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Interval mapping of growth in divergent swine cross

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Abstract. A genomic scan of 18 swine autosomal chromosomes was constructed with 119 polymorphic microsatellite (ms) markers to identify quantitative trait loci (QTL) for 11 growth traits in the University of Illinois Meishan × Yorkshire Swine Resource Family. A significant QTL effect was found for post-weaning average daily gain (ADG) between 5.5 and 56 kg of body weight that mapped between markers *SW373* and *SW1301* near the telomere of Chromosome (Chr) 1 q (SSC1). This QTL effect had a nominal (pointwise) *p*-value of 0.000007, a genome wide *p*-value of 0.012, and accounted for 26% of the F_2 phenotypic variance. The same chromosome region also had significant effects on ADG between birth and 56 kg body weight (*p*-value = .000227), and on ADG between 35 and 56 kg (*p*-value = .00077). These observations suggest that a significant QTL for post-weaning growth resides on SSC1.

Introduction

The focus of genetic selection in the swine industry is on economically important traits that exhibit quantitative variation (Bogart and Taylor 1983; White et al. 1995). To date, most swine selection programs have included at least one growth component that selects animals with greater daily gain. Moderate to high heritabilities of swine growth traits ranging from 30% to 60% have permitted effective genetic improvement programs based solely on phenotypic selection (Lasley 1987; Paszek, unpublished results). However, recent reports addressing the efficiency of marker-assisted selection (MAS) have indicated that an additional annual genetic gain of 8.8% for growth traits could be achieved (Meuwissen and Goddard 1996). Simulated comparisons of selection based on the Best Linear Unbiased Prediction (BLUP) versus BLUP and MAS together showed an additional genetic gain of 64% in the first generation of genetic selection using BLUP and MAS (Henshall and Goddard 1997). Therefore, the use of markers closely associated with QTL is expected to yield genetic improvement over traditional phenotypic selection programs. Several swine chromosomal regions that may contain potential QTL for growth have been reported based on association analysis (Hardge et al. 1996), candidate gene approach (Clamp et al. 1992; Te Pas et al. 1996), or genome scans (Andersson et al. 1994; Andersson-Eklund et al. 1996; Kuryl et al. 1996; Casas-Carrillo et al. 1997; Milan et al. 1998; and Wada et al. 1998). Moreover, Li and Enfield (1989) demonstrated significant differences in growth performance of Yorkshire and Meishan swine. Birth and adult weights for Meishan pigs were equal to 69% and 62% of the respective Yorkshire weights with breed performance means separated by 4 and 9 standard deviations, respectively. Also, breed performance comparisons reported by White et al. (1995) for Meishan and Yorkshire pigs concluded a faster rate of growth from birth to 171 days of age and heavier carcasses of Yorkshire pigs. Thus, in order to map QTL for growth traits in pigs, we conducted a genome scan of autosomal chromosomes, using the University of Illinois Meishan × Yorkshire Swine Resource Family that represents a cross between two phenotypically divergent swine breeds.

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Materials and methods

The University of Illinois Meishan × Yorkshire Swine Resource Family (Schook and Wheeler 1994) was used to provide DNA samples and growth trait data from three generations of animals (grandparents, F_1 and F_2). The statistical method used in this study is applicable for crosses between outbred populations and assumes breed fixation for alternative alleles affecting mapped traits (Haley et al. 1994). However, the assumption of alternative allele fixation in Meishan and Yorkshire swine can not be correctly evaluated without a true test for QTL and genes affecting growth traits in both breeds. Although an assumption of allele fixation in Meishan and Yorkshire may result in decreased power of QTL detection, violation of this assumption does not invalidate QTL analysis, because the mean effects for each of the alternative QTL alleles originating from grandparental breeds are still accurately estimated.

Phenotypic data for nine ADG traits, birth weight, and weight at two weeks of age for 298 F_2 animals were analyzed, and summary statistics are presented in Table 1. The ADG were calculated between body weights for the following standard phases in swine production: weaning weight (average weight of 5.5 kg), nursery (between 5.5 and 35 kg), grower (between 35 and 56 kg) and finishing (between 56 and 105 kg). Three ADG traits, birth to 105 kg, 35 to 105 kg, and 56 to 105 kg body weight, were collected only on male animals (N = 116). Normality tests with a univariate procedure (SAS/STAT, 1990) showed that each trait followed was normally distributed.

