly the same position on SSC 6 for a QTL

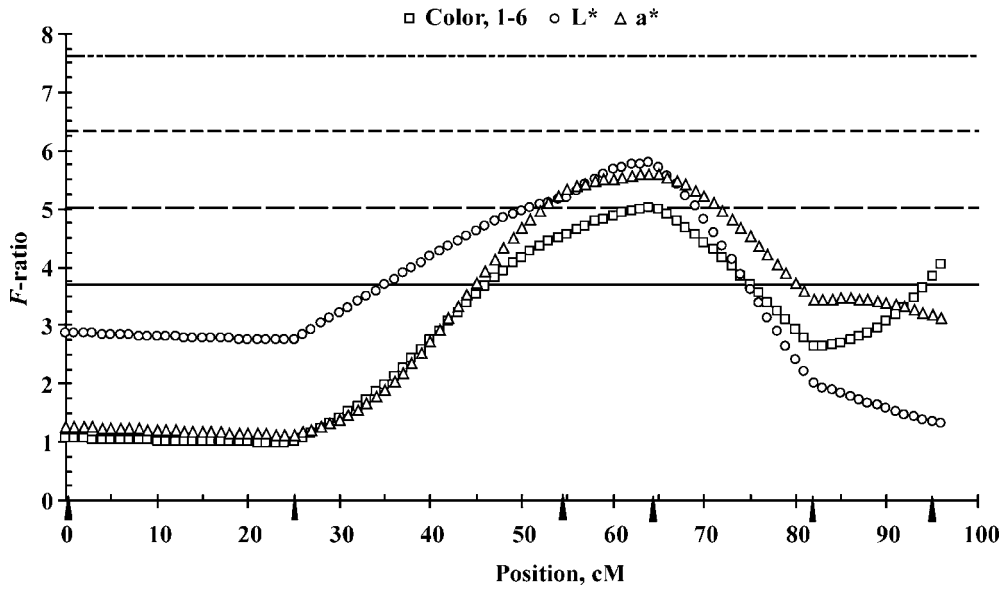

Figure 4. *F*-ratio plots vs. relative positions on SSC 15. Arrows on the x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for the 5% chromosome-wise (—), 1% chromosome-wise (– –), 5% genome-wise (- - -), and 1% genome-wise (— –) significance levels.

affecting intramuscular fat was reported by Ovilo et al. (2002b). This chromosomal region on SSC 6 also affected moisture percentage and was previously reported by Su et al. (2004). A QTL affecting protein percentage was also determined within this region of the chromosome, whereas the QTL on SSC 12 affected moisture percentage. An additional QTL, significant at the 1% genome-wise level for protein percentage, was located on SSC 15. Selection for any of these QTL will directly affect the other 2 traits because these 3 traits are not strictly independent, and similar *F*-ratio curves for fat and moisture percentages observed on SSC 12 (Figure 5) support this association.

Several traits measured are directly related to storage, preparation, and eating quality of chops. One of these was drip loss, and a QTL was found on SSC 9 with an estimated effect that indicated that Duroc alleles caused a higher percentage of drip loss. Cook yield, which measured moisture loss during cooking, had 2 QTL, with one on SSC 5 significant at the 1% chromosome-wise level and an additional one on SSC 15. Rohrer et al. (2005) recently identified a QTL for cook loss percentage at 7 d postmortem in the same region of SSC 15 as the cook yield QTL reported here. Our analyses indicated significant QTL for WBS on SSC 7 and 15, with both significant at the 1% chromosome-wise level. Similar traits, Instron (star probe) force and slice shear force, were reported to have QTL on SSC 15 (Malek et al., 2001a; Rohrer et al., 2005) in similar positions to the WBS QTL in our study, but the QTL on SSC 7 had not been reported previously (Hu et al., 2005). The same 2 QTL regions on SSC 7 and 15 reported here for WBS also affected tenderness and overall tenderness as determined by the trained sensory panel and were significant at the 5% genome-wise level for these 2 important eating quality traits. The QTL on SSC 7 acted in an additive mode of inheritance, where Pietrain alleles led to lower, and less favorable, tenderness scores. On SSC 15, Pietrain alleles from the sire again led to lower tenderness scores. Furthermore, tenderness, overall tenderness, and WBS were controlled by the same chromosomal region on SSC 15 (Figure 6). Malek et al. (2001a) reported a similar position for a tenderness QTL on SSC 15. Additional QTL for both tenderness and overall tenderness were located on SSC 9 and 10. Only one QTL, located on SSC 2, was identified for sensory panel juiciness. A QTL on SSC 2 for juiciness was also reported by Stearns et al. (2005), but it was located more proximal relative to the origin of the map than the QTL discovered here. Additionally, a QTL for off-flavor was located on SSC 2, a chromosome on which Malek et al. (2001a) reported 2 QTL for off-flavor. A QTL significant at the 1% chromosome-wise level that affected connective tissue scores was discovered on SSC 10. Refining the location for these QTL for sensory panel attributes will provide potentially important information for selection of prospective parents in swine populations because these attributes ultimately impact a consumer's dining experience.

