Identification of quantitative trait loci affecting birth characters and accumulation of backfat and weight in a Meishan-White Composite resource population[1]

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ABSTRACT: A search for genomic regions affecting birth characters and accretion of weight and backfat was conducted in a Meishan-White Composite reciprocal backcross resource population. Birth traits analyzed (n = 750) were vigor score, number of nipples, and birth weight. Subsequent measures on gilts and barrows (n = 706) analyzed were weaning weight, 8-wk weight, ADG from 8 to 18 wk of age, ADG from 18 to 26 wk of age, 26-wk weight, and backfat over the first rib, last rib, and last lumbar vertebrae at 14 and 26 (n = 599) wk of age. Feed intake and growth of 92 individually penned barrows were also analyzed. A genomic scan was conducted with microsatellite markers spaced at approximately 20-cM intervals, a least squares regression interval analysis was implemented, and significance values were converted to genomewide levels. No associations were detected for traits measured at birth except for number of nipples, where one significant and two suggestive regions were identified on chromosomes (SSC) 10, 1, and 3, respectively. Early growth was affected by a region on SSC 1 as evidenced by associations with weights collected at weaning and 8 wk of age and ADG from 8 to 18 wk of age. Other regions detected for early growth rate were on SSC 2, 12, and X. Chromosomal regions on SSC 6 and 7 affected ADG from 18 to 26 wk of age. All measures of backfat were affected by regions on SSC 1 and X, whereas SSC 7 consistently affected backfat measures recorded at 26 wk of age. Suggestive evidence for QTL affecting backfat at 14 wk of age was also detected on SSC 2, 6, 8, and 9. These results have improved our knowledge about the genetics of growth rate and fat accretion at the molecular level in swine.

Key Words: Birth, Genome Analysis, Growth, Pigs, Quantitative Trait Loci

 J. Anim. Sci. 2000. 78:2547–2553

Introduction

Gene-mapping technologies have provided scientists the necessary reagents to conduct genomewide searches for genes affecting any phenotype determined in part by the genetic makeup of the animal. Since the publication of genetic maps that comprised primarily microsatellite markers for swine (Archibald et al., 1995; Marklund et al., 1996; Rohrer et al., 1996), several reports have been published on genomic scans for quantitative trait loci (QTL) in swine.

To date, only three publications have reported QTL affecting growth rate in swine using a genomewide scan (Andersson et al., 1994; Casas-Carrillo et al., 1997; Paszek et al., 1999). Andersson et al. (1994) utilized an F_2 population of Large White-European wild boar, Paszek et al. (1999) studied a Meishan-Yorkshire F_2 population, and Casas-Carrillo et al. (1997) used families generated from two F_1 boars produced by crossing lines divergently selected for growth rate (Clutter et al., 1995). There are few similarities between results of these studies. However, one region near the end of chromosome 1q was identified by both Casas-Carrillo et al. (1997) and Paszek et al. (1999) as affecting growth.

No studies have been reported that attempt to identify genes affecting backfat accretion at different stages of the life cycle in pigs. The objective of this research was to detect QTL affecting birth characters, growth rate, backfat accumulation, and feed efficiency in a Meishan-White Composite reciprocally backcrossed resource population.

Material and Methods

A Meishan-White Composite backcross resource population was designed to identify genes affecting

[1]The author would like to acknowledge the swine operations employees for collection of phenotypic data and care of animals, Kris Simmerman for collection of genotype data, and Sherry Kluver for preparation of the manuscript.

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Received December 13, 1999.

Accepted May 29, 2000.

production traits at the USDA, ARS, U.S. Meat Animal Research Center. Matings were designed as described in Rohrer and Keele (1998a). Previous studies (Rohrer and Keele, 1998a,b) used 540 backcross progeny that were slaughtered at approximately 100 kg of live weight. The current study is based on 750 backcross progeny for birth characters and on 706 barrows and gilts, for most traits measured after birth traits were recorded.