The QTL scan was conducted with 119 microsatellite (ms) markers from all 18 swine autosomal chromosomes. Microsatellites were selected based on ease of scoring, heterozygosity in the F_1 animals, and their genetic map location (Rohrer et al. 1996). These linked markers covered 90% of the swine genetic map (Rohrer et al. 1996) at an average marker interval of 24 cM. This interval was assumed to be adequate for QTL detection, as van Ooijen (1992) demonstrated QTLs explaining 5% or 10% phenotypic variance could be detected at 20- to 40-cM marker intervals. According to simulation studies by van Ooijen, up to 79% of QTLs explaining 10% of the phenotypic variance, and up to 29% of QTL explaining 5% of the phenotypic variance, were detected in an F_2 population with N = 200. The F_2 population used in this study included 298 F_2 animals and, therefore, should have adequate power for QTL detection. However, the power of QTL detection also depends on map marker density, the number of informative meioses, the magnitude of genotypic divergence between grand-

Table 1. Growth rates and body weight traits (N = 298).

Trait	Mean	SD	Coefficient of variation	Range (Min ; Max}	Number of SD between Min. and Max.
Average Daily Gain (kg/day)					
Birth to Weaning (t.t kg)	0.179	0.066	0.37	0.020 ; 0.388	5.58
Birth to 35 kg	0.383	0.091	0.24	0.121 ; 0.543	4.62
Birth to 56 kg	0.460	0.098	0.21	0.181 ; 0.667	4.96
Weaning to 35 kg	0.482	0.072	0.15	0.308 ; 0.695	5.41
Weaning to 56 kg	0.552	0.071	0.13	0.385 ; 0.760	5.26
35 kg to 56 kg	0.697	0.129	0.19	0.327 ; 1.228	7.00
Birth to 105 kg[a]	0.551	0.055	0.10	0.382 ; 0.694	5.67
35 kg to 105 kg[a]	0.662	0.093	0.14	0.461 ; 0.933	5.07
56 kg to 105 kg[a]	0.657	0.113	0.17	0.405 ; 0.977	5.06
Body weights (kg)					
Birth weight	1.17	0.21	0.18	0.21 ; 1.48	5.64
Two-week Weight	3.53	0.62	0.18	0.62 ; 1.60	5.78

[a] Trait data collected onlyon males (N = 116).

parental breeds, and the difference between mean allele effects for mapped QTL.

Programs developed by Haley and associates (1994) were used for QTL analysis. These programs implement an interval mapping strategy (Lander and Botstein 1989) with a multilocus regression analysis. The statistical model for each growth trait observed on males and females of the F_2 generation (N = 298) included effects of sex, family, parity, and a covariate. Litter size was used as a covariate for the analysis of birth weight and weight at 2 weeks owing to the variable number of piglets born in each litter (between 8 and 18). Since different litter sizes cause additional variation in birth and 2-week weights of F_2 animals and may bias estimation of QTL effects, body weights at the beginning of each growing phase were used as covariates to account for any bias in the estimation of QTL effects. Birth weight was used as a covariate in analyses of ADG between birth and weaning, birth and 35 kg, and birth and 56 kg. A weaning weight covariate was used in analyses of ADG between weaning and 35 kg, and between weaning and 56 kg. Grower weight (mean 35 kg) was used as a covariate in the analysis of ADG between 35 and 56 kg weights. We analyzed three ADG traits between birth and 105 kg, 35 and 105 kg, and 56 and 105 kg based solely on male records, using a statistical model that included effects of family, parity, and weights at birth, the end of the grower phase (mean 35 kg) and the beginning of the finisher phase (mean 56 kg) as covariates, respectively. Genetic correlations between mapped traits of the University of Illinois Meishan × Yorkshire Swine Resource Family were unknown. Therefore, analyses for each growth trait were conducted independently.

