

A whole genome scan for quantitative trait loci for leg weakness and its related traits in a large F₂ intercross population between White Duroc and Erhualian¹

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ABSTRACT: To detect QTL for leg weakness and its related traits in pigs, a total of 1,484 F₂ pigs were recorded for leg (at 76 and 213 d) and gait scores (at 153 and 223 d) in a White Duroc × Erhualian intercross. The length and weight of the biceps brachii muscle were measured after slaughter at 240 d. A genome scan was performed with 183 microsatellite markers in the population. A total of 42 QTL were detected, including 16 at the 1% genome-wide significant level and 6 at the 5% genome-wide significant level. Thirty-eight of the 42 QTL showed significant additive effects, and 14 had significant dominance effects. At least 2 QTL were

detected for each trait except for leg score at 76 d, for which no QTL was identified. Some of the QTL for leg and gait scores confirmed previous findings. Eighteen QTL were detected for weight and length of the biceps brachii muscle. To our knowledge, this was the first report about QTL for weight and length of the biceps brachii muscle in pigs. Two chromosome regions each on SSC4 and SSC7 showed significant and multiple associations with both leg weakness and growth of the biceps brachii muscle, which are worthwhile for further investigation.

Key words: biceps brachii muscle, gait score, leg score, pig, quantitative trait loci

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INTRODUCTION

Leg weakness is becoming a concern in the pig industry and has resulted in 20 to 50% of eligible boars being culled as breeding animals (Webb et al., 1983; Sternbergen, 1989). Many factors give rise to leg weakness, such as bone and joint diseases, microbial infections, nutritional imbalances, and modern confinement rearing systems (Rothschild and Christian, 1988). Artificial selection for production traits also has adverse effects on leg structure of pigs, impairing leg soundness (Lee et al., 2003). Leg weakness can be evaluated with leg and gait scores and is related to weight and length of the biceps brachii muscle (Draper et al., 1992). As

a multifactorial trait, the heritability of leg weakness is estimated to range from 0.1 to 0.5 (Bereskin, 1979; Webb et al., 1983; Rothschild and Christian, 1988; Jørgensen and Andersen, 2000). The genetic architecture of leg weakness remains poorly understood. Until now, just one paper reported QTL for leg weakness in pigs (Lee et al., 2003).

We have constructed a large-scale White Duroc × Erhualian intercross resource population and have recorded a set of diverse production traits including leg weakness-related traits in this population (Ren et al., 2006). The aim of this study is to identify QTL for leg weakness-related traits, including leg and gait scores, and weight and length of the biceps brachii muscle in the White Duroc × Erhualian resource population.

MATERIALS AND METHODS

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

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Animals

An F₂ resource population was developed by crossing 2 White Duroc founder boars and 17 Erhualian founder sows as described in Ren et al. (2006). Briefly, 9 F₁ boars and 59 F₁ sows were randomly chosen to produce 1,912 F₂ animals in 6 batches. All piglets were weaned at 46 d and then moved into a nursery. Males were castrated at 90 d. Piglets were transferred from the nursery to the provincial performance test station at 120 d (Jiaoqiao, Nanchang, P. R. China). During the testing period (from 120 to 240 d), 10 to 13 animals per pen were housed in 24-m² half-opened pens with solid floors and had ad libitum access to fresh water and a consistent feed containing 3,100 kJ of DE, 16% CP, and 0.78% lysine. All diets were fortified with vitamins and minerals for approximate age of pig. After the fattening period, a total of 1,484 F₂ animals at 240 ± 3 d were slaughtered in a commercial slaughter facility following Chinese industry standards, and weight and length of the biceps brachii muscle dissected from the right front leg were recorded for 498 F₂ animals.

Phenotypic Measurements

A total of 1,484 F₂ animals were evaluated for leg and gait scores in a range of 1 (very poor) to 5 (very good) by a fixed person. The criteria for determining leg and gait scores are given in Figure 1, and the number of animals recorded for each trait is listed in Table 1. Briefly, leg scores were determined according to strength of the leg, damage, and angles of the joints when pigs were walking on a solid concrete pad at 76 ± 13 d and 213 ± 12 d. Videos were taken for F₂ animals at 153 ± 11 d and 223 ± 22 d, from which gait scores were recorded on the basis of walking speed, ease and smoothness of leg movement, and steadiness of the body, especially the hindquarters.

