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A genome scan for loci affecting pork quality in a Duroc–Landrace F_2 population

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Summary

A genome scan was conducted on 370 F_2 Duroc–Landrace pigs. Microsatellite markers ($n = 182$) were genotyped across the entire F_2 population, all F_1 parents and the paternal grandparents. Breed of origin of all chromosomal segments inherited in F_2 progeny were predicted using GenoProb, where genotypic data, genetic maps and extended pedigrees were used as inputs. Statistical tests for quantitative trait loci (QTL) associations were conducted on 41 phenotypes with SAS using output from GenoProb for genotypic data. Fixed effects included sex and age at slaughter. For certain analyses carcass weight, *RYR1* genotype and/or *PRKAG3* genotype were also included as covariates. Subjective and objective measures of pork colour, marbling and tenderness were recorded, as well as measures of carcass fatness and muscularity. Test results were adjusted to a genome-wide level of significance. Five genomic regions presented significant evidence for QTL at chromosome 1 positions 6 cM (intramuscular fat) and 67 cM (Hunter L^*), chromosome 2 position 62 cM (taste panel tenderness), chromosome 17 position 50 (loineye area and image analysis estimated loineye area) and X position 87 cM (carcass weight). Sixty-six suggestive associations were detected. Fourteen of these associations were within the regions with significant QTL on chromosomes 2, 17 and X, and the remaining 52 associations resided in 29 other regions on 13 different chromosomes of the porcine genome. The chromosome 2 region of 60–66 cM was associated with all measures of pork tenderness and the region on chromosome 17 (32–39 cM) was associated with both measures of intramuscular fat and loineye area. After verification, the QTL for marbling and tenderness should be useful in commercial production to improve pork quality as the population was developed from two of the three most utilized breeds of swine in the USA.

Keywords genome scan, markers, pork quality, quantitative trait loci.

Introduction

Selection of commercial pigs for increased muscle mass and decreased backfat has resulted in decreased customer satisfaction of the final meat product. Consumers are most concerned about tenderness and amounts of intramuscular fat in pork (NPPC 1995). Unfortunately, these traits are difficult to assess in live animals requiring progeny testing systems to be designed which are costly and lengthen the generation interval.

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Quantitative trait loci (QTL) scans have been conducted in pigs for several traits (reviewed by Bidanel & Rothschild 2002). Significant QTL have been reported for carcass composition (Andersson *et al.* 1994; Rohrer & Keele 1998a,b; Paszek *et al.* 1999; Malek *et al.* 2001a; Milan *et al.* 2002) and palatability traits (Grindflek *et al.* 2001; de Koning *et al.* 2001; Malek *et al.* 2001b). However, with the exception of Grindflek *et al.* (2001) and Malek *et al.* (2001a,b) most of these studies have used exotic breeds or lines of swine that contribute little to commercial pork production. A thorough evaluation of pork quality traits was conducted in 1995 across US lines of pigs and indicated that Duroc boars clearly excelled in economic merit for a pork quality selection index (NPPC 1995). The 2003 National Barrow Show Progeny Test Results also indicated that Duroc-sired progeny had the greatest values for a pork quality index that included marbling, colour and pH

measurements, while Landrace-sired progeny had the lowest values (D. Anderson and R. Pfortmiller, personal communication).

To this end, we developed a F_2 Duroc–Landrace resource population to identify QTL affecting pork palatability and composition. These two breeds were chosen as extremes for pork quality of the three major commercial breeds (Duroc, Landrace and Yorkshire). Results of this study would be expected to be of immediate use to the commercial pig industry.

Materials and methods

Animals

Fifty F_2 Duroc–Landrace litters were produced from 4 F_1 boars and 50 F_1 females. The F_1 parents were the result of reciprocal crosses between purebred Duroc and Landrace pigs. Tissue samples from the eight paternal grandparents (four Duroc and four Landrace), all F_1 and F_2 pigs were obtained for DNA extraction and genotyping. Eleven of the F_1 sows were paternal half-sibs to an F_1 boar and one F_1 sow was a full-sib to one of the F_1 boars. Pigs were raised under standard commercial production conditions until an approximate live weight of 110 kg. At that point animals were sent to a commercial slaughter facility where they were electrically stunned and processed following industry standards, and composition measurements were recorded. At 24-h postmortem, the left loin of each carcass was removed and delivered to the US Meat Animal Research Center, Meat Research Unit laboratory (Clay Center, NE, USA) where additional measurements and taste panel data were recorded. A total of 370 pigs were included in this study.

Carcass and meat measurements

Pigs were weighed before transport to the abattoir. Carcasses were weighed and scanned by an Animal Ultrasound Services, Inc. CVT scanner (Ithaca, NY, USA), and measures for loin and fat depth were recorded. Percent muscle was estimated from these ultrasound measurements. At *c.* 1-h postmortem, pH of the longissimus muscle was recorded.

Each loin was separated between the 10th and 11th rib. Fat depth at the 10th rib and cross-sectional area of the longissimus at the 10th rib was determined. Scores for firmness/wetness, colour and marbling were recorded as described (NPPC 1991). The surface was also evaluated by a computer image analysis system where total area, total area of fat tissue, total area of muscle tissue, area of longissimus muscle and reflectance of red, blue and green were determined (Shackelford *et al.* 1998). Percentage of fat from the longissimus as well as the density of colour were computed based on the image analysis values. In addition, Hunter reflectance values were determined for the longissimus cross-section where Hunter L^* is a measure of lightness, a^* is a measure of redness and b^* is a measure of yellowness.