Plots of F-ratio statistics for each trait against respective marker intervals served as a basis for the identification of putative QTL by use of nominal (pointwise) significance (p-value < 0.05) and comparison with genome-wide F-ratio thresholds. The F-ratio threshold estimates for concluding genome-wide significant and suggestive evidence for each growth QTL were calculated based on guidelines presented by Lander and Kruglyak (1995). F-ratio thresholds are a function of the genome size, the number of scanned chromosomes, the specific population design (backcross or F_2 design) and the number of observations. An F-ratio greater than 10.74 identified genome-wide significant (F_G) evidence, and F-ratio values between 7.20 and 10.74 indicated genome-wide suggestive (F_S) evidence for the presence of a QTL (based on N = 298). An F-ratio greater than 11.62 for the three ADG traits collected on males (N = 116) identified genome-wide significant evidence, and F-ratio ranging between 7.53 and 11.62 indicated genome-wide suggestive evidence for the QTL.

Results and Discussion

Lander and Kruglyak (1995) proposed a set of guidelines for interpretation of results from complex trait analyses. One of their main goals was to avoid reports of false-positive loci by identifying intervals with the highest statistical support for linkage. F-ratios were compared with genome-wide significant and suggestive F-ratio thresholds, and significant evidence for a QTL affecting ADG between weaning and 105 kg weights on SSC1 was identified (Fig. 1). The identified QTL demonstrated an F-ratio of 12.41 with a corresponding nominal p-value of 0.000007 (Table 2) and a respective genome-wide p-value of 0.012. The QTL effect

Table 2. Growth QTL chromosomal intervals, significance, and effects.

Trait	p-value[a]	% of F_2 variance[b]	Chromosome and map position (cM)	Marker interval	Additive effect ± S.D.[c] (kg)	Dominance effect ± S.D.[d] (kg)
Average Daily Gain (kg/day)						
Weaning (5.5 kg) to 56 kg	0.000007[e]	25.6	SSC1 (209)	SW373–SW1301	0.031 ± 0.007	0.021 ± 0.013*
Birth to 56 kg	0.000227[f]	18.1	SSC1 (214)	SW373–SW1301	0.037 ± 0.009	0.010 ± 0.016
35 kg to 56 kg	0.000770[f]	15.5	SSC1 (206)	SW373–SW1301	0.041 ± 0.013	0.053 ± 0.024*
Body weight (kg)						
Birth weight	0.000462[f]	16.6	SSC4 (33)	SW2509–S0301	–0.046 ± 0.017	0.085 ± 0.028**

[a] Nominal (pointwise) probability of Type-I error (false positives) based on F-ratios calculated with a program by Haley et al. (1994).
[b] Reduction in residual error variance owing to the presence of the QTL.
[c] Deviation between the mean of homozygotes for the Meishan QTL allele and mean of homozygotes for Meishan and Yorkshire QTL alleles.
[d] Deviation between the mean of heterozygotes for QTL alleles and homozygotes for Meishan and Yorkshire QTL alleles.
[e] Genome-wide significant QTL (F-ratio>significance F-ratio threshold).
[f] Genome-wide suggestive QTL (F-ratio>suggestive F-ratio threshold).
* Estimate of dominance effect was different from 0 based on the T-test at p-value<0.05 (T = dominance effect estimate/S.D., degrees of freedom or the full model residual sum of squares).
** Estimate of dominance effect was different from 0 based on the T-test at p-value<0.01 (T = dominance effect estimate/S.D., degrees of freedom for the full model residual sum of squares).