Genotyping and Linkage Map

The entire White Duroc × Erhualian resource population was genotyped for 183 microsatellite markers covering the pig genome as described in Guo et al. (2009), and a linkage map was constructed with CRI-MAP version 2.4 (Green et al., 1994). The number of markers on each chromosome varied from 5 on SSC 18 to 24 on SSC13 with a total length of 2,344.7 cM and an average interval of 13.40 cM.

Statistics

Descriptive statistics of the measured traits were calculated with the MEANS procedure (SAS Inst. Inc., Cary, NC). The differences of leg weakness-related traits between sexes were determined with the TTEST procedure of SAS. The simple phenotypic correlation coefficients between weight and length of the biceps brachii muscle and leg and gait scores were calculated by the CORR procedure of SAS.

The fixed effects and covariates included in QTL models were determined by the GLM procedure of SAS. Sex and batch were included as fixed effects in all QTL models, and carcass weight was used as a covariate in the models for weight and length of the biceps brachii muscle. The QTL analysis was performed with QTL Express at <http://qtl.cap.ed.ac.uk/> (Seaton et al., 2002). The least squares regression method was applied in QTL Express with the assumption that the QTL are fixed for alternative alleles in the 2 founder breeds (Haley et al., 1994). The QTL additive effect was defined as one-half the phenotypic difference between homozygous pigs for the QTL alleles originating from Erhualian and White Duroc. The dominant effect was estimated as the deviation of heterozygous pigs from the mean of the homozygous pigs. Positive values of the additive effect indicate that Erhualian alleles are associated with greater values of the trait and vice versa. The Erhualian allele is dominant over the White Duroc allele when both dominance and additive effects are positive or negative.

Threshold values for suggestive, 5%, and 1% genome-wide significance levels were obtained by a permutation approach with 1,000-iterations (Churchill and Doerge, 1994). The average 5% chromosome-wide significance level was treated as the suggestive significance level. The 95% confidence interval of each QTL was estimated by a bootstrap approach with 2,000 resamplings (Visscher et al., 1996). The percentage of phenotypic variance explained by each QTL was calculated according to the following formula:

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

where $Var\%$ was the percentage of phenotypic variance explained by the QTL; MS_{full} , $MS_{reduce1}$, and MS_{reduce} were the residual mean squares of the models with all QTL, with the rest of the QTL except for a given one, and with no QTL, respectively. Comparing the model with different QTL effects between sexes with the model with equal QTL effects between sexes gave a test for the interaction between the QTL effect and sex (Knott et al., 1998). A significant test indicated that the QTL interacted with sex.

RESULTS AND DISCUSSION

Descriptive Statistics of Phenotypic Traits

The descriptive statistics of leg weakness-related traits are given in Table 1. From 76 to 213 d, front leg scores and rear leg scores dropped significantly by 0.206 ± 0.025 ($P < 0.0001$) and 0.279 ± 0.022 ($P < 0.0001$), respectively. However, no significant difference was observed in gait scores at 153 and 223 d. The reason for this could be that the BW gain from 76 to 213 d is











Attribute	Score				
	1	2	3	4	5
Leg score					
Front leg structure					
Back leg structure					
Strength	very weak	weak	moderate	strong	very strong
Damage	serious	slight	none	none	none
Gait score					
Strides	very small	small	average	large	very large
Even	very uneven	uneven	average	even	very even
Strength	very weak	weak	average	strong	very strong
Speed	very slow	slow	average	fast	very fast
Smooth	very unsmooth	unsmooth	average	smooth	very smooth
Stability of hindquarters	excessive twisting	twisting	average	stable	very stable

Figure 1. Criteria for leg and gait scores (1 = very poor, 5 = very good). Figures were modified from *Pocket Guide for the Evaluation of Structural, Feet, Leg, and Reproductive Soundness in Replacement Gilts* (Stalder et al., 2005).

much more than that during the period from 153 to 223 d (data not shown).

