

A genome scan to detect QTL affecting growth, composition, and meat quality traits in a Berkshire x Yorkshire cross

Jack Dekkers, Jong-Joo Kim, Massoud Malek, Hauke Thomsen, Hakkyo Lee¹, Hong-Hua Zhao, and Max Rothschild

Department of Animal Science and Center for Integrated Animal Genomics
225 Kildee Hall, Iowa State University
Ames, IA, 50011, USA

¹ National Livestock Research Institute, Suwon, Korea

Introduction

The techniques of molecular biology and molecular genetics have rapidly progressed. These methods, coupled with advances in human genetics, have opened new vistas for investigators wishing to identify genes that control quantitative traits (quantitative trait loci or QTL). Also, over the past years, a great deal of progress has been made in development of genetic maps in the pig. For example, a large international mapping effort (Archibald et al., 1994), a USDA/ARS effort (Rohrer et al., 1996) and a U.S. coordinated effort (Rothschild, 1994) have produced several genetic linkage maps for the pig. Based on these linkage maps, several recent studies have reported the discovery of a number of QTL affecting growth and body composition traits in the pig. Andersson et al. (1994) conducted the first genome wide scan for growth and body composition in pigs based on a Wild Boar x Large White cross. They found evidence of QTL on SSC 4 with large effects on growth from birth to 70 kg and for fat deposition. In addition, they found a QTL on SSC 13 affecting early growth. Using the same cross, Marklund et al. (1999) confirmed the presence of QTL on SSC 4 affecting fatness and growth and refined the estimated location of these QTL. Perez-Enciso et al. (2000) also found a significant fatness QTL on SSC 4 in an F₂ cross between Iberian x Landrace pigs. Other crosses to identify and locate QTL in pigs have generally used the Meishan (Chinese) breed crossed to European or American breeds (e.g. Wang et al. 1998, Rohrer and Keele 1998a,b, Paszek et al. 1999, De Koning et al. 2001, Andersson-Eklund et al. 1998, Moser et al. 1999, Bidanel and Rothschild, 2002). Most QTL studies in pigs to-date have involved exotic crosses, which are not of immediate practical interest. Resource families using commercial breeds or lines did not exist at the initiation of the project that will be described here.

Results from the NPPC Genetic Evaluation Program (Goodwin, 1995) revealed that considerable differences in meat quality exist between breeds and that the Berkshire breed, in particular, has very positive meat quality traits. The general use of genes and genetic markers makes it possible to localize the QTL responsible for meat quality traits.

Therefore, the objectives of the first phase of the research that will be described here were to develop a three generation F₂ resource family using the Berkshire and Yorkshire breeds to identify chromosomal regions responsible for breed differences in growth, composition, muscle and meat quality, and sensory quality traits. This initial phase was based on 125 microsatellite markers across the genome and detected over 100 QTL, as described by Malek et al. (2001a,b).

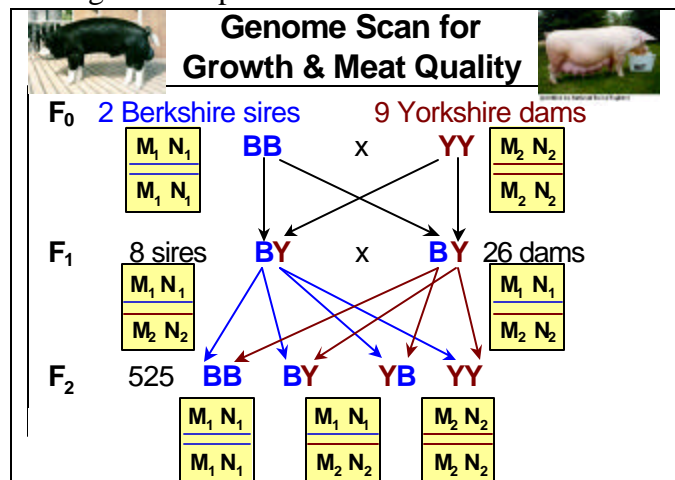
In a second phase, all animals were genotyped for an additional 33 microsatellite markers to increase the number of informative meioses in special regions of interest that appeared to harbor QTL in the initial scan or that had limited marker coverage. Results of the second phase will be described here. In addition to QTL that differ between breeds, this report also describes results of QTL scans designed to detect QTL that segregate within breeds. All analyses presented herein will be for QTL that follow normal Mendelian inheritance. In other words, the effect of the heterozygous genotype (BY) does not depend on whether the B allele was received from the sire or the dam. Results on QTL that exhibit gametic imprinting, for which allele effects do depend on parental origin, will be described in a subsequent paper in these proceedings.

Materials and methods

Population structure

A total of 2 Berkshire boars (chosen with NPPC guidance) and 9 Yorkshire females were used to produce 9 useful F₁ litters. Semen from boar studs was used and sows mated at the ISU Swine Breeding Farm. The two boars used were Casino and Count. From the F₁ litters, 8 boars and 26 females were chosen to produce 65 litters of 525 F₂ animals for genetic and meat trait analysis (Figure 1).

Figure 1. Population structure



Traits measured

A summary of traits evaluated on F₂ pigs is in Tables 1 and 2. Performance data collected included birth weight, 16d weight, ADG from birth to 16 days of age, and ADG from weaning to slaughter. Pigs were weighed at weekly intervals and sent to market at approximately 240 lbs. After slaughter, several carcass traits were evaluated. Measurements were taken primarily at two locations: the Hormel slaughter plant in Austin, Minnesota at 24 hrs after slaughter and the Iowa State University Meat Laboratory in Ames 48 hrs after slaughter. All measurements were taken by trained personnel following the guidelines of the National Pork Producers Council (NPPC, 1991). These data included carcass weight, visual scores for loin muscle marbling, color and firmness, pH, Minolta reflectance, and Hunter L. color scores for ham and loin. Water holding capacity was measured using a piece of filter paper (higher weight is less water holding capacity) and drip loss was calculated using two separate cubes of meat and by collecting the drip over 72 hrs. In addition, a loin chop was taken from each carcass and samples from it were used to evaluate lipid content. Some measurements were taken at 24 hrs post slaughter and repeated at 48 hrs post slaughter.

Table 1. (Based on Malek et al. 2001a) Means and standard deviations for growth and composition traits and expected differences between breed means (Berkshire minus Yorkshire)^a.

Traits Analyzed for QTL Mapping	Mean	Std Dev	Berk -York^a
Birth Weight (kg)	1.55	0.325	NA ^b
16 Day Weight (kg)	4.95	1.311	NA
Average Daily Gain to Weaning (kg/day)	0.24	0.074	0.005
Average Daily Gain on Test (kg/day)	0.69	0.065	0.009
Carcass Weight (kg)	87.08	5.733	NA
Carcass Length (cm)	84.16	2.454	-1.524
Tenth Rib Back Fat (cm)	3.19	0.779	1.016
Lumbar Back Fat (cm)	3.58	0.757	1.016
Last Rib Back Fat (cm)	3.16	0.609	0.664
Average Back Fat (cm)	3.31	0.641	NA
Loin Eye Area (cm ²)	35.59	5.684	-5.548
Additional Traits			
Live Weight at Slaughter (kg)	118.11	6.964	NA
Dressing Percent (%)	73.72	1.95	0.0

^aExpected difference between breed means based on twice the difference observed in crossbreds in the NPPC genetic evaluation program (Goodwin, 1995).

