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QTL analysis of back fat thickness and carcass pH in an F_2 intercross between Landrace and Korean native pigs

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Abstract In this study, we conducted a genome-wide linkage analysis to identify the quantitative trait loci (QTL) that influence back fat thickness and carcass pH in an F_2 intercross between Landrace and Korean native pigs. Eight phenotypes related with back fat thickness and carcass pH were measured in more than 960 F_2 progeny. All experimental animals were subjected to genotypic analysis using 173 microsatellite markers located throughout the pig genome. The GridQTL program, based on the least squares regression model, was used to perform the QTL analysis. We identified 22 genome-wide significant QTL in 9 chromosomal regions (SSC1, 2, 5, 6, 7, 8, 12, 15, and 16) and 29 suggestive QTL in 16 chromosomal regions (SSC2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 14, 15, 16, 17, 18, and X). On SSC5, we detected a QTL affecting back fat thickness that accounted for 4.8 % of the phenotypic variance, which was the highest test statistic (F-ratio = 50.3 under the additive model, nominal P value = 2.5×10^{-12}) observed in this study. Additionally, we showed that there were significant QTL on SSC16 affecting carcass pH traits. In conclusion, the QTL identified in this study together with associated positional candidate genes could play an important role in determining the genetic structure underlying the variation of back fat thickness and carcass pH in pigs.

Keywords Back fat thickness · Carcass pH · Genome-wide linkage analysis · Quantitative trait locus · Landrace and Korean native pigs

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Introduction

Back fat thickness and carcass pH are important economic traits in the pork industry. Back fat thickness is one of the major determinants of the carcass lean meat yield. Decreased back fat thickness tends to be more profitable due to an increased carcass lean meat yield [1]. Carcass pH is a commonly used trait for evaluating pork quality as it is correlated with meat quality traits, such as meat color, water-holding capacity, drip loss, and sensory traits (e.g., juiciness and tenderness). Low pH affects the denaturation of muscle protein and the water-holding capacity. Hence, pork with lower pH values tends to be less desirable. Although a lot of numbers of studies that identified QTLs affecting back fat thickness and pH traits have been performed, the causal mutations for these traits are still unknown [2].

There are two types of Korean native pigs: the native pig raised on the Korean Peninsula and the Jeju native pig raised on Jeju Island. Due to being raised on an island that has been isolated for more than 1,000 years, the Jeju native pig (hereafter, the Jeju native pig is referred to as KNP) has unique genetic properties that are different from those of the pigs raised on the Korea Peninsula [3]. The coat color of KNP is black, and its feed efficiency and growth rate are low, as with most native breeds. However, it has excellent meat quality characteristics, such as solid fat structure, white colored fat, red meat color [4]. Nevertheless, studies regarding what genetic factors affect back fat thickness and meat quality traits, such as carcass pH, of KNP have not yet been performed in detail. Additionally, as in most cases of quantitative traits, back fat thickness and carcass pH are determined by a number of genetic factors; thus, it is difficult to explain phenotypic variance based only on a few known genes.

In this study, using an F_2 intercross between KNP and Landrace pigs, we identified QTL that influence back fat thickness and carcass pH of the *longissimus dorsi* muscle (LDM).

Materials and methods

Animals and genotypic analysis

A three-generation resource population was generated and managed as described by Cho et al. [5]. Briefly, 19 purebred KNP (8 males and 11 females) were crossed with 17 purebred Landrace (8 males and 9 females). From these crosses, 91 F_1 progeny and 1,106 F_2 progeny (568 males and 538 females) from 79 full-sib families were produced. None of the F_2 males were castrated.

A total of 173 informative microsatellite markers, covering the autosomes and X chromosome, were PCR-amplified in 1,233 pigs as described by Cho et al. [5]. Map order and genetic distance were determined using the build option in the CRIMAP software version 2.4 [6]. The total map length was 2348.8 centimorgans (cM). The sex-average autosomal linkage map was used for further QTL analysis, except for the analysis of the X chromosome.

Phenotypic analysis

F_2 pigs were slaughtered in the same commercial slaughterhouse. Prior to slaughter, pigs were fasted for 24 h but with free access to water. These pigs were slaughtered based on age, i.e., the average age at the time of slaughter was 199 days. To measure muscle pH traits, the measurements were conducted during the first 24 h of refrigeration process; sampling of the LDM was performed 1 h (1HPH), 3 h (3HPH), 6 h (6HPH) and 24 h (24HPH) postmortem.