The difference of leg weakness-related traits between sexes are listed in Table 2. No difference was observed in front leg scores at 76 and 213 d between castrated males and intact females. At 213 d, castrated males had decreased values of rear leg scores compared with intact females ($P < 0.05$). Except for values of front legs at 153 d, gait scores were less ($P < 0.01$) in castrated

males than in intact females. The biceps brachii muscle was shorter ($P < 0.05$) in castrated males than in intact females.

It has been reported that weight and length of the biceps brachii muscle were significantly greater in a leg weakness line than in normal and leg soundness lines (Draper et al., 1992). In this study, the gait score of front legs at 223 d showed a negative correlation with the weight ($r = -0.23$, $P < 0.0001$) and length ($r =$

Table 1. Descriptive statistics of leg scores, gait scores, and length and weight of the biceps brachii muscle

Trait ¹	n	Mean	SD	Minimum	Maximum
Front leg score at 76 d	546	4.3	0.3	3.0	4.5
Rear leg score at 76 d	546	4.3	0.3	3.0	4.5
Front leg score at 213 d	1,484	3.9	0.6	2.0	5.0
Rear leg score at 213 d	1,484	3.8	0.6	1.0	5.0
Gait score of front legs at 153 d	543	3.5	0.6	2.0	5.0
Gait score of rear legs at 153 d	543	3.4	0.6	2.0	4.5
Gait score of front legs at 223 d	1,082	3.5	0.6	2.0	4.5
Gait score of rear legs at 223 d	1,082	3.5	0.5	2.0	4.5
Biceps brachii muscle length, cm	498	13.6	1.1	10.7	18.3
Biceps brachii muscle weight, g	498	62.1	12.2	31.9	115.6

¹Leg and gait were scored from 1 (very poor) to 5 (very good).

-0.24, $P < 0.0001$) of the biceps brachii muscle, which was in agreement with the previous report (Draper et al., 1992). However, the front leg score at 213 d had a low and positive correlation with weight ($r = 0.10$, $P < 0.05$) and length ($r = 0.15$, $P < 0.001$) of the biceps brachii muscle. One possible reason is that legs with longer or heavier biceps brachii muscle look stronger, resulting in greater leg scores.

QTL Detection

Details of the QTL detected in this study are given in Table 3. The F -statistic curves indicating significant QTL on SSC 4 and 7 are depicted in Figure 2, and the others are shown in Supplementary Figure 1 (available online at <http://jas.fass.org/content/vol87/issue5/>). In general, a total of 42 QTL were mapped to 14 SSC, including 16 at the 1% genome-wide significance level and 6 at the 5% genome-wide significance level. Thirty-eight of the 42 QTL showed significant additive effects and 14 had significant dominance effects. At least 2 QTL were detected for each trait except for leg score at 76 d, for which no QTL was identified. Eighteen QTL were detected for weight and length of the biceps brachii muscle. To our knowledge, this was the first report about QTL for weight and length of the

biceps brachii muscle in pigs. Two chromosome regions showed multiple associations with both leg weakness and growth of the biceps brachii muscle. One is the *SWR2179* to *SW512* interval on SSC4 (Figure 2a), and the other is in a 6-cM interval flanked by *SW1856* and *S0102* on SSC7 (Figure 2b).

Only one previous study reported QTL for leg and gait scores in a Large White \times Meishan intercross (Lee et al., 2003), and some of the QTL detected were consistent with the results reported here. On SSC2, a QTL for rear leg score at 213 d was identified in a region that was previously identified as a QTL for rear leg score at 85 ± 5 kg. On SSC4, we detected a QTL for gait scores at 223 d close to a previously reported QTL for gait score at 85 ± 5 kg. Moreover, both Lee et al. (2003) and this study mapped a QTL for rear leg score in the middle of SSC7, a QTL for front leg score in the middle of SSC13, and a QTL for rear leg score at the proximal end of SSC16. It should be noted that there are some discrepancies between the 2 studies. On SSC1, we mapped 2 QTL for front leg score at 213 d at 72 and 153 cM, respectively. Lee et al. (2003) detected a QTL for front leg score at a different position (94 cM) on this chromosome. Two suggestive QTL for rear leg score, 1 each on SSC1 and SSC14, and 1 suggestive QTL for front leg score have been found on SSC14. However,