^bNA: Not available

At 48 hours postmortem, a sub-sample of the loin was frozen and sent to the University of Illinois, where glycogen, free glucose, glucose-6-P, and lactate content were measured in $\mu\text{Mol/g}$ (Monin and Sellier, 1985). Postmortem metabolism of elevated glycogen stores results in increased production of lactate, which is a pH lowering by-product of muscle metabolism. Glycolytic potential is a measure of glycogen stores and was calculated as follows: glycolytic potential = $2 \times ([\text{glycogen}] + [\text{glucose}] + [\text{glucose-6-phosphate}]) + [\text{lactate}]$ (Monin and Sellier, 1985; Maribo et al. 1999). Glycolytic potential is expressed in μM lactate equivalents per gram muscle wet weight. In addition

to glycolytic potential and lactate concentration, residual glycogen concentration was used as a trait of interest in this study. Residual glycogen is the glycogen remaining in the muscle that was not converted to lactate and glucose-6-phosphate. Muscle fiber type composition was evaluated in 48-hour postmortem samples from the longissimus dorsi by separation of myosin isoforms on high porosity SDS-PAGE gels (Huff-Lonergan et al. 2001). Results were expressed as the ratio of the density of the IIa band of myosin to the density of the IIb band within a sample. To evaluate the sensory characteristics of the meat, vacuum packaged boneless chops from the longissimus dorsi of each animal were taken 48 hours after slaughter and stored for 10 days at 4°C. Following the storage period, chops were broiled to 71°C and cooking loss was calculated.

Table 2. (Based on Malek et al. 2001b). Means and standard deviations for quality traits on 525 F2 animals and expected differences between breed means (Berkshire - Yorkshire)^a.

Trait (score range)	Score interpretation		N	Mean	St. Dev.	Berk minus York ^a
	Low value	High value				
Subjective carcass evaluations	Pale	Dark	525	3.25	0.48	0.2
Color score (1 – 5)						
Marbling (1 – 5)	Low	High	525	3.80	0.73	0.6
Firmness (1 – 5)	Soft	Firm	525	3.42	0.63	0.4
<i>Light Reflectance</i>						
24-hr Ham Minolta L	Dark	Pale	525	17.47	2.90	NA ^b
24-hr Ham Hunter L	Dark	Pale	525	41.65	3.46	NA
24-hr Loin Minolta L	Dark	Pale	525	21.09	5.20	-0.8
24-hr Loin Hunter L	Dark	Pale	525	44.07	6.12	-0.8
48-hr Loin Minolta L	Dark	Pale	525	22.07	3.24	0.0
48-hr Loin Hunter L	Dark	Pale	525	46.87	3.39	-0.6
<i>Muscle pH</i>						
24-hr Ham pH	Pale	Dark	525	5.89	0.22	NA
24-hr Loin pH	Pale	Dark	525	5.78	0.17	NA
48-hr Loin pH	Pale	Dark	525	5.83	0.19	0.14
<i>Tissue Quality and Water Holding Capacity</i>						
Drip Loss (%)	Low loss	High loss	525	5.84	1.99	-0.84
Water Holding Capacity (g)	Low loss	High loss	525	0.21	0.137	-13.8
Fiber Type I %			513	0.08	0.131	NA
Fiber Type II Ratio			513	1.04	0.77	NA
<i>Glycogen Content of The Loin</i>						
Glycogen content (µmol/g)			519	8.68	3.34	NA
Lactate content (µmol/g)			519	86.67	13.30	NA
Glycolytic Potential (µmol/g)			518	104.00	16.31	NA
<i>Fat Content</i>						
Total Lipid (%)			525	3.23	1.32	0.16
Cholesterol (mg/100g)			525	57.72	8.29	0.6
<i>Instrumental Tenderness</i>						
Instron (Star Probe) Force (kg)	Tender	Tough	513	7.84	1.17	-0.78
<i>Cooking and Sensory Panel Evaluation</i>						
Cooking Loss (%)			513	18.23	4.40	-2.0
Tenderness Score (1-10)	Tough	Tender	488	4.36	0.86	0.48
Juiciness Score (1-10)	Dry	Juicy	513	6.02	1.49	0.0
Chewiness Score (1-10)	Soft	Tough	513	2.42	0.93	-0.32
Flavor score (1-10)	Little	Intense	513	2.85	1.76	0.0
Off Flavor Score (1-10)	None	High	513	1.59	2.03	0.0

^a Expected difference between breed means based on twice the difference observed in crossbreds in the NPPC genetic evaluation program (Goodwin, 1995).

^b NA: Not available.

Instrumental measurement of tenderness of the broiled chops was evaluated using a circular five-pointed star-probe. Sensory evaluation of the broiled chops was done using three highly-trained professional sensory panelists. Samples were evaluated for degree of juiciness, tenderness, chewiness, pork flavor, and off-flavor using a 10-point category scale. The values for each pork chop were averaged across the three panelists. Further details on all traits evaluated can be found in Malek et al. (2001a,b).

DNA isolation and genotyping

Blood samples were collected from all F₂ animals, parents and grandparents and DNA samples collected. Likely parentage (or collection) problems existed on less than 20 F₂ animals and these were discarded for analyses. Prior to genotyping all animals, markers were screened to ensure their accuracy and informativeness in the cross. Genotyping was subcontracted to a commercial laboratory (GeneSeek Inc., Lincoln, NE) to speed the process and minimize costs.

Statistical analyses

Marker linkage maps were computed using Crimap version 2.4 software (Green et al. 1990). The maps were then used for QTL analysis of the 18 autosomes using the following three analyses (see paper on “Principles of QTL Mapping” in these proceedings for details):

- 1) Line cross least squares regression interval mapping (LC) (Figure 2), to detect QTL that differ between breeds.
- 2) Half-sib least squares regression interval mapping (HS) (Figure 3), to detect QTL that segregate within breeds.
- 3) Combined line-cross and half-sib least squares regression interval mapping (COMB) (Figure 4), to combine the power of the LC and HS analyses.