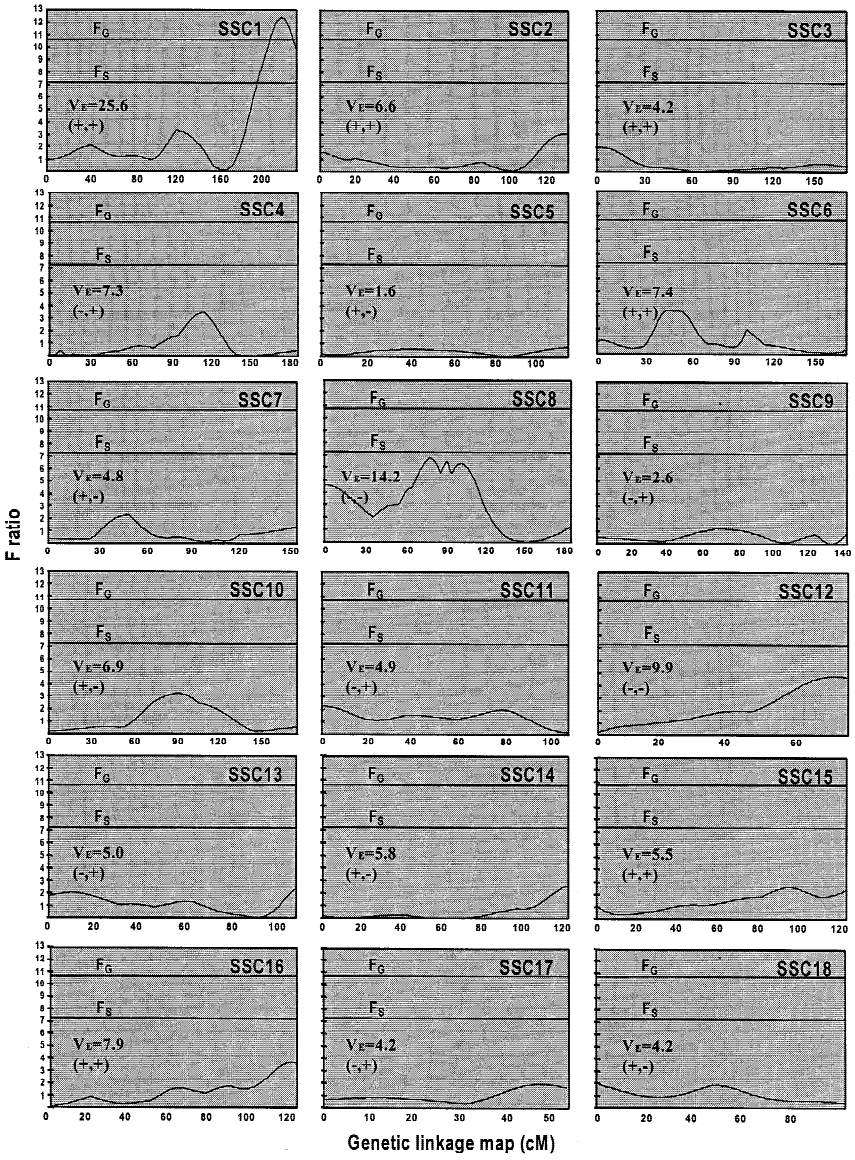

Fig. 1. Genomic QTL Scan for ADG between Weaning (5.5 kg) and 56 kg. F_G = F-ratio threshold for genome-wide significant QTL. F_S = F-ratio threshold for genome-wide suggestive QTL (Lander and Kruglyak 1995). V_E = proportion of variance (in %) explained by a chromosome. (+,+) = direction of QTL effects (additive and dominant).

explained 26% of the phenotypic variance in F_2 animals (Table 2). Estimates of additive QTL effects (Meishan homozygotes deviated from the mean of homozygotes for the alternative QTL allele) indicated a mean superiority of the Meishan QTL allele of 31 g/day. The estimate of the dominance QTL effect (difference of the mean between QTL heterozygotes and mean of QTL homozygotes) indicated mean superiority of 21 g/day of the ADG for QTL heterozygotes. The estimated dominance effect differed from 0 (p-value < 0.05) based on the T-test. The additive and dominance QTL effects were estimated assuming Meishan and Yorkshire populations to be fixed for alternative QTL alleles and suggest superiority of Meishan QTL allele contrary to reports of superior growth performance of Yorkshire breed over the Meishan (Li and Enfield 1989; White et al. 1995). However, estimates of allelic QTL effects in parental populations contradicting phenotypic performance of each population for the studied trait are also known as transgressive variation and may be due to epistatic effects of multiple QTL (Tanksley and McCouch 1997).