Table 2. Differences of leg scores, gait scores, and length and weight of the biceps brachii muscle between males and females

Trait ¹	Male		Female		Male-female, mean \pm SE
	n	Mean \pm SE	n	Mean \pm SE	
FLS76	267	4.27 \pm 0.02	279	4.27 \pm 0.02	0.00 \pm 0.03
RLS76	267	4.32 \pm 0.02	279	4.35 \pm 0.02	-0.03 \pm 0.02
FLS213	783	3.89 \pm 0.02	701	3.86 \pm 0.02	0.03 \pm 0.03
RLS213	783	3.77 \pm 0.02	701	3.83 \pm 0.02	-0.06 \pm 0.03*
FGS153	265	3.47 \pm 0.03	278	3.57 \pm 0.04	-0.01 \pm 0.05
RGS153	265	3.32 \pm 0.04	278	3.54 \pm 0.03	-0.22 \pm 0.05**
FGS223	572	3.41 \pm 0.02	510	3.63 \pm 0.03	-0.22 \pm 0.04**
RGS223	572	3.37 \pm 0.02	510	3.54 \pm 0.02	-0.17 \pm 0.03**
BBL	161	13.42 \pm 0.09	337	13.63 \pm 0.06	-0.21 \pm 0.10*
BBW	161	61.34 \pm 1.01	337	62.42 \pm 0.65	-1.08 \pm 1.17

¹FLS76 = front leg score at 76 d; RLS76 = rear leg score at 76 d; FLS213 = front leg score at 213 d; RLS213 = rear leg score at 213 d; FGS153 = gait score of front legs at 153 d; RGS153 = gait score of rear legs at 153 d; FGS223 = gait score of front legs at 223 d; RGS223 = gait score of rear legs at 223 d; BBL = length of the biceps brachii muscle; BBW = weight of the biceps brachii muscle. Leg and gait were scored from 1 (very poor) to 5 (very good).

* $P < 0.05$; ** $P < 0.01$.

these QTL were not confirmed in this study. Several genome-wide significant QTL, such as the QTL for rear leg score at 213 d on SSC4 and gait score of front legs at 223 d on SSC7, were identified in this study for the first time. These discrepancies could be due to the fact that different founder breeds were used in the 2 resource populations.

A 5% genome-wide significant QTL for weight of the biceps brachii muscle was found at 20 cM on SSC2, and its 95% confidence interval (0 to 66 cM) covered the chromosomal region containing *IGF2*, which is a paternally expressed gene and affects muscle growth in the

pig (Van Laere et al., 2003). We performed the QTL analysis with the imprinting model and found that the QTL for weight of the biceps brachii muscle had a paternally expressed effect (data not shown) and was mapped at a position proximal to *IGF2*. We propose that *IGF2* could be a candidate gene underlying the QTL for weight of the biceps brachii muscle on SSC2.

A prominent QTL on SSC4 showed pleiotropic effects on weight and length of the biceps brachii muscle, gait score at 223 d, and rear leg score at 213 d. This chromosomal region was also significantly associated with limb bone lengths in the White Duroc × Erhual-

Table 3. Details of QTL for leg weakness traits in the White Duroc × Erhualian intercross