Chemical analyses were conducted on a sample of longissimus muscle to determine the amount of moisture and ether-extractable fat within the muscle sample (AOAC 1993). Purge loss on the loin section was also determined. At 48-h postmortem, pH of the longissimus and 48-h drip loss (AMSA, unpublished protocol) were determined. Change in pH was also determined from 1- to 48-h postmortem. At 2- and 7-day postmortem, slice shear force (Shackelford *et al.* 2004) and cooking loss were recorded.

Another chop aged for 7-day postmortem was cooked and evaluated by a trained taste panel. Parameters recorded were measures of overall tenderness, amount of connective tissue, juiciness, pork flavour intensity and off-flavour rating (Wheeler *et al.* 2000). Cooking loss analysed for 7-day postmortem was an average of cooking losses for two chops, one prepared for slice shear force and the other for taste panel assessment. Sarcomere length of the cooked product was determined (Koolmees *et al.* 1986) along with myofibril fragmentation index (Culler *et al.* 1978). Amount of native desmin remaining in the tissue after 7-day postmortem was determined (Wheeler *et al.* 2000) on a limited number of randomly sampled animals ($n = 60$) to evaluate the amount of postmortem protein degradation. Table 1 presents a summary of all traits analysed, their mean, range and standard deviations.

Genotyping procedures

Microsatellite markers were selected from the swine map (Rohrer *et al.* 1996) and tested in the four F_1 boars and their purebred parents for informativeness. Selection of markers to be run across the entire population was based upon location, ease of scoring, number of informative F_1 boars and number of putative breed-specific alleles (alleles only present in animals of one of the founding breeds of the paternal grandparents). For situations where no available marker was informative in at least three F_1 boars, multiple markers in the region were used to increase the information content. The final set of markers that were typed across the entire population included 182 microsatellite markers from the current MARC pig map (http://www.marc.usda.gov). Genotyping reactions were as described (Rohrer *et al.* 1996). The markers used are presented in Supplemental Table S1.

In addition to the microsatellite markers, single-base differences believed to affect pork quality were also assayed. Polymorphisms tested included the *RYR1/R615C* SNP for which the 615C allele causes porcine stress syndrome and pale soft exudative meat (Fujii *et al.* 1991), and four locations in *PRKAG3*, including R200Q for which 200Q causes RN phenotype (Milan *et al.* 2000) and three that potentially affect meat quality (Ciobanu *et al.* 2001), including T30N,

Table 1 Traits measured in the F2 generation used for a quantitative trait loci (QTL) scan, along with the mean performance, measures of variation and the fixed effects that were included in the QTL analysis for each trait.

Symbol	Description	Fixed effects[1]	No. records	Mean	Range	SD	No. QTL
adpth	Ultrasound loin depth	Composition	367	2.4	1.9–3.2	0.2	1
afat	Ultrasound fat depth	Composition	367	0.6	0.3–1.2	0.2	1
apln	Ultrasound predicted percent lean	Composition	367	54.3	50.1–57.7	1.3	1
ckls2	Cooking loss at 2 d postmortem (%)	Palatability	370	21.2	14.2–26.3	2.2	2
ckls7	Cooking loss at 7 d postmortem (%)	Palatability	370	21.5	11.0–29.1	2.7	3
color	Subjective colour score (1–6)	Quality	370	2.6	2–4	0.6	0
cwt	Carcass weight (kg)	Weight	370	84.5	71.9–106.3	6.5	2
drip	Drip loss (%)	Palatability	370	1.97	0.00–7.80	1.46	2
dsmn	Native desmin at 7-day postmortem	Palatability	60	17.5	0.0–89.0	23.9	0
eyb	Image analysis blue colour	Quality	370	40.7	10.7–74.5	9.7	1
eydn	Image analysis total colour density	Quality	370	71.8	39.2–106.6	10.7	2
eyg	Image analysis green colour	Quality	370	39.0	9.3–71.4	10.0	3
eyr	Image analysis red colour	Quality	370	135.8	97.4–177.6	13.0	2
fat10	Tenth rib fat depth (mm)	Composition	370	20.3	7.6–35.6	5.1	2
firmness	Subjective firmness score (1–6)	Quality	370	2.6	1–5	0.9	1
hnta	Hunter *a**	Quality	370	9.4	6.2–12.4	1.2	0
hntb	Hunter *b**	Quality	370	14.9	12.3–18.6	1.2	2
hntl	Hunter *L**	Quality	370	53.8	46.2–62.2	2.5	3
iafat	Image analysis fat content	Composition	370	41 707	11 559–76 748	11 772	1
ialea	Image analysis loin eye area	Composition	370	42 624	28 245–56 532	5086	2
ialean	Image analysis total lean content	Composition	370	86 156	56 001–117 764	9176	2
iaperfat	Image analysis percent fat	Composition	370	33.5	11.1–53.7	7.8	2
iatot	Image analysis total area	Composition	370	123 342	92 014–159 994	11 289	1
imfat	Chemical analysis longissimus fat content (%)	Quality	370	2.7	0.5–6.8	1.1	3
immois	Chemical analysis longissimus moisture content (%)	Quality	370	74.0	65.8–79.9	1.1	4
lea	Loin Eye area (traced; cm^2)	Composition	370	44.5	27.7–62.6	5.8	2
lwt	Live weight (kg)	Weight	368	116.7	102.3–144.8	7.9	2
marb	Subjective marbling score (1–6)	Quality	370	2.2	1–4	0.6	2
mfi	Myofibril framentation index	Palatability	370	55.5	26.8–84.5	9.9	4
ph1	pH 1-h postmortem	Palatability	370	6.09	5.50–6.72	0.24	2
ph48	pH 48-h postmortem	Palatability	370	5.79	5.44–6.45	0.15	2
pHdelta	Change in pH (1 hr–48 hr)	Palatability	370	0.30	−0.60–0.98	0.25	1
purge	Purge loss (%)	Palatability	370	1.44	0.26–3.31	0.63	0
sarc	Sarcomere length (μm)	Palatability	370	1.52	1.11–1.81	0.11	2
ssf2a	Slice shear force 2-day postmortem (kg)	Palatability	370	16.2	6.7–36.6	4.9	2
ssf7a	Slice shear force 7-day postmortem (kg)	Palatability	370	14.4	6.8–33.8	4.7	3
tpact	Taste panel amount of connective tissue score (1–8)	Palatability	370	6.8	5.0–7.7	0.5	2
tpjui	Taste panel juiciness score (1–8)	Palatability	370	5.1	3.4–6.1	0.4	2
tpoff	Taste panel off flavour score (1–8)	Palatability	370	2.8	2.1–3.5	0.2	1
tpot	Taste panel overall tenderness score (1–8)	Palatability	370	5.8	2.4–7.5	0.9	1
tppfi	Taste panel pork flavour intensity score (1–8)	Palatability	370	4.6	3.2–5.6	0.4	1

