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Mapping quantitative trait loci for feed consumption and feeding behaviors in a White Duroc × Chinese Erhualian resource population[1]

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ABSTRACT: To identify QTL for feed consumption and feeding behavior traits in pigs, ADFI, feed conversion ratio (FCR), number of visits to the feeder per day (NVD), and average feeding rate (AFR) were recorded in 577 F_2 animals from a White Duroc × Chinese Erhualian resource population during the fattening period of 120 to 240 d. A whole genome scan was performed with 183 microsatellites covering the pig genome across the entire resource population. A total of 8 QTL were identified on 5 pig chromosomes, including 3 genome-wide significant QTL for FCR on SSC2, 7, and 9, 1 significant QTL for ADFI on SSC3, and 1 for NVD on SSC7. These QTL were identified for the first time, except for the QTL for FCR on SSC2. Four of the 5 significant QTL were adjacent to the known QTL for growth, carcass, and fat deposition traits, supporting the existence of gene(s) with pleiotropic effects on these traits. White Duroc alleles were generally associated with greater phenotypic values, except for those on SSC7 and 9. Comparison of QTL for feed consumption and feeding behaviors indicated that distinct chromosomes had effects on the 2 types of traits. Characterization of causative gene(s) underlying the identified QTL would shed new light on the genetic basis of feed consumption and feeding behaviors in pigs.

Key words: feed intake, feeding behavior, pig, quantitative trait locus

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INTRODUCTION

Feed consumption traits, including ADFI and feed conversion ratio (**FCR**), are economically important traits in pigs and account for a significant proportion of the costs involved in the pig industry. It has been reported that a 5% increase in FCR has an economic impact 4 times as great as a 5% increase in daily BW gain (Okine et al., 2004). Less effort has been devoted to decipher the molecular basis of ADFI, FCR, and feeding behaviors compared with other performance traits. This could be due to the difficulty of phenotype measurement of these traits in a group-housed system. To date, some genes have been found with strong association with feed consumption and growth rate, such as melanocortin-4 receptor (Roehe et al., 2003), *IGF2* (Van Laere et al., 2003), and cholecystokinin type A receptor (***CCKAR***; Houston et al., 2006, 2008). Moreover, genome-wide significant QTL for ADFI and FCR have been identified on SSC 1, 2, 6, 10, and 18 in F_2 populations generated from Pietrain, Meishan, and wild boar crosses (http://www.animalgenome.org/QTLdb/) and a commercial population (Mohrmann et al., 2006; Duthie et al., 2008). Considering the economical importance of feed consumption and limited knowledge about the genetic basis of this trait, further QTL investigation is required using different or larger populations or both.

We have recently constructed a 3-generation resource population by crossing White Duroc boars and Chinese Erhualian sows, and a diverse set of phenotypic traits including ADFI, FCR, and feeding behaviors during the fattening period were recorded. The objective of this study was to identify QTL for traits related to feed consumption and feeding behavior in the White Duroc × Erhualian intercross using a whole genome scan.

MATERIALS AND METHODS

All of the procedures involving animals followed the guidelines for the care and use of experimental animals established by the Ministry of Agriculture of China.

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Animals and Phenotypic Measurement