Figure 2. Statistical model for line cross regression interval mapping

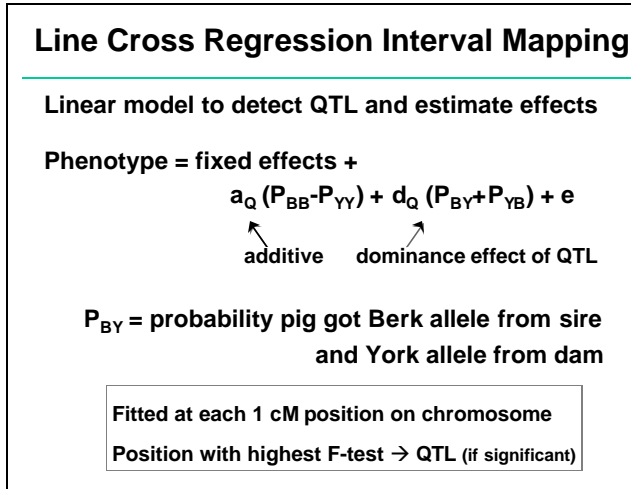


Figure 3. Statistical model for half-sib regression interval mapping

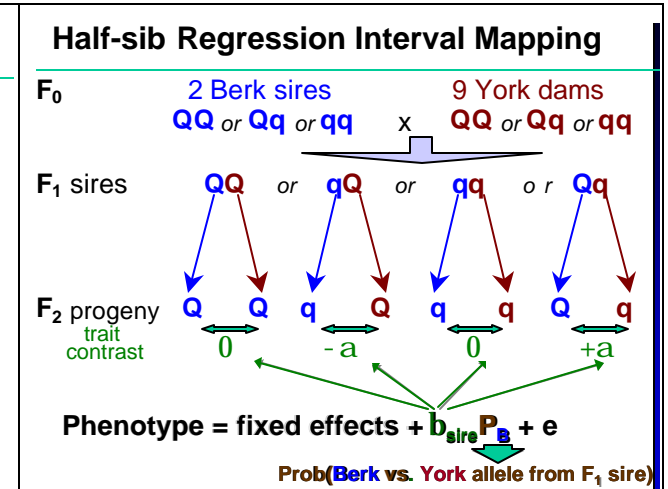
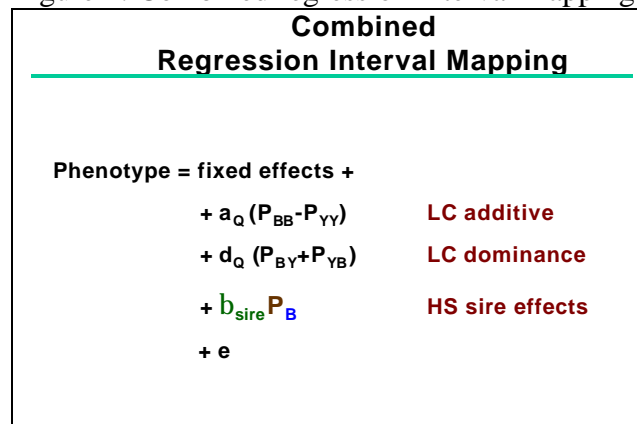


Figure 4. Combined regression interval mapping



Programs developed by Haley et al. (1994) and Knott et al. (1996) were used as the basis for the analyses but were modified as needed.

All models used included sex, year-season, and F1 sire as fixed effects. In addition, litter size was included as a covariate for birth weight, 16 day weight, and growth to weaning. Slaughter age and live weight were included as covariates for all other traits. For meat quality and sensory traits the effect of year-season was removed and the effect for slaughter date was added.

Significance levels were calculated using the permutation test developed by Churchill and Doerge (1994). This was computed for both the individual chromosomal and at the genome-wide level (both at the 5 and 1% levels) based on 10,000 random permutations of the data for each trait separately. The QTL detected at the 5% chromosome-wise level were classified into three categories based on results of the LC, HS, and COMB analyses as follows:

- 1) LC: QTL that are significant for the LC model but not for the HS model. These are QTL that differ in frequency between the breeds but do not show evidence of segregating within the F_0 parents.
- 2) HL: QTL that are significant for the HS model but not for the LC model. These are QTL that segregating within the F_0 parents but do not show evidence of a difference in frequency between the breeds.
- 3) BOTH: QTL that are significant for the COMB model but cannot be classified as LC or HL. These are QTL that show evidence of a difference in frequency between the breeds and of segregation within the F_0 parents.

It must be noted that all results pertain to the specific F_0 parents that were used in this study and may not reflect results for the Berkshire and Yorkshire breeds as a whole, though efforts were made to choose representative animals of the respective breeds.

Results and discussion

Phenotypic data (Tables 1 and 2) conformed to the usual range of measurement scores. A detailed analysis of trait relationships in this population is in Huff-Lonergan et al. (2002). Marker maps calculated based on the initial 125 markers are in Malek et al. (2001a) and agreed well with other published maps. Linkage maps that were derived after adding the 33 new markers were in good agreement with those estimated by Malek et al. (2001a). Map length only changed for SSC2 and was extended by 13 cM because two additional markers were added to the proximal end. Generally, marker order did not change compared to Malek et al. (2001a) except in the rare case where markers were very close together. A summary of QTL that were significant at the 5% chromosome wise level is given in Table 3 by chromosome and in Table 4 by trait.

Table 3. Summary of QTL mapping results by chromosome.

Chromo- some (1 st marker)	Trait	QTL Position	Signif- icance ^b	Type of QTL	QTL variance (% of F2)	Breed QTL effects (in phen. s.d. units)		
						BB ^a	BY	YY
1 (SW1515)	CarcYIELD	50	5%chr-w	HS	4.7			
	LribBFAT	64	*	HS	3.1			
	AVBFAT	59	*	HS	3.2			
	LEA	97	1%chr-w	LC	2.6	0.22	-0.06	-0.22
	MARB	52	5%gen-w	Both	6.6	-0.11	0.26	0.11
	MARB	127	1%gen-w	HS	5.1			
	24HampH	104	*	HS	4.4			
	FIBER-I	89	*	HS	5.2			
	LIPID%	29	*	LC	2.3	-0.21	0.09	0.21
2 (SW2443)	16-d-WT	76	*	LC	4.0	0.02	0.40	-0.02
	ADGearly	77	*	LC	4.3	0.00	0.42	0.00
	10thBFAT	0	****	Both	10.8	0.08	-0.05	-0.08
	LumbBFAT	2	****	Both	11.8	0.15	-0.07	-0.15
	LribBFAT	0	****	Both	8.6	0.12	-0.04	-0.12
	AVBFAT	0	****	Both	13.3	0.14	-0.07	-0.14
	LEA	1	****	Both	10.0	0.04	0.10	-0.04
	24LoinMIN	88	*	LC	3.6	0.20	-0.24	-0.20
	DRIPloss	47	***	Both	7.3	0.08	0.07	-0.08
	WHC	154	*	LC	2.8	0.22	-0.12	-0.22
	FIBER-I	98	**	HS	6.4			
	TENDERness	157	**	LC	3.0	-0.23	-0.13	0.23
	JUICiness	82	*	HS	3.0			
	FLAVOR	157	*	LC	2.8	-0.23	-0.01	0.23
	OFFFLAVOR	50	*	Both	6.4	0.24	0.08	-0.24
OFFFLAVOR	156	*	LC	2.3	0.19	0.14	-0.19	

^a Standard errors ranged from 0.06 to 0.10 phenotypic s.d. for additive effects and from 0.09 to 0.14 phenotypic s.d. for dominance effects.

^b * 5% chromosome-wise
 ** 1% chromosome-wise
 *** 5% genome-wise
 **** 1% genome-wise

Table 3 Continued. Summary of QTL mapping results by chromosome.