[1]Fixed effects fitted for each set of analyses were carcass weight, sex and age at slaughter for Composition; sex and age at slaughter for Weight; sex, age at slaughter and *PRKAG3* haplotype for Palatability; and sex, age at slaughter, tenth rib fat thickness, *RYR1* genotype and *PRKAG3* haplotype for Quality.

G52S and I199V. Sequences were obtained from GenBank (accession nos X68247 and AF214521 for porcine *RYR1* and *PRKAG3*, respectively) and assays were designed to permit genotyping using the MASSArray genotyping platform (Sequenom Inc., San Diego, CA, USA). All animals were homozygous for the *PRKAG3* 200R allele so this SNP was not used in the statistical analyses. Segregation of alleles at the three positions (amino acids 30, 52 and 199) was followed within families to determine the *PRKAG3* haplotypes. Four haplotypes of the three *PRKAG3* SNPs were determined and used in subsequent analyses.

Statistical procedures

GenoProb software (Thallman 2002) evaluated the genotypic data based on an iterative allelic peeling process and

computed probabilities for origin of alleles based on pedigree and marker data (Thallman *et al.* 2001a,b). Updated linkage maps from Rohrer *et al.* (1996) were used to determine distances between adjacent markers. Extended pedigrees of all F_1 parents were included to evaluate breed of origin of maternally and paternally inherited alleles. Initial GenoProb analyses detected suspect genotypes in F_2 animals. After evaluation of all suspect genotypes had been completed, GenoProb was used to determine grandparental origin of marker alleles for each marker and animal. Grandparental origins were converted to probability of having two Duroc derived alleles (DD), two Landrace alleles (LL), a paternal Duroc allele and a maternal Landrace (DL) or a paternal Landrace allele and a maternal Duroc allele (LD) at each marker. These probabilities were then determined for each quarter of a marker interval (mean distance of 3.4 cM) by weighted averages of grandparental origin probabilities at the flanking markers.

Phenotypes were grouped into one of four general categories (Table 1) which were weight, composition, palatability and quality. The weight category was for carcass and live weight analyses. The composition category contained quantitative measurements of subcutaneous fat and longissimus muscle. Palatability traits were measures of water holding capacity, pH, tenderness and taste panel results while the quality category contained subjective and objective measures of intramuscular fat, colour and firmness of the longissimus. An initial analysis of the phenotypes was conducted to determine significant fixed effects to be included in each set of analyses. The initial model included fixed effects of age at slaughter, sex, genotypes at the *RYR1*/R615C SNP and the *PRKAG3* haplotypes. Fixed effects that did not influence any traits included in a set of analyses were removed from the final model. The final model for weight included sex and age as fixed effects while the model for composition included sex, age and carcass weight as fixed effects. For palatability the model included sex, age and *PRKAG3* haplotype and the model for quality included sex, age, tenth rib fat thickness, *RYR1*/R615C SNP and *PRKAG3* haplotypes. No interactions among fixed effects or between QTL and fixed effects were fitted.