The F_1 females were mated to farrow in the spring and fall of 1993. Parity of dam and contemporary groups were completely confounded. Within 24 h after birth, the following measurements were recorded for each piglet: weight, number of nipples, and a subjective vigor score. At the same time, from one-fourth of the litters, two boars were randomly chosen to be retained for breeding (one primary boar and one alternate), and the other males were castrated. Piglets were weaned, weighed, and transported to the nursery at 4 wk of age. Pigs were weighed and transferred to finishing pens at 8 wk of age, at which time half of the females in each litter were randomly selected to be retained to measure ovulation rate and uterine capacity. The selected females were unilaterally ovariohysterectomized at approximately 10 wk of age. Beginning at approximately 14 and 13 wk of age (for spring- and fall-born pigs, respectively), each pig was weighed and had backfat depth estimated by ultrasonography at 4-wk intervals. Backfat estimates were recorded approximately 4 cm off the midline near the first rib, last rib, and last lumbar vertebrae using an A-mode Renco Lean-Meter (Renco Corp., Minneapolis, MN). Animals selected to be slaughtered were transported to the abattoir when they reached approximately 100 kg, and a final weight was recorded. The remaining animals continued to be measured at 4-wk intervals until they were approximately 8 mo of age.

In a preliminary analysis, phenotypic correlations between birth weight, weaning weight, and 8-wk weight were low (< .60). Correlations between these weights and subsequent weights were also low. However, phenotypic correlations between weights recorded after 8 wk of age were considerably higher, and correlations between successive weights were greater than .90. Likewise, phenotypic correlations between successive measures of backfat depth were greater than .80. It was assumed that these high phenotypic correlations were at least partially due to strong genetic correlations resulting from individual genes affecting successive measurements.

To avoid analyzing numerous traits that have high genetic correlations among them, only measurements from developmentally significant ages were analyzed. Birth traits analyzed were vigor score, number of nipples, and birth weight. Subsequent measures on gilts and barrows analyzed were weaning weight, 8-wk weight, ADG from 8 to 18 wk of age, ADG from wk 18 to 26 wk of age, 26-wk weight, and backfat measures at 14 and 26 wk of age over the first rib, last rib, and last lumbar vertebrae. Ultrasonic backfat measurements at 26 wk were not obtained for pigs slaughtered before or at the time of collection of 26-wk measurements, resulting in only 599 observations for these traits. The 26-wk measures were the last ones analyzed because most of the animals scheduled to be slaughtered had already been removed by 30 wk of age and the only slaughter animals remaining were the slowest growing pigs. For animals slaughtered after 22 wk but before their 26-wk measurement, an adjusted 26-wk weight was calculated based on their final weight, age at slaughter, and weight recorded at 22 wk of age. Weights at 0, 4, and 8 wk were included because they are affected by different environmental factors (primarily maternal effects of number of fetuses gestated, number of pigs nursed, and milk production).

Barrows from selected litters born in fall 1993 (n = 92) were individually penned after removal from the nursery building and individual feed intakes were recorded. These animals were fed the same ration and had identical measurements recorded as their contemporaries. Three traits were analyzed for QTL: average daily feed intake, ratio of live weight gain to feed consumed, and ADG on test.

Microsatellite markers used were selected from the map produced by Rohrer et al. (1996) and were previously described (Rohrer and Keele, 1998a). Briefly, 157 microsatellite markers were genotyped across all purebred, F_1, and backcross animals. Markers were selected based on ease of scoring, informativeness, and location in the genome. Intervals between adjacent markers were less than 20 cM whenever possible, and the average marker interval was approximately 17 cM (sex-averaged map distance).

The statistical analyses conducted were as outlined in Rohrer and Keele (1998a). Briefly, a least-squares regression coefficient was fitted for the probability of an animal possessing each possible genotype (Haley et al., 1994). Initially, genotypic tests of significance utilized a 2-df test for additive and dominance genetic effects. When the removal of the dominance term improved the overall genomewide significance of the test, the dominance effect was dropped from the model. Fixed effects fitted for all analyses were breed of sire (breed composition), sex, and contemporary group. Sex and contemporary group were excluded in analyses for individual feed consumption traits. Number of fully formed fetuses was included as a covariate for birth weight and vigor score, whereas number weaned was included as a covariate for weaning weight and 8-wk weight. Including a covariate believed to be genetically correlated with the dependent variable was avoided as it would reduce the power of the genomic scan. The expected number of false-positives was determined based on the methods of Lander and Kruglyak (1995). Parameters used for this study were a rho-value of 1.0, 19 chromosomes, and a genome length of 25 morgans. Results reported meet the criteria of Lander and Krug-