Chromosome (1 st marker)	Trait	QTL Position	Signi- ficance	Type of QTL	QTL variance (% of F2)	Breed QTL effects (in phen. s.d. units)		
						BB	BY	YY
3 (SW274)	LENGTH	123	*	HS	4.4			
	COLOR	72	*	LC	2.6	-0.19	-0.19	0.19
	24HamMIN	32	**	HS	4.4			
	24HamHUNT	30	*	HS	4.3			
	INSTRON	36	*	Both	5.1	0.12	0.33	-0.12
	FLAVOR	9	*	HS	4.6			
	FLAVOR	123	*	Both	5.2	0.18	0.14	-0.18
	OFFFLAVOR	53	*	Both	5.0	0.32	0.11	-0.32
4 (SW2404)	16-d-WT	108	*	Both	4.8	-0.22	-0.14	0.22
	16-d-WT	154	*	HS	4.6			
	ADGearly	108	*	Both	5.1	-0.22	-0.15	0.22
	ADGearly	154	*	HS	4.5			
	CarcYIELD	140	****	LC	5.2	0.30	0.17	-0.30
	LEA	113	*	HS	1.7			
48LoinHUNT	147	*	LC	2.3	0.15	0.21	-0.15	
5 (ACR)	ADGtest	83	*	HS	4.3			
	LENGTH	135	*	Both	5.5	-0.24	0.02	0.24
	LumbBFAT	123	***	Both	6.3	0.38	0.21	-0.38
	LribBFAT	124	***	LC	4.0	0.27	0.13	-0.27
	AVBFAT	126	***	Both	5.7	0.36	0.12	-0.36
	24LoinMIN	133	*	LC	2.8	0.13	-0.29	-0.13
	48LoinMIN	133	*	LC	2.7	0.16	-0.25	-0.16
	48LoinHUNT	133	*	LC	2.4	0.14	-0.24	-0.14
48LoinpH	91	*	LC	3.6	-0.27	0.01	0.27	
6 (SW2535)	10thBFAT	89	*	HS	3.6			
	10thBFAT	134	***	Both	5.3	-0.30	0.20	0.30
	24HampH	50	***	LC	4.2	-0.14	0.36	0.14
	24LoinpH	58	*	Both	5.5	0.13	0.23	-0.13
	LIPID%	137	**	Both	5.4	-0.33	0.34	0.33

Table 3 Continued. Summary of QTL mapping results by chromosome.

Chromo- some (1 st marker)	Trait	QTL Position	Signi- ficance	Type of QTL	QTL variance (% of F2)	Breed QTL effects (in phen. s.d. units)		
						BB	BY	YY
7 (S0025)	10thBFAT	74	*	LC	2.6	0.22	-0.04	-0.22
	10thBFAT	107	**	LC	3.8	0.26	-0.13	-0.26
	LumbBFAT	59	****	LC	6.6	0.36	-0.05	-0.36
	LumbBFAT	104	****	LC	5.5	0.33	-0.05	-0.33
	LribBFAT	73	***	Both	6.4	0.36	-0.05	-0.36
	LribBFAT	107	*	LC	3.4	0.26	-0.03	-0.26
	AVBFAT	72	****	Both	7.3	0.41	-0.07	-0.41
	AVBFAT	105	****	LC	5.5	0.32	-0.09	-0.32
	MARB	134	*	LC	2.6	0.21	0.11	-0.21
	48LoinMIN	84	*	LC	2.5	0.17	-0.21	-0.17
	48LoinHUNT	49	*	HS	4.2			
	48LoinHUNT	84	*	LC	2.6	0.16	-0.23	-0.16
OFFFLAVOR	62	*	HS	4.8				
8 (S0098)	ADGtest	54	*	LC	3.2	-0.19	0.23	0.19
	CarcYIELD	48	****	Both	7.3	-0.12	0.34	0.12
	10thBFAT	58	*	HS	3.1			
	LumbBFAT	70	*	HS	4.6			
	AVBFAT	68	*	HS	3.9			
	LEA	1	***	HS	4.0			
	24HampH	73	*	HS	7.3			
LACTate	0	*	HS	3.9				
9 (SWR68)	16-d-WT	132	***	LC	4.0	0.18	0.31	-0.18
	ADGearly	37	**	LC	3.3	0.12	0.32	-0.12
	ADGearly	132	***	LC	3.9	0.16	0.32	-0.16
	ADGtest	24	*	LC	4.1	0.16	0.33	-0.16
	ADGtest	115	*	Both	4.5	0.29	0.06	-0.29
	CarcYIELD	112	*	HS	4.4			
	MARB	4	*	HS	4.4			
	OFFFLAVOR	79	*	LC	3.2	-0.18	-0.25	0.18
10 (SWR136)	LribBFAT	79	***	Both	5.9	0.31	-0.24	-0.31
	AVBFAT	79	*	Both	4.6	0.34	-0.20	-0.34
	LEA	89	*	Both	3.7	-0.17	-0.23	0.17
	MARB	5	*	LC	3.9	-0.25	-0.18	0.25
	24LoinHUNT	17	*	HS	4.7			
	LIPID%	11	*	Both	4.3	-0.22	0.09	0.22
	INSTRON	0	**	HS	5.1			
	INSTRON	70	***	LC	4.4	-0.29	-0.11	0.29

Table 3 Continued. Summary of QTL mapping results by chromosome.

Chromo- some (1 st marker)	Trait	QTL Position	Signi- ficance	Type of QTL	QTL variance (% of F2)	Breed QTL effects (in phen. s.d. units)		
						BB	BY	YY
11 (S0385)	16-d-WT	32	*	HS	4.1			
	ADGearly	35	*	HS	4.2			
	COLOR	85	***	HS	6.0			
	48LoinMIN	85	*	HS	4.0			
	48LoinHUNT	81	*	HS	4.1			
	24HampH	0	**	HS	5.0			
	48LoinpH	0	**	HS	4.9			
	DRIPloss	0	*	LC	1.8	0.15	-0.16	-0.15
	DRIPloss	69	***	HS	6.7			
	WHC	0	*	HS	4.0			
	WHC	71	*	HS	4.0			
	GLYCogen	6	**	HS	4.1			
	GLYCpot	2	**	HS	3.9			
	FLAVOR	77	*	HS	4.2			
12 (S0229)	CarcYIELD	97	*	LC	3.4	0.14	0.32	-0.14
	10thBFAT	60	**	HS	4.4			
	10thBFAT	97	*	Both	4.4	0.22	-0.10	-0.22
	AVBFAT	91	*	HS	3.8			
	COLOR	34	*	LC	2.3	-0.21	-0.09	0.21
	24HamMIN	44	****	HS	6.0			
	24HamMIN	80	****	HS	6.5			
	24HamHUNT	44	***	HS	5.9			
	24HamHUNT	80	****	HS	6.2			
	48LoinHUNT	0	*	HS	4.1			
LIPID%	43	*	HS	3.7				
13 (SWR1841)	CarcYIELD	67	**	LC	3.2	-0.06	-0.35	0.06
	LENGTH	72	*	HS	1.9			
	LribBFAT	41	*	LC	2.8	0.14	-0.27	-0.14
	WHC	55	*	LC	2.5	0.22	0.05	-0.22
	GLYCogen	72	*	Both	3.4	0.20	-0.20	-0.20
	GLYCpot	72	*	Both	3.3	0.07	-0.24	-0.07
	24HamHUNT	0	*	LC	3.3	-0.07	-0.34	0.07
14 (SW857)	FIBER-I	111	**	HS	5.8			
	INSTRON	35	*	LC	2.5	-0.15	0.23	0.15
	CookLOSS	37	*	LC	2.8	-0.24	-0.01	0.24
	TENDERness	74	*	LC	2.7	0.18	0.20	-0.18

Table 3 Continued. Summary of QTL mapping results by chromosome.