We measured back fat thickness between the 4 and 5th ribs (45RIBBFT), the 11 and 12th ribs (1112RIBBFT), and the last rib and first lumbar vertebrae (THOLUMBFT). In addition, back fat thickness (BFT) was measured according to the rules of the Korea Institute for Animal Products Quality Evaluation (KAPE): BFT = [(back fat thickness between the 11 and 12th thoracic vertebrae) + (back fat thickness between the last thoracic and first lumbar vertebrae)]/2. However, the BFT value was measured within a short time during the process of meat product quality evaluation. For this reason, the BFT value has less accuracy compared to other three back fat thickness values. Measurements of the back fat thickness traits were taken on the left half of the carcass of each animal. The thickness of fat was measured in millimeters.

Statistical and QTL analyses

Before QTL analysis, we obtained descriptive statistics and verified the normal distribution of the phenotypic data. When putative outliers were observed, we omitted them based on the ascertainment of normality using the MINITAB program (Minitab Inc., USA). When necessary, the phenotypic values were transformed by natural logarithm. Pearson correlation coefficients and the significance of each pairwise comparison of traits were also calculated using the MINITAB program.

QTL analysis for each trait was performed using the web-based program GridQTL (http://www.gridqtl.org.uk). The interval mapping model based on the least squares regression method [7] was used for QTL analysis, which included the cofactors of sex, parity, and carcass weight, along with additive and dominance regression variables for the putative QTL. Identification of QTL was based on an *F*-ratio test statistic that was calculated from sums of squares explained by the additive and dominance regression coefficients for the QTL. The *F*-ratios were calculated at 1 cM intervals through the genome. At the QTL peak, we extracted the additive and dominance coefficients of each of the F_2 progeny to evaluate the significance of each additive and dominance effect using the MINITAB program. From this, we selected the final model for QTL analysis. Both the additive and the dominance regression coefficients were included in the QTL model if the effect of the dominance regression coefficient was significant, regardless of the significance level of the additive coefficient. Only the additive regression coefficient was included in the QTL model if the effect of the dominance regression coefficient was not significant. To perform QTL analysis with the X-specific linkage group, the female specific linkage map was used. Genome-wide empirical significance thresholds

of the test statistic (i.e., *F*-ratio) were obtained by 1,000 permutations of data [8]. Genome-wide thresholds for highly significant ($\alpha = 0.01$) and significant linkage ($\alpha = 0.05$) were employed. Suggestive linkage was employed using a 5 % chromosome-wide threshold. The 1.5-LOD (logarithm of odds) drop method was used to estimate support intervals for identified QTL at the suggestive and significant levels of linkage [9].

Results and discussion

Eight traits related to back fat thickness and carcass pH were used to perform the genome-wide linkage analysis to map the QTL. Table 1 shows the descriptive statistics with respect to the measured traits. We identified 22 significant QTL and 29 suggestive QTL (Table 2). In all of the identified QTL affecting back fat thickness, the KNP allele was always associated with higher back fat thickness, whereas the allele from the Landrace was associated with lower phenotypic values. These results are consistent with the observed reduction of back fat thickness in Western breeds through selective breeding. As for carcass pH, Park et al. [4] reported that the pH value of the KNP was higher than that of the Landrace. At the QTL on SSC 2, 6, 10, 11, 14, 16, and 17, the effect of the KNP allele caused an increase in carcass pH. However, the KNP allele also resulted in a decrease in carcass pH at the QTL on SSC3, 5, 7, 18, and the X chromosome. A statistical analysis of the phenotypic data from the F_2 population revealed that a number of the traits were significantly correlated (Supplementary Table 1). For example, 1112RIBBFT was strongly correlated with THOLUMBFT ($r = 0.90$). Positive and significant correlations were also observed among pH traits ($r = 0.65$ or higher), indicating the presence of pleiotropic loci, which may influence multiple phenotypes (e.g., QTL on SSC16 affecting 1HPH, 6HPH and 24HPH).

Back fat thickness

Back fat thickness serves as one of the most important criteria for grading carcass quality. We found significant and suggestive QTL affecting back fat thickness-related traits (BFT, 45RIBBFT, 1112RIBBFT, and THOLUMBFT) in eleven genomic regions (SSC1, 2, 4, 5, 6, 7, 8, 12, 14, 15 and X).