Table 1. Genomewide significant and suggestive associations of chromosomal regions with birth, growth, and backfat accretion measurements

Trait[a]	Location[b]	Degrees of freedom[c]	*F*-ratio	P-genome[d]	Genetic effects[e]	
					a	d
NN	1:123	1; 745	12.4596	2.8×10^{-1}	–.34	—
	3:84	1; 745	15.7855	6.3×10^{-2}	.36	—
	10:80	1; 745	20.5521	7.1×10^{-3}	.45	—
WT4	1:128	1; 700	14.5595	1.1×10^{-1}	.33	—
WT8	1:129	1; 700	34.3404	1.2×10^{-5}	1.37	—
	2:72	1; 700	10.6331	6.4×10^{-1}	.69	—
	X:74	1; 700	11.8645	3.7×10^{-1}	.68	—
EDG	1:134	1; 700	41.5713	4.4×10^{-7}	.051	—
	12:–10	1; 700	10.5870	6.5×10^{-1}	–.029	—
LDG	6:53	2; 697	7.2803	5.5×10^{-1}	–.036	.005
	7:60	1; 698	26.2100	5.3×10^{-4}	.045	—
WT26	1:129	1; 698	25.2736	8.1×10^{-4}	5.18	—
	7:61	1; 698	14.9549	9.2×10^{-2}	3.59	—
14FR	1:136	1; 700	94.8532	2.0×10^{-17}	2.36	—
	X:79	1; 700	71.7844	5.1×10^{-13}	1.94	—
14LR	1:137	2; 699	39.7761	1.7×10^{-13}	1.54	.12
	2:74	1; 700	12.8638	2.4×10^{-1}	.67	—
	7:121	1: 700	9.6702	9.8×10^{-1}	–.68	—
	9:50	1; 700	9.9527	8.7×10^{-1}	.60	—
	X:76	1; 700	59.3500	1.4×10^{-10}	1.35	—
14LL	1:138	2; 699	41.8487	2.9×10^{-14}	1.59	.12
	6:83	2; 699	7.3750	5.1×10^{-1}	.50	.10
	7:57	1; 700	10.3679	7.2×10^{-1}	–.61	—
	8:93	1; 700	9.8392	9.1×10^{-1}	.58	—
	9:44	1; 700	10.9756	5.5×10^{-1}	.70	—
	X:76	1; 700	54.3367	1.3×10^{-9}	1.34	—
26FR	1:133	1; 593	68.2197	3.3×10^{-12}	4.00	—
	7:36	2; 592	12.6677	5.3×10^{-3}	–1.82	–.31
	X:81	1; 593	39.7850	1.1×10^{-6}	2.90	—
26LR	1:136	1; 593	58.7611	2.2×10^{-10}	3.29	—
	7:58	1; 593	20.4728	7.6×10^{-3}	–1.82	—
	X:67	1; 593	37.4407	3.2×10^{-6}	2.48	—
26LL	1:135	1; 593	48.3490	2.3×10^{-8}	3.08	—
	7:58	1; 593	17.4737	3.0×10^{-2}	–1.69	—
	X:75	1; 593	43.3601	2.2×10^{-7}	2.54	—

[a]Traits measured included number of nipples (NN); 4-, 8-, and 26-wk weights (kg) (WT4, WT8, and WT26, respectively); ADG (g/d) from 8 to 18 and 18 to 26 wk of age (EDG and LDG, respectively); and backfat (mm) recorded at 14 and 26 wk of age at the first rib, last rib, and last lumbar vertebra (14 FR, 26FR, 14LR, 26LR, 14LL, and 26LL, respectively).

[b]The position where the test statistic was maximized (expressed as chromosome; position). The position within a linkage group is relative to Rohrer et al. (1996).

[c]Numerator degrees of freedom; denominator (residual) degrees of freedom.

[d]Expected number of false-positives per genome scan as described by Lander and Kruglyak (1995), where G = 25, C = 19, and $\rho = 1.0$. Results with values less than 5.0×10^{-2} should be considered significant, whereas all other associations are only suggestive evidence for QTL (Lander and Kruglyak, 1995).