Trait ¹	SSC	Pos, ² cM	<i>F</i> -value ³	ADD ± SE ⁴	DOM ± SE ⁴	CI ₉₅ ⁵	Var% ⁶
BBL	1	112	7.48*	-0.13 ± 0.05*	0.21 ± 0.07**	13 to 145	1.87
BBW	1	24	12.25***	2.37 ± 0.49***	0.73 ± 0.72	14 to 136	3.15
FGS153	1	41	5.91*	-0.10 ± 0.03**	-0.08 ± 0.05	0 to 159	1.63
FLS213	1	72	9.68**	-0.10 ± 0.02***	0.03 ± 0.03	65 to 124	1.12
FLS213	1	153	7.42*	-0.08 ± 0.02***	0.04 ± 0.04	41 to 159	0.83
RGS153	1	0	6.54*	-0.11 ± 0.03**	0.08 ± 0.05	0 to 134	1.93
BBL	2	56	9.05**	-0.22 ± 0.05***	0.02 ± 0.08	33 to 82	2.33
BBW	2	20	9.12**	-2.24 ± 0.52***	0.13 ± 0.85	0 to 66	2.27
BBW	2	110	7.84*	1.35 ± 0.50**	-2.26 ± 0.79**	40 to 129	1.92
FLS213	2	89	6.64*	-0.08 ± 0.02***	0.03 ± 0.04	26 to 116	0.73
RLS213	2	56	23.04***	-0.13 ± 0.02***	0.07 ± 0.03*	43 to 86	2.72
BBL	3	101	10.78**	0.24 ± 0.05***	0.05 ± 0.08	90 to 128	2.82
FLS213	3	109	12.64***	0.10 ± 0.02***	0.08 ± 0.03*	94 to 124	1.50
BBL	4	61	11.55***	-0.23 ± 0.05***	-0.09 ± 0.07	51 to 84	3.05
BBW	4	72	25.16***	-3.52 ± 0.50***	-1.34 ± 0.76	58 to 77	6.77
FGS223	4	69	11.22***	0.10 ± 0.02***	0.01 ± 0.03	33 to 79	1.48
RGS223	4	55	7.47*	0.07 ± 0.02**	0.07 ± 0.03*	18 to 110	1.06
RLS213	4	60	16.55***	-0.11 ± 0.02***	-0.03 ± 0.03	29 to 80	1.93
BBL	5	114	7.83*	-0.08 ± 0.05	0.24 ± 0.07***	2 to 114	1.97
RLS213	5	72	8.32*	-0.08 ± 0.02***	0.04 ± 0.03	19 to 114	0.91
BBL	7	58	58.73***	0.47 ± 0.05***	0.26 ± 0.07***	58 to 60	16.70
BBW	7	60	30.77***	3.57 ± 0.46***	0.56 ± 0.66	55 to 62	8.34
FGS153	7	59	28.28***	-0.26 ± 0.03***	0.03 ± 0.05	55 to 62	9.13
FGS223	7	58	98.27***	-0.31 ± 0.02***	0.01 ± 0.03	57 to 61	14.03
FLS213	7	57	8.31*	0.05 ± 0.02*	0.09 ± 0.03**	32 to 93	0.92
RGS153	7	63	15.85***	-0.19 ± 0.03***	0.07 ± 0.08	40 to 101	5.14
RGS223	7	62	25.35***	-0.14 ± 0.02***	0.01 ± 0.03	45 to 69	3.98
RLS213	7	57	11.28***	0.08 ± 0.02***	0.04 ± 0.03	55 to 113	1.25
BBL	8	58	10.26**	-0.17 ± 0.05***	0.18 ± 0.07**	0 to 82	2.67
BBW	8	38	12.34***	-2.30 ± 0.49***	-1.16 ± 0.72	21 to 83	3.18
FGS153	8	67	6.77*	0.12 ± 0.03***	0.05 ± 0.05	28 to 145	1.94
FGS223	8	68	6.61*	0.08 ± 0.02***	0.03 ± 0.01	16 to 89	0.79
RGS153	9	2	5.85*	0.04 ± 0.03	-0.16 ± 0.05**	0 to 144	1.67
BBW	10	56	7.05*	-1.93 ± 0.53***	-0.80 ± 0.78	0 to 112	1.69
FGS223	10	35	5.58*	0.03 ± 0.02	-0.11 ± 0.03**	18 to 121	0.66
FLS213	13	76	5.73*	-0.06 ± 0.02**	0.04 ± 0.03	12 to 120	0.61
BBW	15	97	5.83*	-1.64 ± 0.48***	0.47 ± 0.79	0 to 118	1.35
RLS213	16	27	7.2*	-0.02 ± 0.02	0.13 ± 0.04***	17 to 95	0.76
BBL	18	7	7.51*	-0.10 ± 0.05*	-0.24 ± 0.07**	1 to 55	1.88
BBL	X	62	9.04**	-0.23 ± 0.07***	-0.01 ± 0.08	43 to 76	2.32
BBW	X	57	20.64***	-4.61 ± 0.72***	-2.16 ± 0.73**	53 to 60	5.50
RLS213	X	43	7.73*	-0.10 ± 0.03***	-0.05 ± 0.03	16 to 61	0.83