The QTL analyses evaluated the probability of a QTL residing at each marker position and each quartile of an interval. Two different modes of inheritance were tested. One assumed a Mendelian mode of inheritance with coefficients fitted for additive and dominance effects (2 d.f.). The second mode of inheritance fitted imprinting effects with coefficients for allele inherited from sire and dam (1 d.f. each). Tests of significance were adjusted to a genomewide scale for a single analysis through procedures developed by Lander & Kruglyak (1995). Thresholds for 2 d.f. test *F*-ratios were 7.45, 11.00 and 12.95 corresponding to suggestive, significant and highly significant linkage respectively. Thresholds for 1 d.f. test *F*-ratios were 11.25, 18.05 and 21.65 corresponding to suggestive, significant and highly significant linkage respectively. As two separate analyses were conducted, these thresholds are underestimated. However, as the procedures of Lander & Kruglyak (1995) are extremely conservative, the type I error rate of this study should not be greatly inflated. The mode of inheritance that is presented is the one which was the most significant at the genomewide level. Choosing the mode of inheritance with the greatest significance tends to identify more imprinting effects, but it is not biased by preconceived concepts that Mendelian inheritance is most common. Based on the structure of this population, paternal expression may be overestimated for QTL that are not fixed in the founding breeds as each F_1 sire has more progeny than any F_1 dam.

For analyses of the X chromosome, the phenotypic data set was split into male and female F_2 progeny, and analyses were conducted separately. The fixed effects were the same as described above excluding sex as a fixed effect. Analyses of the female data were as described for autosomal QTL scans fitting the Mendelian and imprinting modes of inheritance. For the male data, the QTL effect only included the maternal contribution. Thresholds for significance were slightly higher than those for autosomal tests due to the fewer error degrees of freedom in these analyses.

Results

Fixed effects

The fixed effect that was the most significant for all phenotypes was sex. Barrows grew faster, were heavier and fatter at slaughter, had greater amounts of marbling, and had significantly higher taste panel scores. Age at slaughter was also significantly associated with fatter animals, with more marbling, and with improved tenderness in the cooked product.

Most animals genotyped for the *RYR1* polymorphism were homozygous for the 615R allele. Only a few heterozygous F_2 animals ($n = 17$) were present in the study. Therefore, only one association of this genetic marker was significant (amount of blue intensity of the loineye muscle), but the marker approached significance ($P < 0.10$) for marbling and firmness traits.

Considerable variation was present for the *PRKAG3* gene. Haplotype frequencies in founder animals of the population were 0.56 (Haplotype 1: 30N-52G-199V), 0.27 (Haplotype 2: 30T-52S-199V), 0.09 (Haplotype 3: 30T-52G-199I) and 0.08 (Haplotype 4: 30T-52G-199V) for haplotypes as defined by Ciobanu *et al.* (2001), respectively. Based on the eight paternal grandparents genotyped, haplotype frequencies appeared to be similar in both founding breeds, as the frequencies for Duroc were 0.50, 0.00, 0.25 and 0.25 and the frequencies for Landrace were 0.50, 0.125, 0.25 and 0.125 for Haplotype 1–Haplotype 4 respectively. There were sufficient numbers of animals in six of the ten genotypic

classes for the *PRKAG3* locus, but only five animals were 3/3 homozygous and no animals were 2/2, 2/4 or 4/4. Significant associations of the *PRKAG3* haplotype were with cooking loss traits and for some of the traits associated with pork tenderness.

Genome scan

Six associations reached the genome-wide significant threshold while 66 associations reached the genome-wide suggestive threshold. These associations were localized to 34 genomic regions of *c*. 10 cM or less (Table 2). Five regions contained at least one significant association. Number of associations per genome segment ranged from one to nine. Nineteen genomic segments only had a single association that reached a reportable level of significance.

Four of the 41 traits analysed were not associated with any detected QTL. These traits were subjective score for longissimus colour, Hunter a^* score of the longissimus, amount of native desmin remaining after 7 days of ageing, and purge loss of a section of loin at 48-h postmortem. The most associations detected per phenotype were four (muscle moisture content and myofibril fragmentation index). In general, measures of cooking loss, marbling and objective measures of longissimus tenderness had the most associations identified.

The region with the most associations with phenotypes was on porcine chromosome 17 (SSC17) in the 32–39 cM region. This location was significantly correlated with both measures of loineye area along with seven associations with suggestive evidence for QTL. The suggestive associations were for both measures of marbling (subjective marbling

Table 2 Suggestive and significant quantitative trait loci (QTL) associations identified in the genome scan for genomic regions of *c*. 10 cM or less.