[e]Genetic effects for additive effect of an allele substitution (a) and dominance deviations (d) as described by Falconer (1985). The additive effect is expressed as half the difference between the homozygous Meishan genotype minus the homozygous White Composite genotype. A dash in the column denoted d indicates that this term was removed from the final statistical model.

lyak (1995) for suggestive and significant QTL (expected number of false-positives per genome scan of 1.0 and .05, respectively).

Results and Discussion

All associations, their level of significance, and estimates of their genotypic effects for regions exceeding suggestive evidence of linkage to a QTL are presented in Table 1. Genomic regions are presented as the chromosome (e.g., SSC 1), a colon to separate the values, and the centimorgan position on the map reported by Rohrer et al. (1996). Thus, the genomic region located on chromosome 1 at position 100 to 105 cM would be represented as SSC 1:100–105.

Birth and Weaning Traits. No genomic regions were identified that met our significance criteria for birth weight or vigor score. Two suggestive and one significant region were detected for number of nipples located on porcine chromosomes 1, 3, and 10, respectively. The mode of gene action at all three of these regions was additive. Meishan alleles for the QTL on SSC 3 and

10 increased number of nipples, whereas Meishan alleles for the QTL on SSC 1 reduced number of nipples. The only region identified to affect weaning weight was on SSC 1, with the maximum peak occurring at position 128 (SSC 1:128).

The only other study to search for QTL affecting number of nipples was Wada et al. (1998), in which the researchers identified a region of SSC 3 that affects this trait. Unfortunately, the authors did not report the location of the maximum test statistic, so it cannot be determined whether this region is similar to the suggestive peak detected in this study at SSC 3:84. The significant QTL for number of nipples detected in this study at 10:80 was the same region as an ovulation rate peak detected by Rohrer et al. (1999). This initially would appear to be a useful association; however, the estimates of the genetic effects indicate that the Meishan alleles increase number of nipples but decrease the number of ova ovulated. This type of association would not appear to provide improved reproductive fitness but rather would maintain homeostasis.

Growth and Weight Traits. Only SSC 1:128–134 significantly affected growth prior to 18 wk of age. Two regions (SSC 2:72 and X:74) reached the suggestive level of significance for 8-wk weight. For all three of the described regions, Meishan alleles increased body weight. Average daily gain from 18 to 26 wk of age was significantly affected by SSC 7:60, and suggestive evidence was observed for a QTL on SSC 6:53, with superior growth alleles originating from the Meishan breed for SSC 7:60 and from the White composite for SSC 6:53. The impact of SSC 1:128–134 on 8-wk weight and ADG from 8 to 18 wk of age plus the impact of SSC 7:60 on ADG from 18 to 26 wk of age yielded significant and suggestive effects for 26-wk weight at SSC 1:129 and 7:61, respectively.

The telomeric region on SSC 1q has previously been identified as affecting growth rate by Paszek et al. (1999) and Casas-Carrillo et al. (1997). Although the population of Paszek et al. (1999) comprised swine with breed composition similar to those in the present study, the population of Casas-Carrillo et al. (1997) was different. The present study confirms the findings of Paszek et al. (1999) and Casas-Carrillo et al. (1997). This genomic area has also been identified to contain a gene influencing age at puberty in gilts (Rohrer et al., 1999). Although it cannot be determined whether this association is due to linked QTL or to pleiotropy, body weight and, to some extent, backfat thickness have been known to be associated with age at first estrus in gilts (Young et al., 1978). Further research on this chromosomal region may determine the true nature of this phenotypic correlation.

The results reported for growth traits in the current study identified regions similar to those detected for carcass composition traits by Rohrer and Keele (1998a,b). This implies that the genes that affect growth rate also have major effects on body composition. The causal genes for SSC 1, 7, and X may actually have an influence on energy partitioning rather than on feed conversion.

It is surprising that no evidence of a QTL on SSC 4 for growth traits was detected. This chromosome was first identified and confirmed in a wild boar × Large White population (Andersson et al., 1994; Marklund et al., 1999) and was later confirmed to affect growth in various populations containing Meishan germplasm (Wang et al., 1998; Paszek et al., 1999; Moser et al., 1998). The absence of this association may indicate that for this locus the White Composite founders did not differ from the Meishans, or the study was not large enough to detect the QTL (type II error).