Confidence Intervals

For QTL that were significant at the 5% genome-wise level, 95% confidence intervals were estimated using bootstrapping with resampling in QTL Express (Seaton et al., 2002). These confidence intervals are listed in Table 4. Confidence intervals were not calculated for QTL significant at the 5 or 1% chromosome-wise level

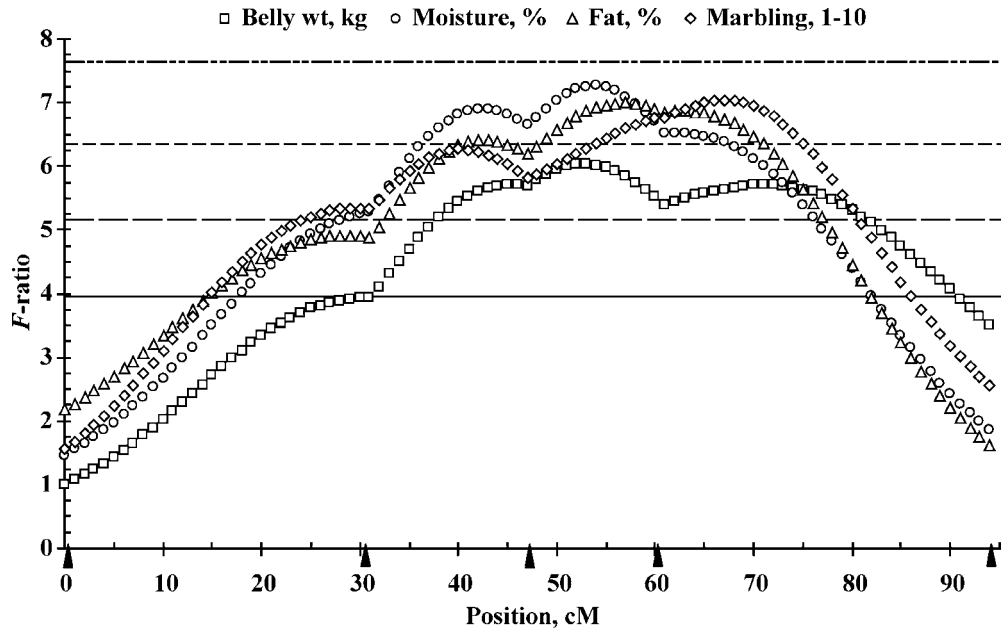

Figure 5. *F*-ratio plots vs. relative positions on SSC 12. Arrows on the x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for the 5% chromosome-wise (—), 1% chromosome-wise (– –), 5% genome-wise (- - -), and 1% genome-wise (— –) significance levels.

because preliminary analyses indicated that many of these intervals tended to encompass the entire chromosome on which they reside.