Porcine chromosome	Position range (cM)	Flanking markers	QTL detected[1]
1	6	*SW1824*	imfat[2]
1	67	*SW1430-SW2432*	hntl[2]
2	0	*SWC9*	ckls7, hntl, pH48
2	60–66	*SW1026-SW776-SW1370*	immois, pH1, ssf7a, tpact, tpot[2]
2	79	*SW1695-S0370*	ssf2a
2	122	*SWR308*	eyg
3	84–87	*SW142-SW2408*	cwt, lwt
4	82–85	*S0107-S0214*	firmness, imfat
5	51	*SW1482-SW2425*	mfi
5	59–67	*SW2425-SW1904-SW2003*	ckls2, hntb, immois, tppfi
5	93	*SW1987-SWR426*	fat10
7	77	*SW1701-SW147*	immois
7	91	*SW147-SW632*	apln
7	126	*SW581-SW2108*	sarc
8	42	*SW905-SW211*	pH48
8	56	*SW211-S0086*	hntb
8	83	*SW2160-SWR1801*	mfi
8	104	*SWR1801-SW61*	marb
9	50–53	*SWR1848-SW2407*	ialean, iaperfat, lea
10	12	*SWR136-SW767*	ialean
10	67	*S0070-SWR158*	afat
13	0–5	*S0282-SWR428*	pH1, mfi
13	31	*SWR428-SW1400*	tpjui
13	53	*SW2448*	immois
14	66–72	*SW1081-SW1557*	drip, eydn, eyg, hntl
15	4–17	*KS169-SW1562*	ckls2, ckls7 eyr, tpact
15	37	*SW1562-SW964*	tpjui
15	47–51	*SW964-SY1*	drip, ssf7a
15	76–81	*SW1683-PRKAG3*	adpth, ckls7, pHdelta, ssf2a
17	9	*SWN335-SW1891*	ssf7a
17	32–39	*S0296-SW2441*	eyb, eydn, eyg, eyr, ialea[2], iatot, imfat, lea[2], marb
X	10	*SW2156-SW980*	mfi, tpoff
X	87–99	*SW1943-SW1608*	cwt[2], ialea, lwt, sarc
X	121	*SJ017*	fat10, iafat, iaperfat

[1]Trait symbols are as defined in Table 1.

[2]Indicates this association exceeded the genome-wise significant QTL threshold.

score and longissimus ether-extractable fat content), total image analysis size of the loin cross-section and all four measures of muscle colour determined by the image analysis system.

The genomic region with the next largest number of associations was SSC2 at 60–66 cM. A significant association was detected for taste panel overall tenderness. This region also presented suggestive evidence for QTL affecting taste panel amount of connective tissue, slice shear force on day 7, pH at 1-h postmortem and longissimus moisture content. A suggestive QTL for day 2 slice shear force was detected further down the chromosome (SSC2 at 79 cM) that may be associated with the same gene(s).

A significant QTL was detected on the X chromosome (87–99 cM) for carcass weight. Suggestive associations of this region were for live weight, loineye area and sarcomere length.

A QTL on SSC1 at 6 cM was significantly associated with longissimus ether-extractable fat content while a region at 67 cM was significantly associated with Hunter L^* reflectance values. Neither of these regions was associated with any other traits at the suggestive level.

Four regions had four suggestive QTL. Chromosome SSC5 at 60–67 cM had suggestive QTL for amount of moisture in the muscle as determined by chemical analysis, cooking loss on day 2, Hunter b^* score and pork intensity flavour determined by the trained sensory panel. Chromosome SSC14 at 66–72 cM was associated with drip loss, Hunter L^*, green and overall density of colour based on image analysis. Chromosome SSC15 at 4–17 cM was associated with both measures of cooking loss, red colour of the longissimus based on the image analysis system and taste panel amount of connective tissue. Further down chromosome 15 at 76–81 cM, suggestive associations were detected for ultrasound loin depth, change in pH, day 2 slice shear force and day 7 cooking loss.

Three genomic regions contained three suggestive associations. The region at 0 cM on SSC2 had suggestive-level QTL for Hunter L^*, 48 h pH and cooking loss on day 7 for taste panel analyses. Chromosome SSC9 at 50–53 cM had suggestive QTL for three different measures of muscle quantity (manually determined loineye area, and image analysis of amount of lean and percent fat in a loin cross-section), and chromosome X at 121 cM was associated with three measures of quantity of fat.

Discussion

Five chromosome regions contained six significant QTL in this study (Table 3). Four of the regions had desirable effects that were contributed by the Duroc breed. For both QTL located on chromosome 1, the Duroc allele increased intramuscular fat (at 6 cM) and decreased the Hunter L^* reflectance value (SSC1 at 67 cM), therefore improving pork quality. Duroc alleles for SSC17 at 32–39 cM significantly increased loineye muscle area as determined by image analysis, and at 87 cM of SSCX Duroc alleles resulted in heavier carcasses. Unexpectedly, the Duroc allele decreased taste panel scores for overall tenderness on SSC2 at 60–66 cM, and this QTL effect coincided with increased force required to shear the cooked product at 7-day postmortem for the suggestive QTL at this location.

Sixty-three associations were detected on autosomal chromosomes (Table 2). Four of five significant associations located on autosomal chromosomes exhibited additive inheritance (Table 3), and nearly half of all autosomal associations were purely additive (29 of 63; Table 4). Two associations had significant additive and dominance contributions to inheritance. Thirteen associations were of paternal origin, eight were of maternal origin and 11 only had a significant dominance effect.

When viewing these results the covariables included in the statistical model affect their interpretation. The most important adjustment was the inclusion of 10th rib fat thickness in the analyses of marbling and intramuscular fat. Thus these QTL are expected to affect intramuscular fat deposition independent of subcutaneous fat deposition. The covariate seemed to appropriately adjust for subcutaneous fat thickness as no QTL for marbling or intramuscular fat content overlapped QTL for measures of subcutaneous fat thickness. Preliminary analyses for intramuscular fat content usually found suggestive QTL at

Table 3 Estimates of quantitative trait loci (QTL) effects for associations exceeding the genome-wise threshold for significant QTL.