Both SSC 1 and 7 affected 26-wk weight; however, it would appear that the age at which these regions affect growth is quite different. Whereas SSC 1:128–134 had its greatest impact on growth between 8 and 18 wk of age, SSC 7:60 apparently did not affect growth rate until after 18 wk of age. There was no evidence of SSC 1 affecting growth rate after 18 wk of age, but, due to its effect on prior growth rate, SSC 1 was still a significant factor for 26-wk weight. The age at which SSC 7 affected growth rate could reflect changes in gene expression due to sexual maturation or processes associated with puberty.

Backfat Accumulation Traits. At 14 wk of age, SSC 1:136–138 and X:76–79 significantly affected all three measures of backfat depth. Suggestive evidence for linkage to QTL was identified at SSC 2:74, 7:121, and 9:50 for 14-wk last-rib fat depth and at positions 6:83, 7:57, 8:93, and 9:44 for 14-wk last-lumbar fat depth. At 26 wk of age, SSC 1:133–136, 7:55–58, and X:67–81 significantly affected backfat at all three anatomical positions measured. The only other chromosomal region exceeding the set criteria was SSC 7:34–39. Meishan alleles at all genomic locations except those on SSC 7 increased backfat depth.

The results for backfat depth at 26 wk of age were similar to those of Rohrer and Keele (1998a). This was expected because most of the animals from the previous study (450 out of 540 animals from Rohrer and Keele, 1998a) were included in the current study. The current study included backfat measures for 148 gilts retained for breeding that were not included in the previous study. In general, the associations were much more significant in the current study than in the previous study. The increase in significance could be due to the additional phenotypic records, difference in phenotypes measured, or the elimination of the dominance effect (excluding the analysis of 26-wk first-rib fat depth at SSC 7). Because the hogs slaughtered were skinned, there is a greater potential for measurement error in backfat depth from carcass measurements.

Chromosome 7 has previously been identified as containing a QTL affecting body composition in studies using Meishan germplasm (Moser et al., 1998; Rohrer and Keele, 1998a; Wang et al., 1998). Results have been somewhat consistent with Meishan alleles associated with leaner carcasses. A striking similarity

among most of these studies is the presence of a "double peak" in the profile of the test statistic for backfat traits (Moser et al., 1998; Rohrer and Keele, 1998a; Wang et al., 1998). The first peak tends to maximize about 20 cM before the major histocompatibility complex (**MHC**; position, 58 cM), whereas the second, and usually greater peak, is maximized at or near the MHC (Moser et al., 1998; Rohrer and Keele, 1998a; Wang et al., 1998). This same phenomenon was observed for growth traits by Milan et al. (1998). The presence of this same phenomenon in four discrete populations provides supporting evidence that SSC 7 actually contains two loci that affect backfat accretion in swine. However, the power of any of these data sets alone is probably not sufficient to statistically confirm this hypothesis. Contrary to the backfat F-ratio profiles (Figure 1) and the results from Milan et al. (1998), the current study identified a single peak on SSC 7 for growth traits that is maximized 5 cM after the MHC.

Individual Feeding Traits. No associations were detected that exceeded the criteria of Lander and Kruglyak (1995) for suggestive linkage. However, the lack of significant results for these traits was expected due to the limited number of animals with phenotypic measurements. Four associations were detected that were nominally significant at $P < .01$ (Table 2). For daily feed intake, two regions were identified at SSC 1:119 and 5:71. Both regions displayed additive inheritance, but Meishan alleles at 1:119 tended to increase daily feed intake, whereas Meishan alleles at 5:71 decreased daily feed intake by a similar amount (approximately .25 kg/d). Chromosome 1 also had an effect on feed efficiency, with a maximum peak located at the other end of the chromosome (1:30) as the region affecting growth and backfat. Finally, ADG on test was associated with SSC 8:58, with the Meishan allele increasing ADG by 15 g/d.

This is the only study reported to look for QTL affecting feed conversion. Despite the fact that none of these findings reached suggestive levels of significance for the traits measured on pigs that were individually fed, interesting observations can be made. The putative QTL detected on SSC 8 for ADG on test is in the same vicinity as cholecystokinin type A receptor (Clutter et al., 1998). Cholecystokinin and its receptors have been shown to be involved in the control of appetite (Anika et al., 1981) and would be a logical positional candidate gene. However, this location did not affect early or late ADG in group-penned pigs or feed intake in individually penned pigs. Either this association is a false-positive or ADG in individually penned swine is controlled by different genes than ADG in group-penned swine.