On SSC1, we detected several significant QTL for the four back fat thickness-related traits (100–109 cM). These QTL explained up to 2.7 % of the phenotypic variance. Furthermore, these QTL regions overlapped with the QTL regions reported in previous studies [10–13]. In the QTL region for 45RIBBFT on SSC1 (109 cM), there is a gene encoding the melanocortin receptor type 4 (MC4R), which is known to be closely related to fatness and growth [14]. In addition, studies on the association of the p.Asp298Asn mutation in the *MC4R* gene with fatness and growth rate were reported for various populations [15, 16]. However, there are also contradictory reports indicating the lack of an association between this mutation and fatness traits [17, 18].

On SSC2, two highly significant QTL for BFT (78 cM) and 45RIBBFT (26 cM) were detected, and they explained up to 1.9 % of the phenotypic variance. Milan et al. [19] reported a QTL affecting back fat thickness between the 3rd and 4th ribs on SSC2 in an F_2 intercross between Meishan and Large White pigs. This QTL overlapped with our QTL region for 45RIBBFT. To our knowledge, the QTL on SSC2 for BFT (78 cM), 1112RIBBFT (81 cM), and THOLUMBFT (82 cM) are novel. The *lipid storage droplet protein 5* gene (*LSDP5*; also known as *perilipin 5*, *PLIN5*) is located in this novel QTL region. *PLIN5* is member of the perilipin family; this family of proteins coat intracellular lipid storage droplets and protect them from lipolytic degradation [20]. Wang et al. [21] reported that *PLIN5* has a negative regulatory role in lipid droplet

Table 1 Number, mean, SD, and range of back fat thickness and carcass pH of the KNP × Landrace intercross population

Traits	Abbr.	*N*	Mean	SD	Min	Max
Backfat thickness (KAPE, mm)	BFT	1,014	22.93	6.897	6	48
Between 4 and 5th thoracic (mm)	45RIBBFT	1,046	34.02	7.623	7	60
Between 11 and 12th Thoracic (mm)	1112RIBBFT	1,046	27.99	7.579	5	55
Between thoracic and lumbar (mm)	THOLUMBFT	1,046	26.15	7.154	5	49
pH 1 h post mortem[a]	1HPH	964	1.77	0.047	1.67	1.93
pH 3 h post mortem[a]	3HPH	965	1.77	0.048	1.65	1.94
pH 6 h post mortem	6HPH	965	5.89	0.318	5.24	6.97
pH 24 h post mortem[a]	24HPH	965	1.74	0.048	1.65	1.93

For the number of animals (*N*)