Porcine chromosome	cM (CI)	Trait	Inheritance	Effect[1] (SE)	*F*-ratio	Nominal *P*
1	6 (0–12)	imfat	Sire	0.41 (0.09)	19.316	1.47E-05
1	67 (42–79)	hntl	Additive	−0.84 (0.19)	19.195	1.56E-05
2	62 (60–64)	tpot	Additive	−0.33 (0.06)	26.182	5.09E-07
17	39 (32–49)	ialea	Additive	1566 (321)	23.791	1.61E-06
17	39 (36–50)	lea	Additive	1.6 (0.4)	18.391	2.31E-05
X	87 (80–97)	cwt	Additive	3.6 (0.7)	23.742	2.33E-06

CI, confidence interval based on a 1 LOD drop from the peak *F*-ratio.

[1]Effects are expressed as a deviation of Duroc–Landrace alleles in the units presented in Table 1.

Table 4 Estimates of quantitative trait loci (QTL) effects for associations of suggestive QTL.

Porcine Chromosome	cM (CI)	Trait	Inheritance	Effect[1] (SE)	*F*-ratio	Nominal *P*
2	0 (0^2–9)	ckls7	Addtive	−0.73 (0.22)	11.304	8.58E-04
2	0 (0^2–7)	hntl	Additive	−0.78 (0.20)	14.892	1.35E-04
2	0 (0^2–13)	ph48	Additive	0.05 (0.01)	15.726	8.85E-05
2	60 (50–68)	ssf7a	Additive	1.44 (0.36)	15.667	9.12E-05
2	61 (56–67)	tpact	Additive	−0.15 (0.04)	17.037	4.57E-05
2	66 (60–78)	immois	Mendel	$a = -0.25$ (0.08); $d = 0.30$ (0.11)	9.105	1.38E-04
2	66 (59–76)	ph1	Dominance	0.09 (0.03)	11.459	7.91E-04
2	79 (71–91)	ssf2a	Additive	1.34 (0.38)	12.492	4.63E-04
2	122 (112–122^2)	eyg	Additive	−2.61 (0.74)	12.960	3.64E-04
3	84 (51–95)	cwt	Dam	2.7 (0.7)	14.562	1.59E-04
3	87 (47–99)	lwt	Dam	3.1 (0.9)	12.434	4.75E-04
4	82 (67–118)	firm	Dominance	−0.41 (0.12)	12.141	5.55E-04
4	85 (75–118)	imfat	Dominance	−0.37 (0.11)	11.922	6.22E-04
5	51 (35–66)	mfi	Dam	4.53 (1.22)	13.559	2.67E-04
5	59 (40–63)	hntb	Sire	0.43 (0.12)	12.811	3.93E-04
5	62 (43–67)	ssf2c	Dam	−0.89 (0.25)	12.923	3.70E-04
5	64 (51–82)	immois	Sire	−0.42 (0.11)	14.735	1.47E-04
5	67 (59–90)	tppfi	Additive	0.11 (0.03)	12.804	3.94E-04
5	93 (68–108)	fat10	Additive	1.5 (0.4)	15.284	1.10E-04
7	77 (57–99)	immois	Sire	0.40 (0.11)	11.577	7.45E-04
7	91 (77–108)	apln	Mendel	$a = -0.20$ (0.09); $d = 0.23$ (0.07)	7.549	6.13E-04
7	126 (108–139)	sarc	Dominance	0.05 (0.01)	14.651	1.53E-04
8	42 (23–60)	ph48	Sire	0.07 (0.02)	13.222	3.17E-04
8	56 (27–72)	hntb	Additive	−0.32 (0.09)	11.792	6.66E-04
8	83 (72–100)	mfi	Dam	−4.23 (1.13)	13.664	2.53E-04
8	104 (95–121)	marb	Dominance	0.23 (0.07)	11.636	7.22E-04
9	50 (37–56)	lea	Dominance	−1.05 (0.31)	11.362	8.31E-04
9	53 (41–64)	ialean	Dominance	−1714 (510)	11.276	8.69E-04
9	53 (41–59)	iaperfat	Dominance	1.69 (0.45)	14.352	1.78E-04
10	12 (4^2–44)	ialean	Dominance	1931 (525)	13.546	2.68E-04
10	67 (52–91)	afat	Additive	0.04 (0.01)	11.555	7.51E-04
13	0 (0^2–16)	mfi	Additive	−3.31 (0.84)	15.606	9.41E-05
13	5 (0^2–21)	ph1	Additive	−0.08 (0.02)	11.848	6.46E-04
13	31 (0–59)	tpjui	Additive	−0.11 (0.03)	11.442	7.98E-04
13	53 (45–58)	immois	Dominance	−0.39 (0.11)	13.097	3.39E-04
14	66 (61–91)	eydn	Sire	−3.95 (1.12)	11.280	8.69E-04
14	66 (55–81)	hntl	Sire	−1.04 (0.26)	15.693	9.02E-05
14	69 (58–86)	eyg	Sire	−4.25 (1.11)	13.184	3.24E-04
14	72 (55–101^2)	drip	Sire	−0.57 (0.17)	12.308	5.08E-04
15	4 (4^2–11)	eyr	Additive	−3.59 (0.99)	13.549	2.69E-04
15	14 (4^2–27)	ckls7	Sire	−1.08 (0.29)	13.386	2.92E-04
15	14 (4^2–45)	ssf2c	Sire	−0.82 (0.24)	11.363	8.31E-04
15	17 (6–61)	tpact	Additive	0.13 (0.04)	12.419	4.80E-04
15	37 (9–66)	tpjui	Additive	0.12 (0.03)	14.240	1.88E-04
15	47 (32–66)	drip	Dam	−0.54 (0.16)	11.267	8.74E-04
15	56 (27–82)	ssf7a	Additive	−1.32 (0.39)	11.741	6.83E-04
15	76 (66–82)	ckls7	Additive	−0.81 (0.21)	15.458	1.01E-04
15	77 (68–98)	adpth	Additive	0.05 (0.01)	15.294	1.10E-04
15	112 (101–121^2)	dph	Sire	−0.10 (0.03)	13.737	2.43E-04
15	112 (101–121^2)	ssf2a	Dominance	−2.20 (0.59)	14.154	1.97E-04
17	9 (0^2–23)	ssf2a	Sire	−1.87 (0.56)	11.283	8.66E-04
17	32 (26–38)	imfat	Dam	0.36 (0.09)	15.313	1.09E-04
17	32 (26–35)	marb	Dam	0.22 (0.06)	16.211	6.94E-05
17	34 (18–49)	eyb	Additive	2.65 (0.74)	11.746	6.82E-04
17	34 (18–49)	eydn	Additive	2.97 (0.81)	12.450	4.73E-04