A 3-generation resource population was created and managed as described by Ren et al. (2009). Briefly, 2 White Duroc sires and 17 Erhualian dams were mated to produce F_1 animals in 2001, from which 9 F_1 boars and 59 F_1 sows were intercrossed (avoiding full-sib mating) to produce 983 F_2 males and 929 F_2 females in 6 batches from 2003 to 2006. To obtain large full-sib families, each F_1 sow was usually mated to the same boar in different batches. Males and females were weaned at 46 d, and the males were castrated at 90 d. All piglets were raised at the experimental farm of Jiangxi Agricultural University (Nanchang, P. R. China) until 100 d. Subsequently, 577 F_2 individuals, including 365 boars and 212 gilts, were transferred to Jiangxi Swine Performance Test Station (Nanchang, P. R. China) for measurements of feed consumption and feeding behaviors during the fattening period from 120 to 240 d. These animals were group-housed in half-open cement-floor pens each with 10 to 12 animals (an average of 2 m^2 per pig) and fed an ad libitum diet containing 16% CP, 3,100 kJ of DE, and 0.78% lysine until harvest. All diets were fortified with vitamins and minerals appropriate for the age of the pig. Water was provided ad libitum. Each animal was marked with a unique tag, which was recognized by the ACEMA64 electronically recorded feeding system (ACEMO, Pontivy Cedex, France). With this system, every time an individual visited the feeder, the animal number and the BW of individual, the total feed consumption during the visit, and the visit times per day were recorded. Feed consumption-related traits, including ADFI, FCR, number of visits to the feeder per day (**NVD**), and average feeding rate (**AFR**), were measured throughout the testing period. The FCR was calculated from total feed consumption divided by BW gain. Phenotypic measurements of carcass length, small intestinal length, and fat deposition traits were performed from pigs slaughtered at a commercial abattoir at 240 ± 3 d as described in Ma et al. (2009).

Microsatellites and Genotyping

Microsatellite markers were initially selected from the USDA-MARC linkage map (Rohrer et al., 1996) to genotype all founder and F_1 animals in the White Duroc × Erhualian resource population. A final set of 183 informative markers at approximate 20-cM intervals covering the pig genome were selected and genotyped across the entire resource population. Genomic DNA was extracted from ear or tail tissues using a standard phenol/chloroform method and quantified with a DU640 spectrophotometer (Beckman, CA). All DNA samples were diluted to a standard concentration of 20 ng/μL in 96-well plates. Primers for each marker were labeled with fluorescent dyes of FAM, HEX (Aoke, Beijing, China), or NED (ABI, Foster City, CA). Amplifications were performed in a 15-μL mixture containing 40 ng of genomic DNA, 0.3 U of Taq polymerase (Takara, Dalian, China), 10× supplied buffer, 1.5 m*M* $MgCl_2$, 0.2 m*M* of each dNTP, and 10 pmol of each primer. The PCR conditions were as follows: predenaturation at 94°C for 3 min; 38 cycles of 94°C for 20 s, optimal annealing temperature for 20 s and 72°C for 30 s and a final extension at 72°C for 8 min. The PCR products were recorded with a 3130XL Genetic Analyzer and analyzed with GeneMapper Software Version 3.7 (ABI).

Statistical Analysis

Genotype data were first analyzed with CRIMAP version 2.4 (Green et al., 1990) to construct a whole-genome linkage map as described previously (Guo et al., 2009). The QTL analysis was performed by composite interval mapping based on a least squares regression approach (Haley et al., 1994) and implemented via QTL Express available at http://qtl.cap.ed.ac.uk. The option F_2 ANALYSIS was used to detect single QTL with additive and dominance effects on 18 autosomes and additive effects on the X chromosome. Factors significantly affecting the traits measured were determined with PROC GLM (SAS Institute Inc., Cary, NC). Pen, sex, and batch were included as fixed effects and BW at 120 d as a covariate in the QTL analysis model. The QTL analysis was fitted at 1-cM intervals along each chromosome, and the *F*-ratio for the QTL effect was calculated at each point. The position reaching the greatest *F*-ratio was considered as the position of the QTL. Detected QTL in the current population were fixed as the genetic background in the next round of QTL identification. It was assumed that founder breeds were fixed for alternative alleles at a QTL, and 2 alleles at a putative QTL at a given location were denoted by Q and q. Probabilities of QTL genotypes, denoted by Prob(QQ), Prob(Qq), and Prob(qq), were computed from the observed marker genotypes flanking the QTL. The additive and dominance effects of a QTL at a given position were defined as the deviation of animals homozygous for the White Duroc allele or heterozygotes from the mean of the 2 homozygotes, respectively. The genome-wide and chromosome-wide significance thresholds for QTL were estimated by a permutation test with 1,000 random data shuffles as described by Churchill and Doerge (1994). The empirical 95% confidence intervals (**CI**) were evaluated by a bootstrapping approach with 1,000 iterations (Visscher et al., 1996). Percentage of variance (***Var%***) explained by each QTL was calculated using the following formula:

$$Var\% = \frac{(MS_{reduce1} - MS_{full})}{MS_{reduce}} \times 100,$$

where MS_{full}, $MS_{reduce1}$, and MS_{reduce} were the residual mean squares of the models with all detected QTL, with the rest of the detected QTL except for the 1

Table 1. Summary of the feeder traits from 120 to 240 d in the White Duroc × Erhualian resource population

Trait	n	Mean	SD
ADFI, g/d	494	2,168	470
Feed conversion rate	395	3.75	0.57
Number of visits per day	478	8.90	3.90
Average feeding rate, g/sec	474	0.70	0.20

currently under consideration, and without any of the detected QTL, respectively.

RESULTS AND DISCUSSION

Phenotypic means and SD of the measured traits are given in Table 1. A whole-genome linkage map was constructed with a total length of 2,344.7 cM and an average marker interval of 12.1 cM (Guo et al., 2009). The marker order was generally consistent with that on the USDA-MARC reference map (Rohrer et al., 1996), except for *KS502* and *SWR2189* on SSC13. The suggestive (5% chromosome-wide), 5%, and 1% genome-wide significance thresholds were 5.27, 8.50, and 10.47, respectively. A total of 8 QTL for the measured traits were identified on 5 chromosomes (Table 2), including one 1% genome-wide significant QTL on SSC2 and 2 on SSC7, and two 5% genome-wide significant QTL on SSC3 and 9. Moreover, 3 suggestive QTL were identified on SSC8 and 9 (Table 2). The statistic *F*-curves indicating genome-wide significant QTL are shown in Figure 1.

Most of genome-wide significant QTL in this study were adjacent to previously reported QTL for growth, carcass, and fatness traits (see below). Moreover, the significant QTL for ADFI on SSC3 and FCR on SSC2 and SSC7 overlapped with the QTL for ADG in the current population (data not shown). As highly correlated traits (Supplemental Table 1; http://jas.fass.org/content/vol87/issue11/), there might be gene(s) with pleiotropic effects on FCR, ADFI, growth, carcass, and fatness traits in these QTL regions. However, QTL for feed consumption and feeding behavior were always found in different chromosomal regions, which may be due to low correlations among these traits in this population (Supplemental Table 2; http://jas.fass.org/content/vol87/issue11/) and indicate a different genetic basis of feed consumption and feeding behaviors.

QTL for ADFI

Only 1 genome-wide significant QTL was detected for ADFI in this study. This significant QTL was found at 74 cM on SSC3 (Figure 1B), explaining 3.82% of the phenotypic variance. To our knowledge, this QTL was found for the first time. The chromosomal region around 74 cM overlapped with the previously reported QTL for fatness traits (Beeckmann et al., 2003b), for ADG in a Large White × Meishan intercross (Bidanel et al., 2001), and in the current population (data not shown). The White Duroc allele at this locus was associated with greater phenotypic values.

On SSC1, a significant QTL for ADFI has been characterized in a Meishan × White composite resource population (Rohrer, 2000) and a European wild boar × Pietrain intercross (Beeckmann et al., 2003c), respectively. In addition, previous studies have revealed significant QTL for ADFI on SSC2 (Houston et al., 2005; Duthie et al., 2008) and SSC6 (Mohrmann et al., 2006). However, these QTL were not confirmed in this study. Moreover, several suggestive effects for ADFI have been evidenced on SSC1, 4, 5, 9, 13, 14, 16, and X in an F_2 population from Pietrain, Meishan, and wild boar crosses (http://www.animalgenome.org/QTLdb/). These suggestive QTL were not replicated herein, either.