[a] Transformed phenotypic data values using natural logarithm

Table 2 Summary of QTL for back fat thickness and carcass pH

SSC	Traits	Position (cM)	*F*-ratio[a]	Mode of inheritance[b]	95 % SI[c]		Var %[d]	A ± SE[e]	D ± SE[f]
					cM	Marker			
1	BFT	100	14.9*	A	46–118	*SW64–SW974*	1.5	0.923 ± 0.239	
	45RIBBFT	109	14.3**	AD	83–126	*SW2035–SW1957*	2.7	1.387 ± 0.283	−1.013 ± 0.453
	1112RIBBFT	101	23.1**	A	83–114	*SW2035–SW803*	2.2	1.247 ± 0.259	
	THOLUMBFT	100	17.4**	A	41–112	*SW64–SW803*	1.7	1.041 ± 0.249	
2	BFT	78	19.7**	A	68–87	*SW776–S0370*	1.9	1.163 ± 0.262	
	45RIBBFT	26	18.6**	A	0–60	*SW2623–SW776*	1.8	1.275 ± 0.296	
	1112RIBBFT	81	11.3†	A	71–105	*SW776–SW1879*	1.1	0.923 ± 0.274	
	THOLUMBFT	82	10.1†	A	69–105	*SW776–SW1879*	1.0	0.852 ± 0.269	
	24HPH	8	7.8†	A	0–82	*SW2623–S0370*	0.8	0.007 ± 0.002	
3	3HPH	113	6.9†	AD	98–131	*SW2047–SW1327*	1.4	−0.003 ± 0.002	0.012 ± 0.003
4	BFT	86	10.0†	A	37–126	*SWR73–MP77*	1.0	0.769 ± 0.243	
	THOLUMBFT	48	11.1†	A	28–104	*S0301–MP77*	1.1	0.864 ± 0.260	
5	BFT	60	50.3**	A	51–81	*SW1482–SW963*	4.8	1.842 ± 0.260	
	45RIBBFT	55	16.9**	A	30–78	*SW1482–SW963*	1.6	1.160 ± 0.282	
	1112RIBBFT	58	15.7**	A	37–84	*SW1482–SW963*	1.5	1.131 ± 0.286	
	THOLUMBFT	60	20.2**	AD	49–75	*SW1482–SW963*	3.8	1.643 ± 0.272	0.884 ± 0.422
	3HPH	111	7.5†	A	74–150	*SW2003–SW967*	0.8	−0.006 ± 0.002	
6	45RIBBFT	41	22.8**	A	27–48	*SW2406–APR8*	2.1	1.290 ± 0.271	
	1112RIBBFT	41	12.8*	A	21–61	*SW2406–SW492*	1.2	0.950 ± 0.265	
	THOLUMBFT	40	13.8*	A	19–53	*S0035–APR8*	1.3	0.957 ± 0.258	
	3HPH	86	6.9†	AD	75–96	*SW492–S0059*	1.4	0.005 ± 0.002	0.010 ± 0.003
7	BFT	64	12.5*	A	22–112	*SW1354–SW2108*	1.2	0.886 ± 0.251	
	1112RIBBFT	62	17.8**	A	31–78	*S0064–SW147*	1.7	0.63 ± 0.278	
	THOLUMBFT	63	11.1†	A	16–112	*SW1873–SW2108*	1.1	1.139 ± 0.270	
	6HPH	92	8.1†	A	66–146	*S0102–SW764*	0.8	−0.046 ± 0.016	
8	BFT	41	10.3**	AD	6–55	*SW2410–SW933*	2.0	1.092 ± 0.286	0.970 ± 0.476
	45RIBBFT	32	12.6†	A	0–57	*SW2410–SW933*	1.2	1.103 ± 0.311	
	1112RIBBFT	47	12.0†	A	1–75	*SW2410–SW444*	1.1	1.136 ± 0.328	
	THOLUMBFT	41	16.6**	A	17–60	*S0353–SW933*	1.8	1.212 ± 0.298	
10	6HPH	96	9.0†	A	63–135	*SW2195–SW2067*	0.9	0.044 ± 0.015	
11	1HPH	49	10.3†	A	12–81	*SW1632–SW1135*	1.1	0.009 ± 0.003	
	3HPH	46	6.2†	A	0–81	*SW1460–SW1135*	0.6	0.007 ± 0.003	
	24HPH	35	12.5†	A	15–61	*SW1632–SW703*	1.3	0.008 ± 0.002	
12	45RIBBFT	106	11.1**	AD	99–115	*S0106–SWR1021*	2.1	0.965 ± 0.265	1.183 ± 0.417
	1112RIBBFT	107	5.8†	AD	97–115	*S0106–SWR1021*	1.1	0.418 ± 0.264	1.240 ± 0.421
	THOLUMBFT	105	7.7†	AD	97–114	*S0106–SWR1021*	1.5	0.302 ± 0.243	1.384 ± 0.377
14	BFT	14	8.3†	A	0–40	*SW857–S0162*	0.8	0.742 ± 0.257	
	45RIBBFT	70	5.6†	AD	60–89	*SW2519–SW2515*	1.1	0.687 ± 0.265	0.844 ± 0.389
	THOLUMBFT	23	10.9†	A	4–53	*SW857–SW2519*	1.0	0.998 ± 0.302	
	6HPH	40	10.8†	A	12–63	*SW857–SW886*	1.1	0.051 ± 0.015	
15	BFT	123	12.6*	A	67–152	*SW1989–SWR2121*	1.2	0.919 ± 0.259	
	45RIBBFT	117	15.3*	A	79–138	*SW1263–S0040*	1.5	1.066 ± 0.273	
	1112RIBBFT	119	12.2†	A	73–140	*SW1263–S0040*	1.2	0.923 ± 0.264	
16	1HPH	67	7.0†	A	38–97	*SW419–S0105*	0.7	0.006 ± 0.002	
	6HPH	67	14.8*	A	54–88	*SW1809–S0105*	1.5	0.056 ± 0.015	
	24HPH	71	14.7*	A	56–91	*SW1809–S0105*	1.5	0.009 ± 0.002	
17	24HPH	0	6.2†	A	0–50	*SWR1004–SW1031*	0.6	0.005 ± 0.002	