Chromo- some (1 st marker)	Trait	QTL Position	Signi- ficance	Type of QTL	QTL variance (% of F2)	Breed QTL effects (in phen. s.d. units)		
						BB	BY	YY
15 (SW1416)	10thBFAT	66	*	LC	2.2	-0.15	-0.21	0.15
	LribBFAT	30	**	HS	4.9			
	FIRMness	67	*	HS	3.9			
	24LoinHUNT	54	*	LC	2.6	-0.23	0.01	0.23
	24LoinHUNT	102	**	LC	4.0	-0.25	0.18	0.25
	48LoinMIN	72	****	Both	8.2	-0.41	0.11	0.41
	48LoinHUNT	73	****	Both	7.8	-0.40	0.12	0.40
	24HampH	81	****	LC	4.2	0.28	-0.09	-0.28
	24LoinpH	84	****	LC	5.9	0.34	-0.03	-0.34
	48LoinpH	44	***	LC	5.0	0.28	-0.21	-0.28
	48LoinpH	73	***	LC	3.7	0.27	-0.08	-0.27
	DRIPloss	52	***	LC	3.5	-0.23	0.19	0.23
	GLYCogen	4	*	LC	2.7	-0.19	0.18	0.19
	GLYCogen	95	*	Both	5.0	-0.19	0.11	0.19
	GLYCpot	76	*	LC	2.8	-0.24	0.01	0.24
	INSTRON	49	**	LC	4.5	-0.28	0.15	0.28
	INSTRON	73	*	LC	2.9	-0.24	0.06	0.24
	TENDERness	74	*	Both	5.7	0.46	-0.02	-0.46
	FLAVOR	100	*	LC	3.6	0.22	-0.22	-0.22
	OFFFLAVOR	53	*	LC	3.2	-0.23	0.14	0.23
16 (SW2411)	GLYCogen	51	*	LC	2.3	-0.21	0.03	0.21
17 (SW335)	16-d-WT	7	*	Both	4.6	-0.01	-0.21	0.01
	ADGearly	7	*	Both	4.6	0.00	-0.21	0.00
	COLOR	81	**	Both	5.8	0.20	-0.20	-0.20
	48LoinMIN	86	***	Both	6.8	-0.24	0.20	0.24
	48LoinHUNT	86	***	Both	6.4	-0.22	0.18	0.22
	LACTate	89	*	LC	2.8	-0.12	0.29	0.12
	GLYCpot	86	*	LC	2.6	-0.09	0.30	0.09
	OFFFLAVOR	82	*	LC	2.5	-0.15	0.24	0.15
18 (SW1023)	10thBFAT	1	*	LC	1.8	-0.19	0.03	0.19
	AVBFAT	7	*	Both	4.0	-0.33	0.04	0.33
	24LoinMIN	35	*	LC	2.6	-0.05	-0.31	0.05
	GLYCogen	29	*	HS	4.0			

Table 4. Significant QTL by trait.

Chr	Trait	QTL Position	Significance ^c	Type of QTL	QTL variance (%)	Breed QTL effects (SD)			Breed difference B-Y in SD ^b
						BB ^a	BY	YY	
2	16-d-WT	76	*	LC	4.0	0.02	0.40	-0.02	
4		108	*	Both	4.8	-0.22	-0.14	0.22	
4		154	*	HS	4.6				
9		132	***	LC	4.0	0.18	0.31	-0.18	
11		32	*	HS	4.1				
17		7	*	Both	4.6	-0.01	-0.21	0.01	
Sum			#QTL: LC/HS/Both		2 / 2 / 2	26.3	-0.03	0.36	
2	ADGearly	77	*	LC	4.3	0.00	0.42	0.00	
4		108	*	Both	5.1	-0.22	-0.15	0.22	
4		154	*	HS	4.5				
9		37	**	LC	3.3	0.12	0.32	-0.12	
9		132	***	LC	3.9	0.16	0.32	-0.16	
11		35	*	HS	4.2				
17		7	*	Both	4.6	0.00	-0.21	0.00	
Sum		#QTL: LC/HS/Both		3 / 2 / 2	29.9	0.05	0.70	-0.05	0.07
5	ADGtest	83	*	HS	4.3				
8		54	*	LC	3.2	-0.19	0.23	0.19	
9		24	*	LC	4.1	0.16	0.33	-0.16	
9		115	*	Both	4.5	0.29	0.06	-0.29	
Sum		#QTL: LC/HS/Both		2 / 1 / 1	16.1	0.26	0.62	-0.26	0.22
1	CarcYIELD	50	*	HS	4.7				
4		140	****	LC	5.2	0.30	0.17	-0.30	
8		48	****	Both	7.3	-0.12	0.34	0.12	
9		112	*	HS	4.4				
12		97	*	LC	3.4	0.14	0.32	-0.14	
13		67	**	LC	3.2	-0.06	-0.35	0.06	
Sum		#QTL: LC/HS/Both		3 / 2 / 1	28.2	0.25	0.48	-0.25	N/A
3	LENGTH	123	*	HS	4.4				
5		135	*	Both	5.5	-0.24	0.02	0.24	
13		72	*	HS	1.9				
Sum		#QTL: LC/HS/Both		0 / 2 / 1	11.8	-0.24	0.02	0.24	-0.78

^a Standard errors ranged from 0.06 to 0.10 phenotypic s.d. for additive effects and from 0.09 to 0.14 phenotypic s.d. for dominance effects.

^b Expected difference between breed means based on twice the difference observed in crossbreds in the NPPC genetic evaluation program (Goodwin, 1995).

^c * 5% chromosome-wise
 ** 1% chromosome-wise
 *** 5% genome-wise
 **** 1% genome-wise

Table 4 Continued. Significant QTL by trait.

Chr	Trait	QTL Position	Significance	Type of QTL	QTL variance (%)	Breed QTL effects (SD)			Breed difference B-Y in SD
						BB	BY	YY	
2	10thBFAT	0	****	Both	10.8	0.08	-0.05	-0.08	
6		89	*	HS	3.6				
6		134	***	Both	5.3	-0.30	0.20	0.30	
7		74	*	LC	2.6	0.22	-0.04	-0.22	
7		107	**	LC	3.8	0.26	-0.13	-0.26	
8		58	*	HS	3.1				
12		60	**	HS	4.4				
12		97	*	Both	4.4	0.22	-0.10	-0.22	
15		66	*	LC	2.2	-0.15	-0.21	0.15	
18		1	*	LC	1.8	-0.19	0.03	0.19	
Sum		#QTL: LC/HS/Both		4 / 3 / 3	41.9	0.15	-0.30	-0.15	1.61
2	LumbBFAT	2	****	Both	11.8	0.15	-0.07	-0.15	
5		123	***	Both	6.3	0.38	0.21	-0.38	
7		59	****	LC	6.6	0.36	-0.05	-0.36	
7		104	****	LC	5.5	0.33	-0.05	-0.33	
8		70	*	HS	4.6				
Sum		#QTL: LC/HS/Both		2 / 1 / 2	34.8	1.22	0.03	-1.22	1.58
1	LribBFAT	64	*	HS	3.1				
2		0	****	Both	8.6	0.12	-0.04	-0.12	
5		124	***	LC	4.0	0.27	0.13	-0.27	
7		73	***	Both	6.4	0.36	-0.05	-0.36	
7		107	*	LC	3.4	0.26	-0.03	-0.26	
10		79	***	Both	5.9	0.31	-0.24	-0.31	
13		41	*	LC	2.8	0.14	-0.27	-0.14	
15		30	**	HS	4.9				
Sum		#QTL: LC/HS/Both		3 / 2 / 3	39.2	1.47	-0.51	-1.47	1.24
1	AVBFAT	59	*	HS	3.2				
2		0	****	Both	13.3	0.14	-0.07	-0.14	
5		126	***	Both	5.7	0.36	0.12	-0.36	
7		72	****	Both	7.3	0.41	-0.07	-0.41	
7		105	****	LC	5.5	0.32	-0.09	-0.32	
8		68	*	HS	3.9				
10		79	*	Both	4.6	0.34	-0.20	-0.34	
12		91	*	HS	3.8				
18		7	*	Both	4.0	-0.33	0.04	0.33	
Sum			#QTL: LC/HS/Both		1 / 3 / 5	51.2	1.23	-0.25	

Table 4 Continued. Significant QTL by trait.