In conclusion, numerous QTL that control economically important traits of carcass composition and meat quality were revealed in this F_2 Duroc × Pietrain resource population. These QTL are extremely important because they give us insight into traits that are not easily measured in breeding animals, but add value to pork products, and will become even more important as the traits they influence achieve greater economic value. Many QTL for meat quality, with both desirable and undesirable alleles, existed in the Duroc and Pietrain breeds utilized in this study, and desirable QTL could be incorporated systematically into breeding schemes, as these 2 populations are already a major

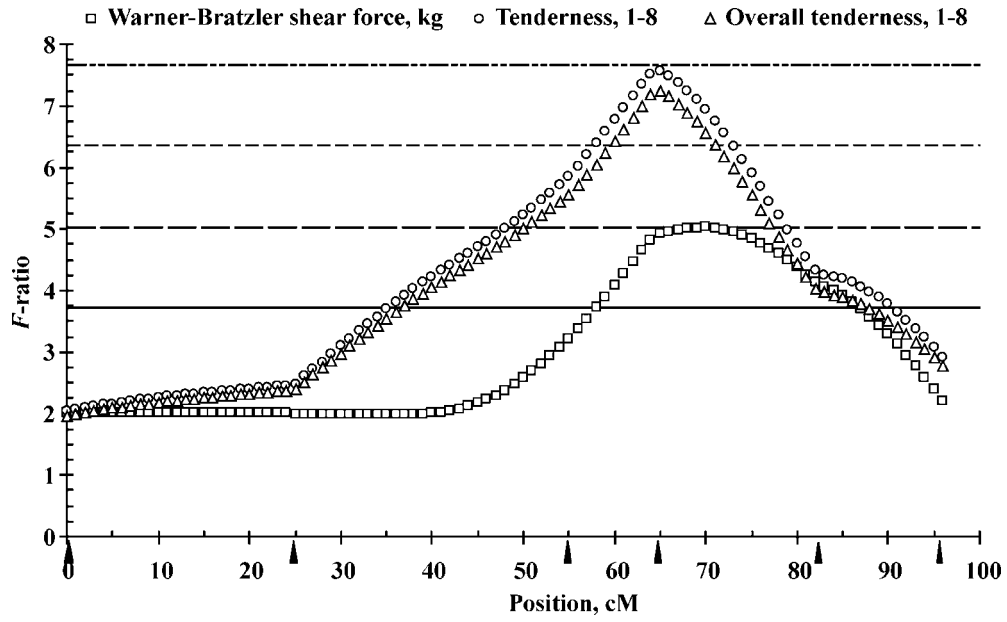

Figure 6. *F*-ratio plots vs. relative positions on SSC 15. Arrows on the x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for the 5% chromosome-wise (—), 1% chromosome-wise (– –), 5% genome-wise (- - -), and 1% genome-wise (— –) significance levels.

Table 4. Position and 95% confidence interval lower and upper limits of carcass and meat quality QTL significant at the 5% genome-wise level

Chr[1]	Trait	Position, cM	Lower limit, cM	Upper limit, cM
1	Spareribs wt	172	146	184
3	45-min pH	91	43	149.5
3	Loin wt	114	88	156
4	Hot carcass weight	12	0	61
4	Off-farm BW	13	0	61
5	24-h carcass temperature	117	12	123
6	a*	24	4	117
6	Marbling	116	94	144
6	Fat	117	96	144
6	Ham wt	121	113	175
6	Tenth-rib backfat	125	118	148
6	Last lumbar vertebra backfat	129	99	146
6	Carcass length	139	99	144
6	Loin wt	141	122	149
6	Last-rib backfat	144	0	173.5
6	Protein	150	30	164
6	LM area	156	80.5	166
6	24-h carcass temperature	176	81	181
7	Carcass length	67	41	152
7	Dressing percent	70	56	80
7	Number of ribs	124	106	144
12	Fat	57	12	75
12	Marbling	67	17	79
14	Belly wt	114	36	117
15	Protein	57	46	71
15	L*	60	41	67
15	Overall tenderness	65	34	93
15	Tenderness	65	33	86.5

[1]Chr = chromosome.

part of commercial pig production. Chromosomal regions of interest discovered in these populations are being subjected to further analyses, and refinement of QTL positions may lead to their incorporation into selection programs for prospective parents and subsequently increase value in these pork products.

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