Table 2 continued

SSC	Traits	Position (cM)	*F*-ratio[a]	Mode of inheritance[b]	95 % SI[c]		Var %[d]	A ± SE[e]	D ± SE[f]
					cM	Marker			
18	6HPH	17	5.3[†]	AD	0–37	*SWR1004–SW1920*	1.1	−0.040 ± 0.017	0.070 ± 0.031
X	45RIBBFT	67	11.9[†]	A	17–102	*SW949–SJ017*	2.4	1.340 ± 0.389	
	1112RIBBFT	74	9.6[†]	A	1–123	*SW949–SJ017*	1.9	1.276 ± 0.413	
	24HPH	123	12.6[†]	A	78–123	*SW2434–SJ017*	2.7	−0.009 ± 0.003	

[a] Test statistic and level of [†]suggestive and significant ([*] 0.05, [**] 0.01) thresholds

[b] A represents additive effect; AD represents additive and dominance effects

[c] 95 % support intervals estimated by the 1.5-LOD drop method. Flanking markers for the QTL support intervals

[d] Var % is the reduction in residual variance of the F_2 population obtained by inclusion of a QTL at the given position

[e] Additive effect and standard error. A positive value means the Jeju native pig allele has an increase effect on a trait, and a negative value indicates that the Landrace allele has an increase effect on a trait

[f] Dominance effect and standard error

hydrolysis by binding and inhibiting adipose triglyceride lipase activity at the lipid droplet surface under basal conditions. *PLIN5* also plays a critical role in oxidative tissues (e.g., heart and skeletal muscle) by protecting mitochondria from a rapid increase of fatty acid during lipolysis. A previous study reported that the *IGF2* gene on SSC2 was associated with back fat thickness [22]. However, the genetic map of our study does not include the *IGF2* locus. Thus, further studies using the map with the *IGF2* locus are necessary to evaluate the effects of the *IGF2* gene on back fat traits.

On SSC5, we identified highly significant QTL affecting the four BFT-related traits (55–60 cM). The test statistic for BFT was 50.3 (nominal P value $= 2.5 \times 10^{-12}$) with only an additive effect, which was the highest F-ratio observed in this study (Fig. 1a). These QTL explained up to 4.8 % of the phenotypic variance. These QTL regions overlapped with the QTL regions identified by Kim et al. [23] and Guo et al. [24].

On SSC6, significant QTL for 45RIBBFT (41 cM), 1112RIBBFT (41 cM) and THOLUMBFT (40 cM) were identified. These QTL explained up to 2.1 % of phenotypic variance and showed only an additive effect. They also overlapped with the QTL region reported by Fontanesi et al. [25]. The *FTO* obesity-associated gene has been considered a strong positional candidate gene for fatness in this region. *FTO* was reported to have a strong association with BMI and other obesity-related traits in humans [26]. Association of the *FTO* gene with intramuscular fat (IMF) deposition, feed conversion rate, BFT and marbling score have been reported in pigs [12, 25].

On SSC7, we identified significant QTL affecting BFT (64 cM) and 1112RIBBFT (62 cM). These QTL showed only an additive effect and accounted for up to 1.7 % of the phenotypic variance. Our QTL regions overlapped with the