Figure 2 presents specific ms intervals for identified QTL based on autosomal genome-wide significance and suggestive evidence. The significant QTL for ADG between weaning and 56 kg was detected between SW373 and SW1301 on SSC1. Suggestive QTL for ADG between birth and 56 kg weights, and 35 and 56 kg, were also observed within the same marker interval on SSC1. QTL for the deposition of backfat as well as loin eye area and carcass length were recently located within the same marker interval on SSC1 (Rohrer and Keele 1998a, 1998b). Genetic correlations between swine ADG, deposition of backfat, loin eye area, and carcass length determined from performance data of commercial pig lines (Paszek, unpublished results) suggest pleiotropic effects of the identified QTL or multiple QTL within the SSC1 region. The analysis of the University of Illinois Swine Resource Family F_2 data for three growth rates showed high phenotypic correlations (0.79 between weaning to 56 kg, and birth to 56 kg ADGs; 0.78 between weaning to 56 kg and 35 to 56 kg weight ADGs; 0.76 between birth to 56 kg and 35 to 56 kg weight ADGs), which may in part be due to genetic correlations resulting from pleiotropy of the identified QTL. True pleiotropic effects of a QTL on mapped traits accounted for in multi-trait mapping methods would result in greater power for QTL detection.

Estimates of dominance effects for ADG between weaning to 56 kg and 35 to 56 kg were different from 0 (p-value < 0.05) (Table 2) and provide evidence for significant non-additive effects of the identified QTL on SSC1. The dominance effect estimated for ADG between 35 to 56 kg was nearly twice as large as the estimate for dominance effect of ADG between weaning to 56 kg

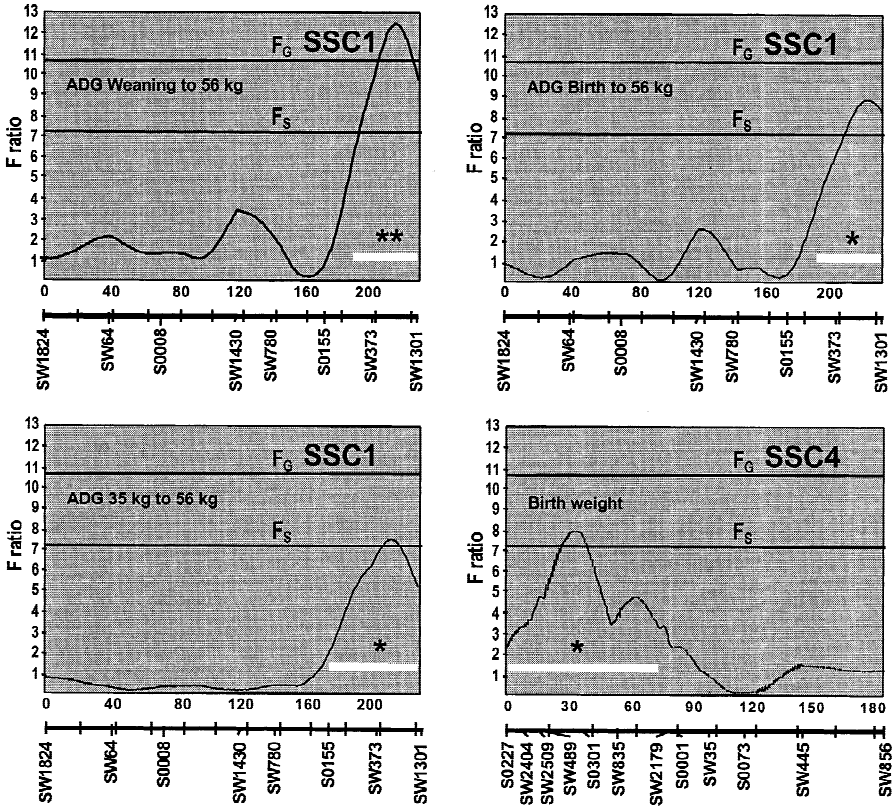

Fig. 2. Significant** and suggestive QTL* for growth traits on SSC1 and SSC4 based on genome-wide evidence. White horizontal bar = 95% confidence interval for QTL position. F_G = F-ratio threshold for genome-wide significant QTL, and F_S = F-ratio threshold for genome-wide suggestive QTL (Lander and Kruglyak 1995).

and was consistent with overdominance based on the observation of a greater mean for heterozygotes than for homozygote animals inheriting Meishan or Yorkshire alleles.