The region on SSC 1 that has been identified in this study and others (Paszek et al., 1999; Casas-Carello et al., 1997) to affect growth rate may affect appetite

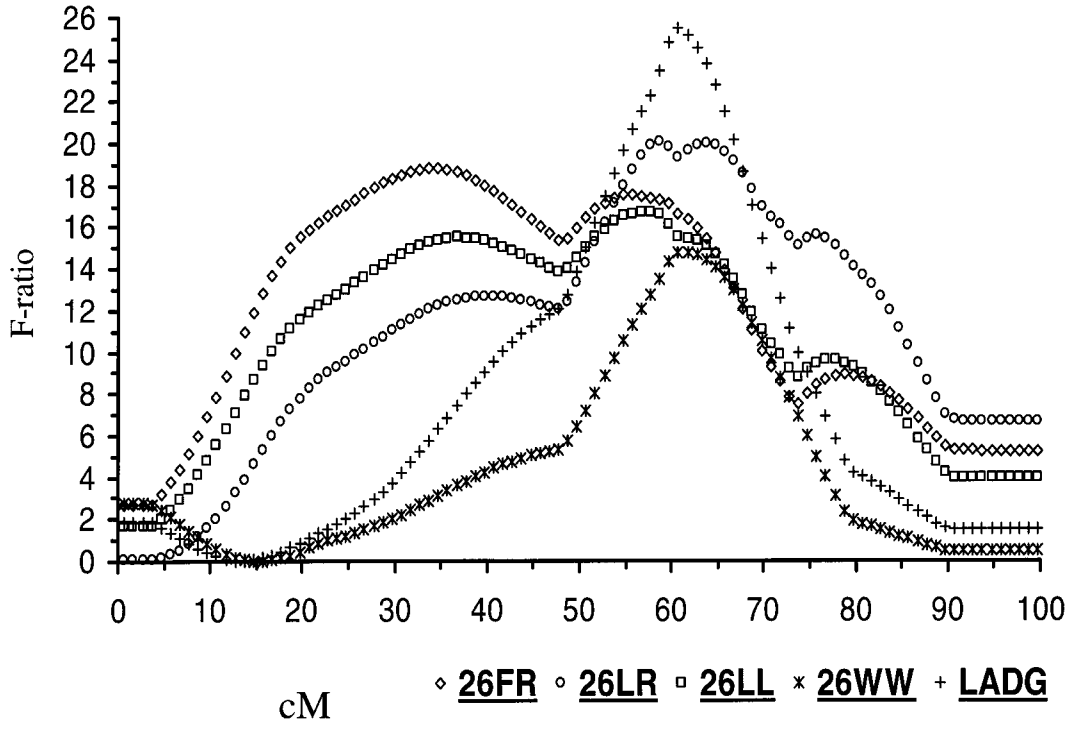

Figure 1. *F*-ratio profiles for QTL analyses on SSC 7. Traits included were ADG from 18 to 26 wk of age (LADG), weight at 26 wk (26WW), and ultrasonic backfat estimates recorded at 26 wk over the first rib, last rib, and last lumbar vertebrae (26FR, 26LR, and 26LL, respectively). All analyses plotted had 1 numerator degree of freedom for ease of comparison despite the fact that the model presented in Table 1 for 26FR had 2 numerator degrees of freedom. The threshold for genomewide significance is approximately 16.0.