¹FLS213 = front leg score at 213 d; RLS213 = rear leg score at 213 d; FGS153 = gait score of front legs at 153 d; RGS153 = gait score of rear legs at 153 d; FGS223 = gait score of front legs at 223 d; RGS223 = gait score of rear legs at 223 d; BBL = length of biceps brachii muscle; BBW = weight of biceps brachii muscle.

²Position along each chromosome.

³Significance levels: *suggestive; **5% genome-wide; ***1% genome-wide.

⁴* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

⁵95% confidence interval.

⁶Percentage of phenotype variance explained by the QTL.

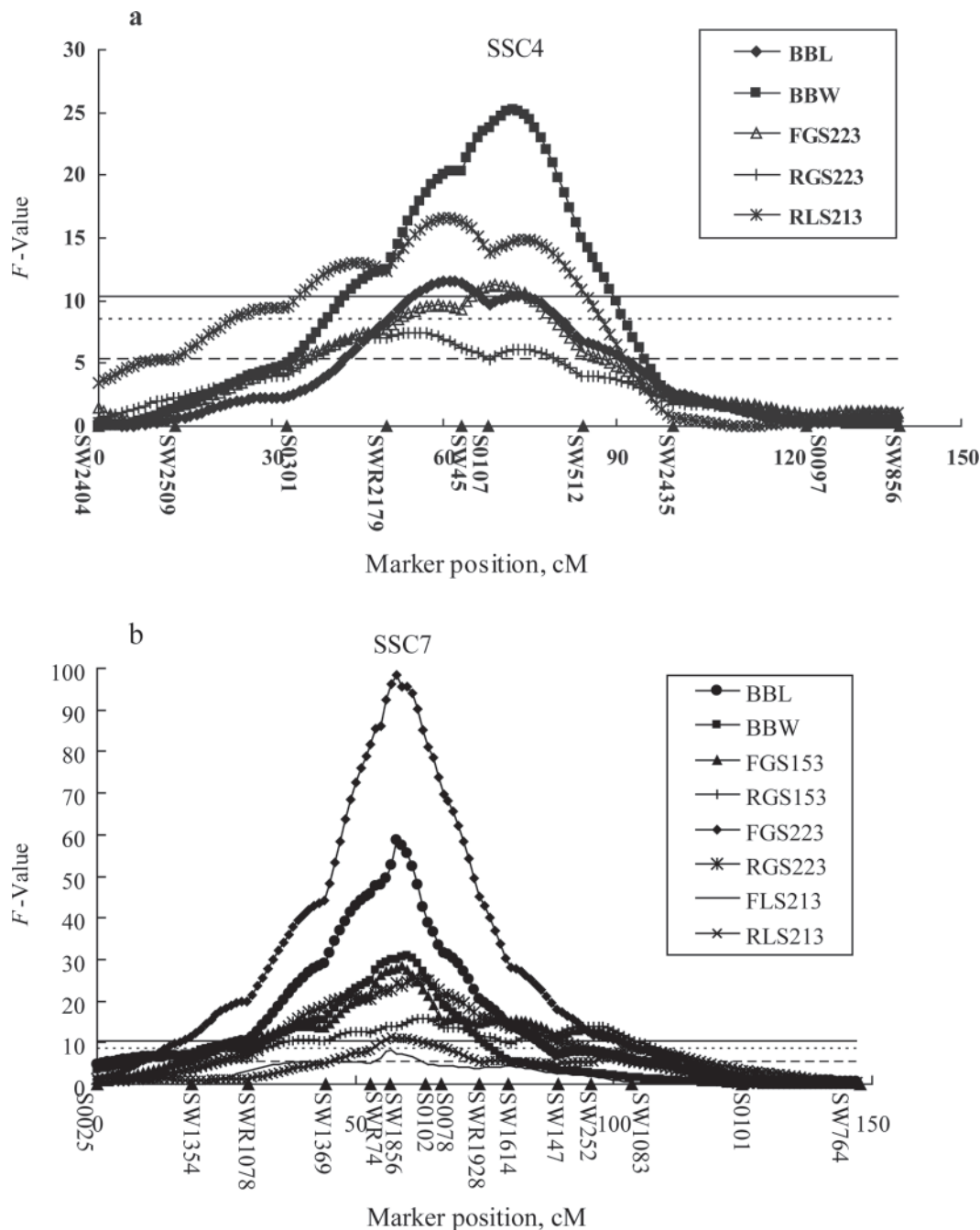


Figure 2. Evidence of significant QTL for leg scores, gait scores, and weight and length of biceps brachii muscle on pig chromosomes 4 (a) and 7 (b). Marker positions along each chromosome were indicated in cM on the x-axis, and the y-axis showed *F*-values. The suggestive, 5% genome-wide, and 1% genome-wide significance levels were indicated by the horizontal dashed, dotted, and solid lines, respectively. FLS213 = front leg score at 213 d; RLS213, rear leg score at 213 d; FGS153 = gait score of front legs at 153 d; RGS153 = gait score of rear legs at 153 d; FGS223 = gait score of front legs at 223 d; RGS223 = gait score of rear legs at 223 d; BBL = length of the biceps brachii muscle; BBW = biceps brachii muscle weight.

ian intercross (Mao et al., 2008). The co-localization of the QTL for leg weakness-related traits and limb bone length was also observed on SSC7, on which the QTL for front gait score at 223 d was the most significant QTL detected in this study. These observations implied that the corresponding causative gene(s) on SSC4 and SSC7 could affect growth of the limb bones, biceps brachii muscle, and soundness of legs.