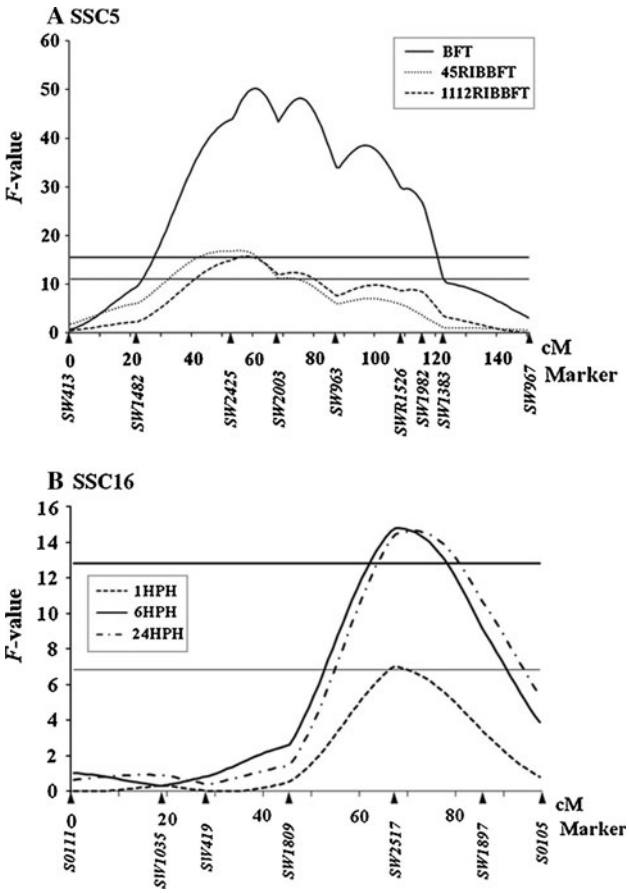

Fig. 1 QTL profiles for backfat thickness and carcass pH traits. The *y-axis* represents the *F*-value testing the hypothesis of a single QTL in a given position on the chromosome. Marker map with genetic distance between microsatellite markers in Kosambi cM is given on the *x-axis*. The *thick horizontal line* indicate the 1 % genome-wise significant threshold and *thin horizontal line* indicate the 5 % genome-wise significant threshold. **a** Test statistic *curves* for the BFT QTL on SSC5 **b** Test statistic *curves* for meat pH QTL on SSC16. Trait abbreviations are given in Table 1

regions identified by Guo et al. [24] and Chen et al. [27]. Interestingly, Chen et al. [27] highlighted *SLC39A7* as a candidate gene in one of these QTL regions. According to that study, the c.205G > A polymorphism of *SLC39A7* was closely linked to *SW1856* in a F_2 population from a Large White and Meishan cross, and it was reported to be significantly associated with fatness.

On SSC8, highly significant QTL for BFT (41 cM) and THOLUMBFT (41 cM) were identified. These QTL explained up to 2.0 % of phenotypic variance. These particular QTL regions overlapped with the regions identified by De Koning et al. [28] and Vidal et al. [29].

On SSC12, we detected a significant QTL affecting 45RIBBFT (106 cM), and this QTL accounted for 2.1 % of the phenotypic variance. This QTL region overlapped with the region reported by Thomsen et al. [10].

Significant additive QTL for BFT (123 cM) and 45RIBBFT (117 cM) were identified on SSC15. These QTL explained up to 1.5 % of the phenotypic variance. These QTL regions also overlapped with the QTL regions identified by Thomsen et al. [10].

Meat pH

The pH of meat can impact meat color, microbial growth, and water-holding capacity (WHC). WHC, which indicates the ability of meat to retain water following physical treatment, is closely associated with meat texture and moisture percentage. We analyzed the QTL for the pH of the LDM at different time points and identified significant and suggestive QTL affecting carcass pH-related traits (1HPH, 3HPH, 6HPH, and 24HPH) in twelve chromosomal regions (SSC2, 3, 5, 6, 7, 10, 11, 14, 16, 17, 18 and X). On SSC16, significant QTL for 6HPH (67 cM) and 24HPH (71 cM) were detected. These QTL accounted for up to 1.5 % of the phenotypic variance. The significant QTL affecting carcass pH found in this study overlapped with the suggestive QTL affecting meat pH identified by Duan et al. [30].

In this study, we performed a genome-wide QTL analysis for back fat thickness and meat quality traits using an F_2 intercross between KNP and Landrace pigs. Many significant QTL regions were identified for back fat thickness, but only one significant QTL was found for pH. These results indicate that the phenotypic differences between the parental lines may not be significant enough for pH-related traits. Another possible explanation for different number of significant QTL for back fat thickness and pH is that there could be different number of genetic factors with large or small effects on the two traits.

The results from this study not only detected a novel chromosomal region (i.e., QTL on SSC2 for BFT, 1112RIBBFT, THOLUMBFT) but also validated previously reported QTL (e.g., QTL on SSC5 for BFT; QTL on SSC16 for 6HPH) that were significantly associated with back fat thickness and carcass pH in pigs. The results presented herein could play an important role in investigating the genetic structure of phenotypic variation of back fat thickness and meat pH.

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