Chr	Trait	QTL Position	Significance	Type of QTL	QTL variance (%)	Breed QTL effects (SD)			Breed difference B-Y in SD
						BB	BY	YY	
1	LEA	97	**	LC	2.6	0.22	-0.06	-0.22	
2		1	****	Both	10.0	0.04	0.10	-0.04	
4		113	*	HS	1.7				
8		1	***	HS	4.0				
10		89	*	Both	3.7	-0.17	-0.23	0.17	
Sum		#QTL: LC/HS/Both		1 / 2 / 2	22.1	0.10	-0.19	-0.10	-1.12
3	COLOR	72	*	LC	2.6	-0.19	-0.19	0.19	
11		85	***	HS	6.0				
12		34	*	LC	2.3	-0.21	-0.09	0.21	
17		81	**	Both	5.8	0.20	-0.20	-0.20	
Sum		#QTL: LC/HS/Both		2 / 1 / 1	16.8	-0.19	-0.48	0.19	0.43
1	MARB	52	***	Both	6.6	-0.11	0.26	0.11	
1		127	****	HS	5.1				
7		134	*	LC	2.6	0.21	0.11	-0.21	
9		4	*	HS	4.4				
10		5	*	LC	3.9	-0.25	-0.18	0.25	
Sum		#QTL: LC/HS/Both		2 / 2 / 1	22.6	-0.14	0.19	0.14	0.91
15	FIRMness	67	*	HS	3.9				0.69
Sum		#QTL: LC/HS/Both		0 / 1 / 0	3.9				
3	24HamMIN	32	**	HS	4.4				
12		44	****	HS	6.0				
12		80	****	HS	6.5				
Sum		#QTL: LC/HS/Both		0 / 3 / 0	16.9				N/A
3	24HamHUNT	30	*	HS	4.3				
12		44	***	HS	5.9				
12		80	****	HS	6.2				
14		0	*	LC	3.3	-0.07	-0.34	0.07	
Sum		#QTL: LC/HS/Both		1 / 3 / 0	19.6	-0.07	-0.34	0.07	N/A
2	24LoinMIN	88	*	LC	3.6	0.20	-0.24	-0.20	
5		133	*	LC	2.8	0.13	-0.29	-0.13	
18		35	*	LC	2.6	-0.05	-0.31	0.05	
Sum		#QTL: LC/HS/Both		3 / 0 / 0	9.0	0.28	-0.84	-0.28	-0.20
10	24LoinHUNT	17	*	HS	4.7				
15		54	*	LC	2.6	-0.23	0.01	0.23	
15		102	**	LC	4.0	-0.25	0.18	0.25	
Sum		#QTL: LC/HS/Both		2 / 1 / 0	11.3	-0.48	0.19	0.48	-0.17

Table 4 Continued. Significant QTL by trait.

Chr	Trait	QTL Position	Significance	Type of QTL	QTL variance (%)	Breed QTL effects (SD)			Breed difference
						BB	BY	YY	B-Y in SD
5	48LoinMIN	133	*	LC	2.7	0.16	-0.25	-0.16	
7		84	*	LC	2.5	0.17	-0.21	-0.17	
11		85	*	HS	4.0				
15		72	****	Both	8.2	-0.41	0.11	0.41	
17		86	***	Both	6.8	-0.24	0.20	0.24	
Sum		#QTL: LC/HS/Both		2 / 1 / 2	24.2	-0.34	-0.15	0.34	0.00
4	48LoinHUNT	147	*	LC	2.3	0.15	0.21	-0.15	
5		133	*	LC	2.4	0.14	-0.24	-0.14	
7		49	*	HS	4.2				
7		84	*	LC	2.6	0.16	-0.23	-0.16	
11		81	*	HS	4.1				
12		0	*	HS	4.1				
15		73	****	Both	7.8	-0.40	0.12	0.40	
17		86	***	Both	6.4	-0.22	0.18	0.22	
Sum		#QTL: LC/HS/Both		3 / 3 / 2	34.0	-0.16	0.04	0.16	0.19
1	24HampH	104	*	HS	4.4				
6		50	***	LC	4.2	-0.14	0.36	0.14	
8		73	*	HS	7.3				
11		0	**	HS	5.0				
15		81	****	LC	4.2	0.28	-0.09	-0.28	
Sum		#QTL: LC/HS/Both		2 / 3 / 0	25.0	0.14	0.27	-0.14	N/A
6	24LoinpH	58	*	Both	5.5	0.13	0.23	-0.13	
15		84	****	LC	5.9	0.34	-0.03	-0.34	
Sum		#QTL: LC/HS/Both		1 / 0 / 1	11.4	0.47	0.20	-0.47	N/A
5	48LoinpH	91	*	LC	3.6	-0.27	0.01	0.27	
11		0	**	HS	4.9				
15		44	***	LC	5.0	0.28	-0.21	-0.28	
15		73	***	LC	3.7	0.27	-0.08	-0.27	
Sum		#QTL: LC/HS/Both		3 / 1 / 0	17.2	0.27	-0.28	-0.27	0.88
2	DRIPloss	47	***	Both	7.3	0.08	0.07	-0.08	
11		0	*	LC	1.8	0.15	-0.16	-0.15	
11		69	***	HS	6.7				
15		52	***	LC	3.5	-0.23	0.19	0.23	
Sum		#QTL: LC/HS/Both		2 / 1 / 1	19.3	0.01	0.09	-0.01	-0.48

Table 4 Continued. Significant QTL by trait.