Table 4 Continued

Porcine Chromosome	cM (CI)	Trait	Inheritance	Effect[1] (SE)	*F*-ratio	Nominal *P*
17	34 (20–49)	eyg	Additive	2.83 (0.77)	12.585	4.41E-04
17	34 (17–51)	eyr	Additive	3.41 (0.97)	11.664	7.12E-04
17	35 (28–47)	iatot	Additive	2446 (666)	13.493	2.76E-04
X	10 (3–30)	mfi	Additive	4.37 (1.27)	11.915	6.92E-04
X	10 (1–36)	tpoff	Additive	0.10 (0.03)	11.451	8.74E-04
X	87 (80–97)	lwt	Additive	3.6 (0.9)	17.622	4.14E-05
X	87 (80–109)	sarc	Additive	0.05 (0.01)	11.363	9.14E-04
X	99 (12–127)	ialea	Additive	−2086 (619)	11.347	9.18E-04
X	121 (77–127[2])	fat10	Additive	2.0 (0.6)	12.143	6.14E-04
X	121 (116–127[2])	iafat	Additive	4394 (1230)	12.769	4.48E-04
X	121 (114–127[2])	iaperfat	Additive	3.01 (0.87)	12.060	6.40E-04

CI, confidence interval based on a 1 LOD drop from the peak *F*-ratio.

[1]Effects are expressed as a deviation of Duroc–Landrace alleles in the units presented in Table 1.

[2]Indicates that the confidence interval extends beyond the area spanned by the genetic markers genotyped.

many of the locations that affected subcutaneous fat thickness.

For measures of body composition, carcass weight was included as a covariate. Therefore, these QTL effects are expected to affect the trait reported relative to a constant carcass weight. For analyses of palatability and quality, genotypic data were included. If the allele frequencies for the founding breeds differed significantly for either genetic marker, then the genotypic information could remove variation because of a QTL in that location of the genome. However, the frequency of the *RYR1* 615C allele was very rare, and the frequencies of the four different haplotypes for *PRKAG3* were quite similar in the four purebred Duroc and Landrace pigs genotyped, indicating that these covariates should not dramatically affect these results.

The regions containing imprinted QTL in this study (Table 4) had not been associated with imprinting in other publications in swine (de Koning *et al.* 2000; Dekkers *et al.* 2003). For many of these regions there was only a single imprinted QTL detected. However, five of these regions were supported by multiple suggestive imprinted QTL and have interesting features. Region SSC3 at 84–87 cM had suggestive QTL affecting live and carcass weight for maternally inherited alleles. Paternal expression was highly supported for four longissimus traits on SSC14 at 66–72 cM for measures of reflectance (Hunter L^*), green and colour density recorded by image analysis equipment as well as drip loss. SSC17 at 32–39 cM exhibited imprinting effects where maternally expressed alleles were associated with marbling and intramuscular fat. This specific location also possessed seven other QTL with additive modes of inheritance. Finally, SSC5 at 59–67 cM had four suggestive QTL, two that were paternally expressed (Hunter b^* and intramuscular moisture content), one that was maternally expressed (cooking loss on day 2) and one that was additive (pork flavour intensity).

Some imprinted QTL regions may actually be due to the structure of the data set. First, because all paternal grandparents were available for analyses, and breed of origin of most of the maternally inherited alleles were predicted by GenoProb, there is less ambiguity in paternally inherited alleles than in maternally inherited alleles, and therefore, more significant associations from the paternally inherited alleles are possible than for the maternally inherited alleles. Another feature of the genotypic data is that markers were selected to maximize the number of heterozygous sires, and no information from the dams was considered. This resulted in average marker heterozygosity for sires of 87% and 77% for dams. However, heterozygosity of sires and dams were similar in regions with maternal or paternal expressed QTL. Finally, the analyses assumed that QTL were fixed within the parental breeds. Deviations from this assumption along with sampling could lead to a region where the QTL will be segregating in a disproportionate larger number of F_1 parents of one sex resulting in an apparent imprinting mode of inheritance.