Table 2. Genomic regions nominally significant at $P < .01$ for traits measured on individually fed barrows

Trait[a]	Location[b]	Degrees of freedom[c]	*F*-ratio	*P*-value	Genetic effects[d]	
					a	d
DFI	1:119	1; 89	9.7157	2.5×10^{-3}	249.2	—
	5:71	1; 89	8.8292	3.8×10^{-3}	–260.6	—
FEF	1:30	1; 89	7.1786	8.8×10^{-3}	–.021	—
TDG	8:58	2; 88	6.3640	2.6×10^{-3}	15.4	–20.5

[a]Traits analyzed were daily feed intake (DFI, g), feed efficiency (FEF) expressed as kg of gain/kg of feed consumed, and ADG on test (TDG, g/d).
[b]The position where the test statistic was maximized (expressed as chromosome position). The position within a linkage group is relative to Rohrer et al. (1996).
[c]Numerator degrees of freedom; denominator (residual) degrees of freedom.
[d]Genetic effects for additive effect of an allele substitution (a) and dominance deviations (d) as described by Falconer (1985). A dash in the column denoted d indicates that this term was removed from the final statistical model.

because the region identified for daily feed intake (1:119) is in the growth and backfat regions identified on SSC 1, with maximum test statistics located between 128 and 136 cM. Furthermore, the Meishan alleles tended to increase feed intake, body weight, and backfat depth.

General Discussion. This study represents a genomewide analysis for 14 traits. The only adjustment made for multiple comparisons was on a within-trait basis (genomewide levels of significance). If a Bonferroni adjustment is used assuming 14 independent traits, all of the significant QTL would remain significant except those for 26-wk weight, number of nipples, and all associations of SSC 7 for backfat depth at 26 wk of age. However, use of the Bonferroni adjustment based on 14 independent traits would be overly conservative because many of the traits analyzed are assumed to be highly correlated, both genetically and phenotypically. Thus, the thresholds set for this study were assumed sufficient.

Breed comparisons between Meishan and "western-type" pigs have revealed that Meishan germplasm produces more rapid early growth rate (prior to 8 wk of age), slower growth rates at later ages, and an increased backfat depth at 80 to 100 kg of live weight (Haley et al., 1992; Young, 1992a,b). The QTL detected in this study tended to conform to these observations with the exception of the region(s) detected on SSC 7. It is interesting to note that this locus tended to exhibit transgressive variation for all traits studied (late growth rate and backfat accretion). It is difficult to assess the actual portion of the breed differences that have been accounted for by the detected QTL for birth, growth, and backfat characteristics, but more loci that affect these traits exist.

The methods implemented to minimize Type I error have reduced the power of this study to detect more QTL. Actual QTL could have been overlooked in this study for many reasons. First, the analysis assumes that each breed is fixed for alternate alleles at the QTL. Deviation from this assumption can greatly reduce the power of the statistical test. However, statistical methods to alleviate this assumption are not as well tested and are computationally more demanding. Another condition under which a QTL may not be detected is if the magnitude of the effect is not large enough to yield an *F*-ratio greater than the critical value. The only ways to detect QTL with smaller effects are to increase population size or reduce error variance by adding effects (fixed or random) to the statistical model. Finally, if the genetic model used in the analysis does not reflect the true genetic model, some QTL will not be detected. In general, the methodology to detect epistatic loci has not been developed and, due to the mating structure of this population, models that account for genomic imprinting could not be tested.

Two reports have identified a paternally imprinted allele that affects carcass composition near the insulin-like growth factor-II gene located on SSC 2pter in Large White × Pietrain and Large White × wild boar populations (Nezer et al., 1999; Jeon et al., 1999). Due to the mating structure of this population, the effect from this locus would be completely confounded with the breed of sire term included in the statistical model. In preliminary analyses, removal of this term from the statistical model yielded numerous false-positives throughout the genome because half of the variation due to breed effects was confounded with the additive genetic variance at the QTL.

In summary, this study has increased our knowledge about the genetic mechanisms controlling birth, growth, and backfat characteristics; however, additional studies need to be conducted in populations composed of different germplasm to substantiate these findings as well as to identify other QTL that affect these traits. Further studies on the QTL identified in this research need to be evaluated to determine whether they would be useful in commercial swine populations and to identify the gene that is responsible for the observed effect. More QTL need to be identified for growth and body composition to determine the importance of epistatic and other genetic effects on quan-

titative traits and to increase the benefits of marker-assisted selection.

Implications

These results provide more information about the genetics of growth rate and fat accretion in swine. The two regions that affected growth rate (chromosomes 1 and 7) have previously been identified as affecting backfat depth and trimmed retail product yield in the same population. By increasing the knowledge of the traits that these quantitative trait loci affect, scientists will be better equipped to select positional candidate genes to study. These locations need to be assessed in commercial populations of swine to determine their utility in the swine industry.

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