2	WHC	154	*	LC	2.8	0.22	-0.12	-0.22	
11		0	*	HS	4.0				
11		71	*	HS	4.0				
13		55	*	LC	2.5	0.22	0.05	-0.22	
Sum		#QTL: LC/HS/Both 2 / 2 / 0			13.2	0.44	-0.07	-0.44	-0.12
1	FIBER-I	89	*	HS	5.2				
2		98	**	HS	6.4				
14		111	**	HS	5.8				
Sum		#QTL: LC/HS/Both 0 / 3 / 0			17.3				N/A
11	GLYCogen	6	**	HS	4.1				
13		72	*	Both	3.4	0.20	-0.20	-0.20	
15		4	*	LC	2.7	-0.19	0.18	0.19	
15		95	*	Both	5.0	-0.19	0.11	0.19	
16		51	*	LC	2.3	-0.21	0.03	0.21	
18		29	*	HS	4.0				
Sum		#QTL: LC/HS/Both 2 / 2 / 2			21.4	-0.40	0.12	0.40	N/A
8	LACTate	0	*	HS	3.9				
17		89	*	LC	2.8	-0.12	0.29	0.12	
Sum		#QTL: LC/HS/Both 1 / 1 / 0			6.8	-0.12	0.29	0.12	N/A
11	GLYCpot	2	**	HS	3.9				
13		72	*	Both	3.3	0.07	-0.24	-0.07	
15		76	*	LC	2.8	-0.24	0.01	0.24	
17		86	*	LC	2.6	-0.09	0.30	0.09	
Sum		#QTL: LC/HS/Both 2 / 1 / 1			12.7	-0.26	0.07	0.26	N/A
1	LIPID%	29	*	LC	2.3	-0.21	0.09	0.21	
6		137	**	Both	5.4	-0.33	0.34	0.33	
10		11	*	Both	4.3	-0.22	0.09	0.22	
12		43	*	HS	3.7				
Sum		#QTL: LC/HS/Both 1 / 1 / 2			15.8	-0.76	0.52	0.76	0.13
3	INSTRON	36	*	Both	5.1	0.12	0.33	-0.12	
10		0	**	HS	5.1				
10		70	***	LC	4.4	-0.29	-0.11	0.29	
14		35	*	LC	2.5	-0.15	0.23	0.15	
15		49	**	LC	4.5	-0.28	0.15	0.28	
15		73	*	LC	2.9	-0.24	0.06	0.24	
Sum		#QTL: LC/HS/Both 4 / 1 / 1			24.6	-0.84	0.67	0.84	-1.04
14	CookLOSS	37	*	LC	2.8	-0.24	-0.01	0.24	
Sum		#QTL: LC/HS/Both 1 / 0 / 0			2.8	-0.24	-0.01	0.24	N/A

Table 4 Continued. Significant QTL by trait.

Chr	QTL Trait	Position	Significance	Type of QTL	QTL variance (%)	Breed QTL effects (SD)			Breed difference B-Y in SD
						BB	BY	YY	
2	TENDERness	157	**	LC	3.0	-0.23	-0.13	0.23	
14		74	*	LC	2.7	0.18	0.20	-0.18	
15		74	*	Both	5.7	0.46	-0.02	-0.46	
Sum		#QTL: LC/HS/Both		2 / 0 / 1	11.4	0.42	0.05	-0.42	0.42
2	JUICiness	82	*	HS	3.0				0.00
Sum			#QTL: LC/HS/Both		0 / 1 / 0	3.0			
2	FLAVOR	157	*	LC	2.8	-0.23	-0.01	0.23	
3		9	*	HS	4.6				
3		123	*	Both	5.2	0.18	0.14	-0.18	
11		77	*	HS	4.2				
15		100	*	LC	3.6	0.22	-0.22	-0.22	
Sum			#QTL: LC/HS/Both		2 / 2 / 1	20.4	0.16	-0.09	
2	OFFFLAVOR	50	*	Both	6.4	0.24	0.08	-0.24	
2		156	*	LC	2.3	0.19	0.14	-0.19	
3		53	*	Both	5.0	0.32	0.11	-0.32	
7		62	*	HS	4.8				
9		79	*	LC	3.2	-0.18	-0.25	0.18	
15		53	*	LC	3.2	-0.23	0.14	0.23	
17		82	*	LC	2.5	-0.15	0.24	0.15	
Sum			#QTL: LC/HS/Both		4 / 1 / 2	27.4	0.19	0.46	

In total, 160 QTL were detected for the 39 traits evaluated. In many cases the same chromosomal region was significant for several correlated traits. These may represent QTL with pleiotropic effects on those traits. Of the 160 QTL, 65 were classified as LC QTL, representing QTL that were not segregating within the F₀ parents but did have a different frequency when comparing the Berkshire grandsires to the Yorkshire granddams. A total of 55 QTL were classified as HS, reflecting QTL that did not differ in frequency between the Berkshire and Yorkshire grandparents but were segregating within the breeds. The remaining 40 QTL could not be classified as either LC or HS.

A detailed discussion of many of the QTL classified as LC in the present analysis is in Malek et al. (2001a,b). Here, we will limit our discussion to several general observations.

Individual QTL explained from 1.9 to 13.3% of the phenotypic variance in the F₂. When summing across QTL identified for a given trait, the identified QTL explained up to 51% of the F₂ variance for average backfat. It should be noted that these variance estimates may be biased upward because of the estimation procedure and double-counting when multiple QTL are identified on the same chromosome for the same trait.

For QTL classified as LC or BOTH, estimates of the average effect of Berkshire versus Yorkshire alleles could be obtained and these are presented in Tables 3 and 4. It is of interest to compare these to what we would expect based on overall breed differences, which are also presented in Table 4. Results show that estimates of QTL effects often were in the same direction as the breed difference. For example, for backfat traits, the Berkshire alleles (BB genotype) tended to increase backfat, consistent with the breed difference. However, for other QTL, breed QTL effects were in an opposite direction of the breed difference. For example, for marbling (Table 4), Berkshires are expected to have higher scores, yet for two of the three QTL with significant breed differences, the Berkshire allele resulted in lower marbling score. These discrepancies could result from the Berkshire and Yorkshire F₀ parents used in the cross not being representative of their breeds. Alternatively, these could represent real breed differences for these QTL, with so-called cryptic alleles, and reflect the substantial genetic variation that is still present within each of the breeds.

Many QTL classified as LC or BOTH also showed substantial amounts of dominance. For example, for the marbling QTL at position 52 on chromosome 1 (Table 1), the heterozygote had a substantially greater marbling score than either homozygote. These could represent real effects that explain presence of heterosis for the trait. It must also be realized, however, that all results presented are estimates and have substantial standard errors.

When evaluating the results presented in Tables 3 and 4, it must be realized that the genome scan approach employed here has some limitations with regard to its ability to provide accurate estimates of both QTL position and effects. Nevertheless, the results presented here will enable further evaluation of the identified QTL regions to attempt to identify the individual genes responsible for the traits through candidate gene or fine-mapping approaches, as will be discussed in a subsequent paper in these proceedings (Rothschild et al., 2003). In addition, the QTL regions will enable their initial use in strategies for marker-assisted selection, as will be discussed in a later paper.

Acknowledgments

This work was made possible through financial support from an industry consortium consisting of the National Pork Board, the Iowa Pork Producers Association, the Iowa Purebred Swine Council, Babcock Genetics, Danbred USA, Monsanto Choice Genetics, PIC/Sygen, Seghers Genetics USA, and Shamrock Breeders, and by a grant from USDA/CSREES IFAFS, grant # 00-52100-9610. Additional financial support was provided from the Iowa Agriculture and Home Economics Experimental Station, Ames, project no. 3600. Several additional ISU faculty, staff, and students contributed to the success of this project, including Drs. Tom Baas, Lauren Christian, Steve Lonergan, Elisabeth Huff-Lonergan, Rohan Fernando, Ken Prusa, Zhiliang Hu, Daniel Ciobanu, Yang Zhang, and Peiqi Chen, and Ms. Jeanine Helm, Ms. Chris Fedler, Mr. Marlan Braet, and Mr. John Newton and personnel at the ISU Bilsland swine breeding farm.