QTL for FCR

Four chromosomes showed effects on FCR, including 3 genome-wide significant QTL on SSC2, 7, and 9.

Table 2. Details of QTL for feed intake and feeding behaviors identified in the White Duroc × Erhualian resource population

SSC	Position, cM	Trait[1]	*F*-value[2]	Additive effect ± SE[3]	Dominance effect ± SE[4]	95% CI, cM	Variance,[5] %
2	20	FCR	14.5***	−0.24 ± 0.05	0.10 ± 0.07	0 to 26	5.96
3	74	ADFI	10.4**	115.10 ± 26.00	35.20 ± 39.50	34 to 106	3.82
7	59	FCR	18.3***	0.25 ± 0.04	−0.04 ± 0.06	31 to 65	7.63
	47	NVD	14.3***	−1.10 ± 0.30	1.20 ± 0.40	26 to 68	5.50
8	6	FCR	8.4*	−0.05 ± 0.01	−0.30 ± 0.07	0 to 99	3.27
9	0	FCR	10.2**	−0.08 ± 0.04	−0.25 ± 0.06	0 to 128	4.06
	73	NVD	6.8*	1.00 ± 0.30	−0.30 ± 0.40	0 to 102	2.40
	127	AFR	5.4*	−0.10 ± 0.10	0.10 ± 0.10	7 to 144	1.63

[1]FCR, NVD, and AFR indicate feed conversion ratio, number of visits per day, and average feeding rate from 120 to 240 d, respectively.
[2]Significance levels determined by permutation test: *5% chromosome-wide significance level; **5% genome-wide significance level; ***1% genome-wide significance level.
[3]The positive additive effect means that White Duroc-originated alleles are associated with increased phenotypic values or vice versa.
[4]The positive dominance effect indicates that White Duroc-originated alleles are dominant over Erhualian-originated alleles or vice versa.
[5]Percentage of the phenotypic variance explained by the QTL.