In the present study, no QTL were found for leg scores at 76 d. A possible reason for this could be that leg

scores at 76 d were not divergent in the experimental population. It was observed that the SD of leg scores at 76 d was about one-half that at 213 d (Table 1).

Different QTL for leg and gait scores at different growth age stages were observed in this study, reflecting distinct genes engaged in the development of the leg structure. These QTL need further studies to fine map them using additional markers and populations, and closely linked genetic markers may be identified in the QTL regions.

Table 4. Interactions between QTL for leg weakness traits and sex

Trait ¹	SSC ²	Position, cM	F-value ²	Sex	ADD ± SE ³	DOM ± SE ⁴
FLS213	3	109	7.84***	Male	0.04 ± 0.03	0.09 ± 0.05
				Female	0.15 ± 0.03***	0.08 ± 0.05
FGS223	4	69	7.23***	Male	0.05 ± 0.03	0.05 ± 0.01
				Female	0.16 ± 0.03***	0.01 ± 0.05
BBL	18	7	6.46*	Male	-0.01 ± 0.06	-0.16 ± 0.10
				Female	-0.31 ± 0.09***	-0.43 ± 0.13***

¹FLS213 = front leg score at 213 d; FGS223 = gait score of front legs at 223 d; BBL = length of biceps brachii muscle.

²Significance levels: *suggestive; **5% genome-wise; ***1% genome-wise.

³Additive effects and their SE (*** $P < 0.001$).

⁴Dominance effects and their SE (*** $P < 0.001$).

Interactions Between QTL and Sex

As shown in Table 4, only 3 QTL had an interaction with sex. Two QTL each for front leg score at 213 d on SSC3 and gait score of front legs at 223 d on SSC4 showed additive effects only in females. The QTL for length of the biceps brachii muscle on SSC18 had no effect in castrated males but had additive and dominance effects in females.

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