Analyses of the X chromosome only detected QTL for performance in females. All loci appeared to have additive inheritance. Power to detect QTL on the X chromosome was reduced by splitting the data set into male and female progeny.

Only a few of the QTL detected in the present study appear to overlap with previously reported QTL. One of the six significant QTL (Table 3) has previously been detected in other populations. The QTL detected at SSC1 at 67 cM for Hunter L^* was also found by de Koning *et al.* (2001). Another location with direct evidence of concordance was SSC14 at 66–69 cM, where QTL for colour score (de Koning *et al.* 2001) and Hunter L^* reflectance (Malek *et al.* 2001b) overlap with suggestive QTL for image analysis green colour and Hunter L^* in the present study. The region SSC15 at 51 cM in this study had a suggestive QTL for slice shear

force at 7-day postmortem, which overlaps QTL for taste panel tenderness scores and STAR probe tenderness of Malek *et al.* (2001b). Finally, a QTL affecting reflectance values in a half sib model (de Koning *et al.* 2001) may be similar to a suggestive QTL for Hunter L^* in this study on SSC2 at 0 cM.

Other similarities that are less definitive include two QTL for water holding capacity on chromosomes 2 and 13 (Malek *et al.* 2001b), which could be similar to suggestive QTL for intramuscular moisture content QTL in this study (SSC2 at 60–66 cM and SSC13 at 53 cM). A QTL for ham and loin pH from Malek *et al.* (2001b) on chromosome 15 is located near a suggestive QTL for change in pH in this study (SSC15 at 76–81 cM). Malek *et al.* (2001a) reported a QTL for 10th rib fat thickness close to a suggestive QTL for the same trait in our data at SSC5 at 93 cM. A QTL for 8-week weight in a Meishan–White Composite population (Rohrer 2000) is near the QTL for live weight at slaughter and carcass weight in this study on ChrX at 84–87 cM.

Four chromosomes with significant QTL were supported by multiple associations with correlated traits. Chromosome 2 presented the best support for a QTL affecting tenderness located in the physical region of 2q1.1–2.1. This region was associated with slice shear force at 7-day postmortem, measures of tenderness in the trained sensory panel and most likely shear force at 2-day postmortem (position SSC2 at 79 cM). This region of pig chromosome 2 has homologies to the short arm of human chromosome 19 and the long arm of human chromosome 5. Calpastatin is an inhibitor of the calpain family of proteases which are important in postmortem tenderization (Koohmaraie 1992) and it resides on HSA5q15–21. Recently, Ciobanu *et al.* (2004) have reported significant linkage disequilibrium between alleles of calpastatin and measures of firmness and tenderness in four commercial lines of pigs. These results combined may indicate the causative variation lies somewhere near the calpastatin gene located on human chromosome 5 position 96 Mb (Build 35 of human genome).

Chromosome 17 displayed convincing evidence of a QTL for musculature and body composition. Unfortunately, the public comparative map for this region of the pig genome is not well defined. A possible positional candidate for this QTL could be *MNTRA1* that is located on human chromosome 4 and pig chromosome 17. However, other candidates exist, including a QTL that affects body composition in both humans (Lembertas *et al.* 1997; Lee *et al.* 1999; Hunt *et al.* 2001) and mice (Lembertas *et al.* 1997; Mehrabian *et al.* 1998; Rocha *et al.* 2004) and that resides on the long arm of human chromosome 20, which is known to be homologous to pig chromosome 17 (Goureau *et al.* 1996). Possible positional candidate genes for this QTL may be *agouti signalling protein* (*ASIP*) and *CCAAT/enhancer-binding protein-beta* (*CEBPB*; Lee *et al.* 1999).

Chromosomes 15 and X had multiple regions with QTL associations. One possibility for associations of chromosome 15 with many pork quality traits and tenderness could be undiscovered alleles of *PRKAG3*. However, there could also be other genes residing on chromosome 15 that also affect pork quality traits. The results on chromosome X are likely due to different genes located across the chromosome. The fact that most QTL were only detected in female progeny may aid in selecting positional candidate genes. While QTL for fat deposition have been found around the centromere on chromosome X in multiple studies using Meishan germplasm, our results for fat deposition were located towards the end of the q arm and are unlikely to be caused by the same gene(s). However, the growth QTL in this study is located near the centromere and may be caused by the same or neighbouring gene as the backfat QTL in Meishan populations, but the difference in traits could be due to the background genotype of the animals. As the X chromosome results are based on a limited number of records, additional research needs to be completed to determine more precisely the location and mode of inheritance for these QTL before many resources are invested into follow-up studies.

While this study utilized commercially relevant germplasm, validating these QTL in other populations is necessary to verify that the identified QTL were not false positives or just an anomaly of the selected parental animals of the population. Furthermore, validation in populations with less linkage disequilibrium than this F_2 population will permit resolving the location of the QTL to a much smaller interval, resulting in genetic markers that will be more robust across different populations of pigs. Identification of the nucleotide variation that causes the observed phenotypic effect will result in the most accurate predictive genetic markers for all commercial pig populations.

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Supplementary Material

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

Table S1 Microsatellite markers used to interrogate the porcine genome.