A genome-wide suggestive QTL contributing to birth weight was detected on SSC4 between ms SW489 and S0301 (Fig. 2). The estimated additive effect suggested a lower birth weight for homozygotes inheriting Meishan allele from boars in comparison with the mean of homozygote animals for Meishan and Yorkshire alleles. The lower birth weight of Meishan piglets is in agreement with larger litter sizes observed in Meishan pigs (Li and Enfield 1989). The dominance effect estimate is almost twice as large as the additive effect estimate (0.085 vs. 0.046) and illustrates a difference of non-additive effects between identified QTL on SSC4 and SSC1 (Table 2).

None of the remaining traits met criteria for claiming significant or suggestive linkage to the markers examined. However, with nominal significance, several regions of interest were identified. Additional investigations of data from other populations are necessary to determine whether these regions contain QTL associated with studied traits.

Several genomic regions affecting the variance of the traits studied are shown in Fig. 3. Regions based on the nominal test p-value < 0.05 as well as highest nominal probability for a QTL (p-value < 0.001) were identified. Reported effects of SSC4 on body weight and growth rate were confirmed at nominal significance (Fig. 3; Andersson-Eklund et al. 1996; Kuryl et al. 1996; Wada et al. 1998; Milan et al. 1998). Casas-Carrillo et al. (1997) reported nominally significant (p-value < 0.05) effects of SSC1, SSC2, SSC3, SSC8, and SSC12 on post weaning ADG. Figure 3 presents regions of those chromosomes identified based on nominal significance for putative QTL for ADG from weaning to 35 kg, weaning to 56 kg, 35 to 56 kg, 35 to 105 kg, and birth to 105 kg. A region on SSC8 was identified based on high nominal significance for ADG between weaning and 35 kg and weaning and 105 kg (nominal p-value = 0.0019 and 0.0014, respectively) and included several F-ratio peaks in the interval defined by SW1345 and S0086 (Fig. 3).

A genetic interval for growth rate between birth and 30 kg of body weight was identified by Andersson and colleagues (1994) near ms S0084 on SSC13. We also detected a region affecting ADG between birth and 35 kg on SSC13 located between ms S0068 and SW398 (Fig. 3). The use of similar marker sets in future genomic QTL scans in different resource populations may provide opportunity for verification and extension of QTL between resource populations.

This study identified several regions on SSC2, SSC4, SSC8, and SSC13 that were consistent with QTL regions previously reported (Andersson et al. 1994; Andersson-Eklund et al. 1996; Kuryl et al. 1996; Casas-Carillo et al. 1997; Wada et al. 1998; Milan et al. 1998) when evaluated with nominal criteria. We have identified a significant QTL for growth rate measured by ADG on SSC1 and a suggestive QTL for ADG and birth weight on SSC1 and SSC4 based on the genome-wide criteria proposed by Lander and Kruglyak (1995). The QTL contributing to ADG on SSC1 accounted for 26% of the phenotypic variance. Further dissection of these intervals will require additional markers within the intervals and the use of multi-trait methods in QTL analyses that account for genetic correlations among the traits. Confirmation of the putative QTLs from this study will also be required and could be improved with use of similar marker sets and common analyses of multiple data sets. A more robust estimate of the economic significance of this locus in MAS procedures could also be made in commercial swine populations segregating the traits of interest.

In summary, this study reports genetic loci affecting growth rate on SSC1 in domestic swine *(Sus scrofa).* Although the findings are reported for swine, they provide initial direction for dissecting growth as a complex mammalian trait. The Mouse Genome Database at The Jackson Laboratory (http://www.informatics.jax.org/homology.html) reports three candidate genes from regions of mouse and human genomes homologous to SSC1 (GAS—Growth