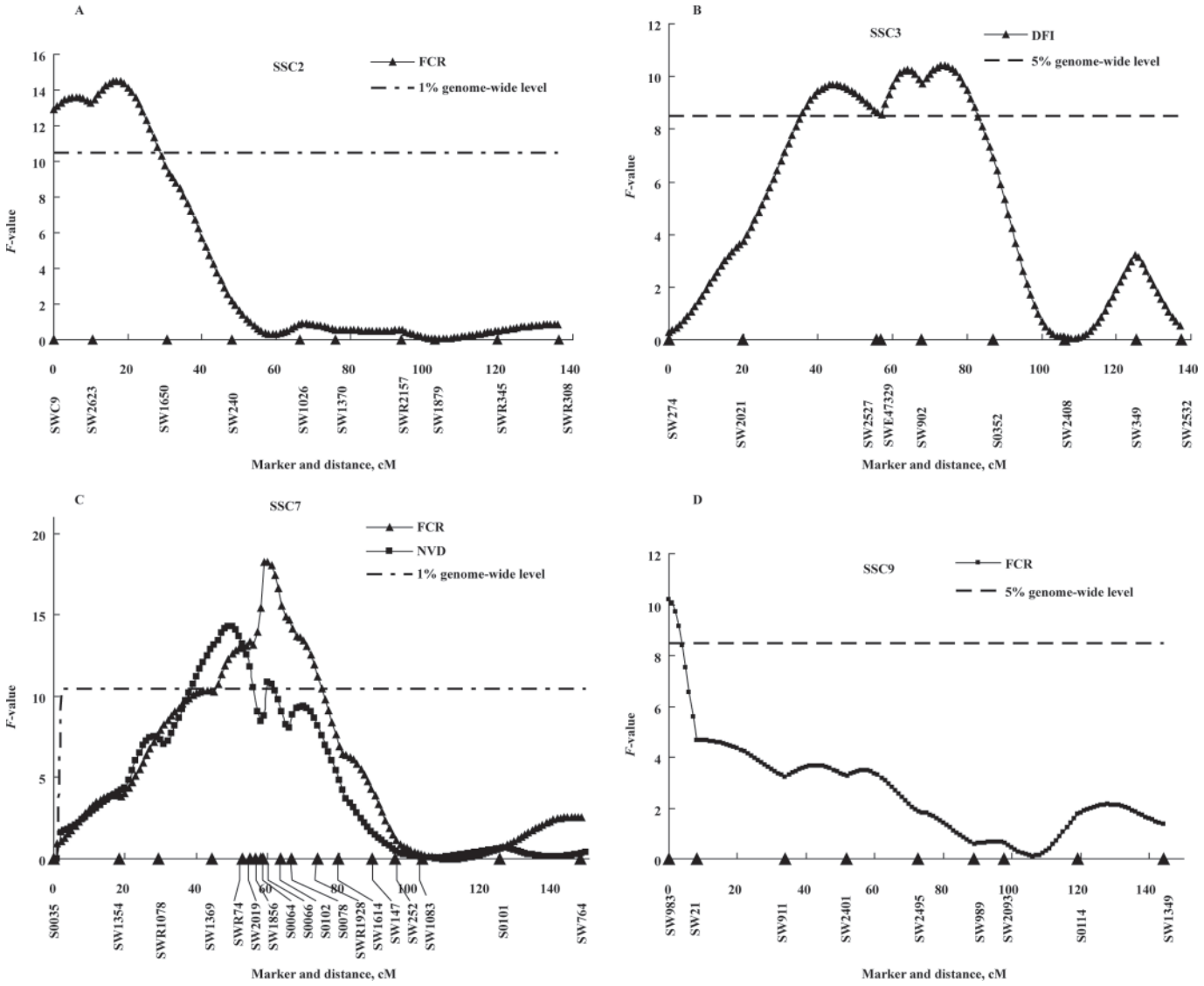

Figure 1. Statistic *F*-curves indicating genome-wide significant QTL for feed consumption and feeding behaviors on SSC2 (A), SSC3 (B), SSC7 (C), and SSC9 (D). Markers and distance in cM are given on the x-axis, and *F*-values are indicated on the left y-axis. The 1 and 5% genome-wide significance levels are indicated by distinct dashed lines. FCR, NVD, and DFI indicate feed conversion ratio, number of visits per day, and daily feed intake from 120 to 240 d, respectively.

The QTL on SSC2 (Figure 1A) explained 5.96% of the phenotypic variance, and the White Duroc allele at this locus was associated with greater feed conversion efficiency. This genomic region overlapped with the previous significant QTL for FCR in a commercial population (Duthie et al., 2008) and for ADFI in the Meishan × Large White intercrosses (Houston et al., 2005), and for ADG in the current population (data not shown). Moreover, numerous QTL for fatness, carcass composition, and fatness traits have been mapped around this region (http://www.animalgenome.org/QTLdb/). We found that FCR was significantly correlated with carcass and fatness traits in the current population (Supplemental Table 1; http://jas.fass.org/content/vol87/issue11/). Whether these traits are affected by the same gene or different loci in the QTL region needs further investigation. The *IGF2* gene (Van Laere et al., 2003), a parentally expressed gene with a large effect on fatness and growth traits, lies close to this QTL on SSC2. We hypothesized that the *IGF2*-intron3-G3072A causal mutation could have a pleiotropic effect on FCR. We found that all Chinese Erhualian founder sows are *GG* homozygotes and White Duroc boars are alternatively *AA* homozygotes at the causative mutation site in this resource population. However, a significant imprinting effect was not found on SSC2 by analyzing with the imprinting QTL model in this F_2 population (data not shown), indicating that the *IGF2* causative mutation is not responsible for FCR in this study. A distinct causative variant on the P arm of SSC2 is likely to explain the observed effect on FCR.