References

- Andersson L., C. S. Haley, H. Ellegren, S. A. Knott, M. Johansson, K. Andersson, L. Andersson-Eklund, I. Edfors-Lilja, M. Fredholm, I. Hansson, J. Hakansson, and K. Lundstrom. 1994. Genetic mapping of quantitative trait loci for growth and fatness in pigs. *Science* 263: 1771-1774.
- Andersson-Eklund, L., L. Marklund, K. Lundstrom, C.S. Haley, K. Andersson, I. Hansson, M. Moller, and L. Andersson. 1998. Mapping quantitative trait loci for carcass and meat traits in a Wild boar x Large White intercross. *J. Anim. Sci.* 76: 694-700.
- Archibald, A., J. Brown, S. Couperwhite, H. McQueen, D. Nicholson, C. Haley, W. Coupieters, A. van de Weghe, A. Stratil, A. Wintero, M. Fredholm, N. Larson, V. Nielsen, D. Milan, N. Woloszyn, A. Robic, M. Dalens, J. Riquet, J. gellin, J.-C. Caritez, D. Hue, G. Burgaud, L. Ollivier, J.-P. Bidanel, M. Vaiman, C. Renard, H. Geldermann, R. Davoli, D. Ruyter, E. Verstege, M. Groenen, W. Davies, B. Hoyheim, A. Keiserud, L. Andersson, H. Ellegren, M. Johansson, L. Marklund, R. Miller, D. Dear, E. Signer, A. Jeffreys, C. Moran, P. Le Tissier, Muladno., M.Rothschild, C. Tuggle, D. Vaske, J. Healm, H.-C. Liu, A. Rahman, T.-P. Yu, R. G. Larson, and C. Schmitz. 1994. The PiGMaP consortium linkage map of the pig (*Sus scrofa*). *Mammalian Genome* 6: 157-175.
- Bidanel, J. P., and M.F. Rothschild. 2002. Current Status of Quantitative Trait Locus Mapping in Pigs. *Pig News and Information* 23 (2): 39N-53N.
- Churchill G.A., and R.W. Doerge. 1994. Empirical threshold values for quantitative trait mapping. *Genetics* 138: 963-971.
- De Koning, D. J., B. Harlizius, A. P. Rattink, M. A. M. Groenen, E. W. Brascamp, and J. A. M. van Arendonk. 2001a. Detection and characterization of quantitative trait loci for meat quality traits in pigs. *J. Anim. Sci.* 79: 2812-2819.
- Green, P., K. Falls, and S. Crooks. 1990. Documentation for CRIMAP, version 2.4. Washington Univ. School of Medicine, St. Louis, MO.
- Goodwin R, and S. Burroughs. 1995. Genetic evaluation terminal line program results. National Pork Producer Council, Des Moines, Iowa.
- Huff-Lonergan, E., T. J. Baas, M. Malek, J. C. M. Dekkers, K. Prusa, and M. F. Rothschild. 2001. Correlations among selected pork quality traits. *J. Anim. Sci.* 80: 617-627.
- Haley, C.S., S.A. Knott, and J.M. Elsen. 1994. Mapping quantitative trait loci in crosses between outbred lines using least squares. *Genetics* 136: 1195-1207.
- Knott, S.A., J.M. Elsen, and C.S. Haley. 1996. Methods for multiple-marker mapping of

quantitative trait loci in half-sib populations. *Theor. Appl. Genet.* 93: 71-80.

Malek, M., J.C.M. Dekkers, H.K. Lee, T.J. Baas, and M.F. Rothschild. 2001a. A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. I. Growth and body composition. *Mamm. Genome.* 12: 630–636.

Malek, M., J.C.M. Dekkers, H.K. Lee, T.J. Baas, K. Prusa, E. Huff-Lonergan, and M.F. Rothschild. 2001b. A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. II. Meat and muscle composition. *Mamm. Genome* 12: 637–645.

Maribo H., S. Stoier, and P.F. Jorgensen. 1999. Research Note: Procedure for determination of glycolytic potential in porcine m. longissimus dorsi. *Meat Sci* 52: 191-193.

Marklund L., P. Nystrom, S. Stren, L. Andersson, and E. Andersson .1999. Confirmed quantitative trait loci for fatness and growth on pig chromosome 4. *Heredity* 82: 134-141.

Monin G. and Sellier. 1985. Pork of low technological quality with a normal rate of muscle pH fall in the immediate post-mortem period: The case of the Hampshire breed. *Meat Sci* 13, 49: 63.

Moser, G., G. Reiner, E. Mueller, P. Beeckmann, G. Yue, M. Dragos, H. Bartenschlager, S. Cepica, A. Stratil, and H. Geldermann. 1999. Status of genome and QTL mapping in the Hohenheim F2 pig-families. *Proc. European. Animal Production.*

NPPC. 1991. Procedures to Evaluate Market Hogs. National Pork Producers Council, Des Moines Iowa.

Pasek, A., P. Wilkie, G. Flickeenger, G. Rohrer, L. Alexander, C. Beattie, and L. Schook. 1999. Interval mapping of growth in divergent swine cross. *Mammal. Genome.* 10: 117-122.

Perez-Enciso M., A. Clop, J.L. Noguera, C. Ovilo, Folch J.M., et al. 2000. A QTL on pig chromosome 4 affects fatty acid metabolism: Evidence from an Iberian by Landrace intercross. *J Anim Sci* 78: 2525-2531.

Rohrer, G.A., L.J. Alexander , Z. Hu, T.P.L. Smith, J.W. Keele, and C.W. Beattie. 1996. A comprehensive map of the porcine genome. *Genome Res.* 6: 371-391.

Rohrer, G.A., and J. Keele. 1998. Identification of quantitative trait loci affecting carcass composition in swine I. Fat deposition traits. *J. Anim. Sci.* 76: 2247-2254.

Rothschild. M. F. 1994. Genome mapping in livestock: A journey, not a destination. *Proceedings of the Future Genetics for the Animal Industry, St. Louis, MO, May 4.* ISU publication.

Rothschild M.F., D. Ciobanu, S. Lonergan, and K. Stalder. 2003. Identification of Genes for Carcass Merit and Meat Quality in the Pig. NSIF Proceedings (in press).

Rothschild, M. F., C. Jacobson, D.A. Vaske, C. Tuggle, L. Wang, T. Short, G. Eckardt, S. Sasaki, A. Vincent, D.G. McLaren, O. Southwood, H. van der Steen, A. Mileham, and G. Plastow. 1996. The Estrogen Receptor locus is associated with a major gene influencing litter size in pigs. *Proc. Nat. Acad. Sci. (USA)* 93: 201-205.

Rothschild, M.F., H.-C. Liu, C.K. Tuggle, T.-P. Yu, and L. Wang. 1995. Analysis of chromosome 7 genetic markers for growth and carcass performance traits. *J. Anim. Breed. Genet.* 341-348.

Wang, L., T.P. Yu, C.K. Tuggle, H.C. Liu, and M.F. Rothschild. 1998. A directed search for quantitative trait loci on chromosomes 4 and 7 in the pig. *J. Anim. Sci.* 76: 2560-2567.