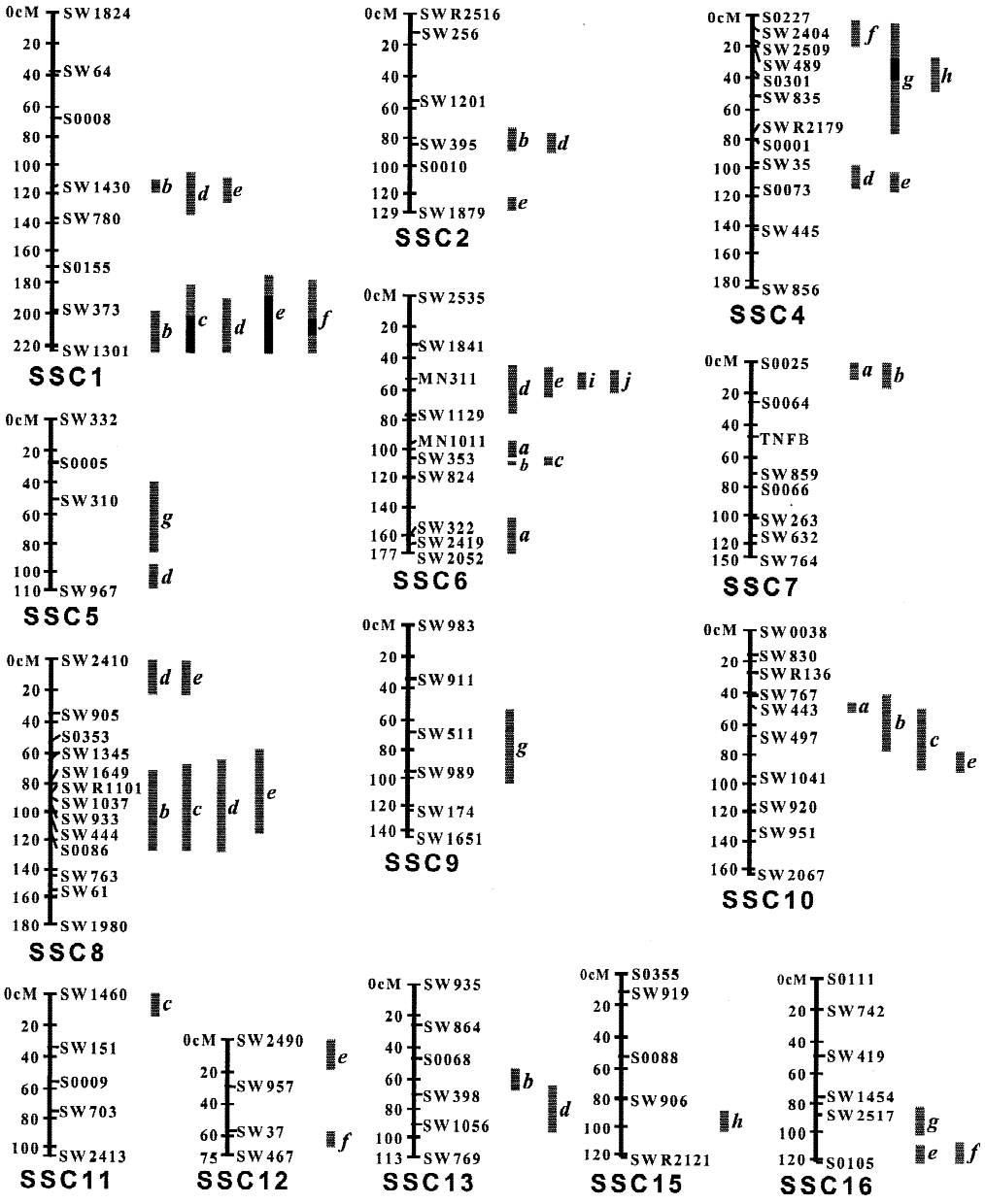

Fig. 3. Genomic regions for growth traits based on nominal (pointwise) significance of p-value < 0.05 (grey vertical bar) and p-value < 0.001 (black vertical bar). **a**–growth rate between birth and weaning (5.5 kg), **b**–growth rate between birth and 35 kg, **c**–growth rate between birth and 56 kg, **d**–growth rate between weaning and 35 kg, **e**–growth rate between weaning and 56 kg, **f**–growth rate between 35 kg and 56 kg, **g**–birth weight, **h**–2-week weight, **i**–growth rate between 35 kg and 105 kg, **j**–growth rate between birth and 105 kg.

Arrest-Specific Gene-1; TGFBR1—Transforming Growth Factor-Beta Receptor, Type 1; and IGF1R—Insulin-like Growth Factor 1 receptor) and, therefore, helps to identify major genetic factors affecting mammalian growth.

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