On SSC7, abundant QTL for diverse traits have been identified around the major histocompatibility complex region (http://www.animalgenome.org/QTLdb/). Hence, high-density markers around this region were used in this study to diminish the confidence interval

of the expected QTL. A 1% genome-wide significant QTL for FCR was identified at 59 cM on SSC7 (Figure 1C), which explained 7.63% of the phenotypic variance. To our knowledge, it is the first time to identify a QTL for FCR on SSC7. This region also showed a significant effect on ADG in the current experimental population (data not shown). Unexpectedly, the White Duroc alleles on SSC7 were associated with increased FCR, which was in contrast with the breed characteristics and the observations at the other QTL detected in this study. The unusual effect in this region has also been found for other performance traits in other experimental crosses. As proposed previously (de Koning et al., 1999), the reasons for this discrepancy could be 1) the Western alleles are recessive and remain at a reasonable frequency in the commercial breeding stock; 2) the allele, although undesirable for feed conversion efficiency, might have a favorable effect on other production traits.

A suggestive QTL for FCR was identified at 6 cM on SSC8, which explained 3.27% of the phenotypic variance. In a Meishan × Pietrain intercross (Beeckmann et al., 2003a), a suggestive QTL for FCR was also found on this chromosome, whereas it is far from the peak of the current QTL. The *CCKAR* gene maps to a region close to the QTL on SSC8 in this study. It has been shown that a g.179A > G polymorphism in the 5′-untranslated region of this gene is significantly associated with ADFI, ADG (Houston et al., 2006), and feeding rate (Houston et al., 2008). Whether this QTL effect is caused by the *CCKAR* g.179A > G polymorphism requires further investigation. Additionally, previously reported QTL for FCR have been identified on SSC3, 5, 6, 13, and 18 in different populations (http://www.animalgenome.org/QTLdb/), which were not confirmed in this study.

On SSC9, a 1% genome-wide significant QTL for FCR was identified at the end of the P arm for the first time (Figure 1D), explaining 4.06% of the phenotypic variance. This chromosomal region was far from the QTL observed for NVD and AFR in this population. We noticed that no QTL for growth and fatness traits were found in this region (data not shown).

QTL for Feeding Behavior

Only one genome scan has been performed to identify QTL for feeding behavior-related traits including NVD and AFR before this study (Houston et al., 2005), but no QTL have been found for NVD. In this study, a 1% genome-wide significant QTL for NVD was identified at 47 cM on SSC7 for the first time (Figure 1C), explaining 5.50% of the phenotypic variance. This chromosomal region was adjacent to the previously reported significant QTL for carcass length (Yue et al., 2003) and the significant QTL for FCR in this study. In addition, a suggestive QTL for NVD was identified at 73 cM on SSC9. For AFR, only one suggestive QTL was identified on SSC9 in this study, explaining 1.63% of the phenotypic variance. This QTL region overlapped with previously reported QTL for ADG during the fattening period in a Meishan × Large White intercross (Quintanilla et al., 2002). This region was also adjacent to previous QTL for FCR and fat-to-meat ratio in a wild boar × Pietrain intercross (Cepica et al., 2003). Houston et al. (2005) have reported QTL for AFR on SSC3, 7, 12, and 14, which were not confirmed in this study. This discrepancy may be due to the different genetic basis of founder animals or the complexity of behavior traits.

In summary, we detected 8 QTL for 4 traits related to feed consumption, including three 1% genome-wide significant QTL on SSC2 and 7 and two 5% genome-wide significant QTL each on SSC3 and 9. These QTL were identified for the first time, except the QTL for FCR on SSC2. Most of genome-wide significant QTL were adjacent to known QTL for growth, carcass, and fatness traits. Further studies are required to fine map these QTL with additional markers and populations. Investigation of the causative gene(s) underlying the identified QTL may shed new light on the genetic basis of feed consumption and feeding behaviors in pigs.

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