QTL mapping for body shape and conformation measurements on BTA1 in Japanese Black cattle

Aduli Enoch Othniel MALAU-ADULI[1, 4*], Tomomi NIIBAYASHI[2], Takatoshi KOJIMA[2], Kazunaga OSHIMA[2], Yasushi MIZOGUCHI[3] and Masanori KOMATSU[1,]

[1] Department of Animal Breeding and Reproduction, National Institute of Livestock and Grassland Science, Tsukuba, Ibaraki 305-0901, Japan.

[2] Laboratory of Animal Breeding and Reproduction, Department of Livestock and Grassland Science, National Agricultural Research Centre for Western Region, Oda, Shimane 694-0013, Japan.

[3] Shirakawa Institute of Animal Genetics, Nishigo-nura, Fukushima, Japan.

[4] Present address: School of Agricultural Science, University of Tasmania, Private Bag 54 Hobart, Tasmania 7001, Australia.

*Corresponding author: Tel: +61-3-6226-2717

Fax: +61-3-6226-2642

E-mail: Aduli.MalauAduli@utas.edu.au, aduli40@yahoo.co.uk

Running Title: Body conformation QTL in Japanese Black cattle

ABSTRACT

The detection and mapping of segregating QTL influencing withers height, hip height, hip width, body length, chest width, chest depth, shoulder width, lumbar width, thurl width, pin bone width, rump length, cannon circumference, chest girth, abdominal width and abdominal girth at weaning was conducted on chromosomal regions of bovine chromosome one. QTL analysis was performed by genotyping half-sib progeny of five Japanese Black sires using microsatellite DNA markers. Probability coefficients of inheriting allele 1 or 2 from the sire at specific chromosomal locations were computed. The phenotypic data of progeny were regressed on these probability coefficients in a within-common-parent regression analysis using a linear model that included fixed effects of sex, parity and season of birth as well as age as a covariate. F-statistics were calculated every 1cM on a linkage map. Permutation tests of 10,000 iterations were conducted to obtain chromosome-wide significance thresholds. A significant QTL for chest width was detected at 91cM in Family 3. The detection of this QTL boosts the prospects of implementing marker-assisted selection for body conformation traits in Japanese Black beef cattle.

KEYWORDS: Beef cattle, body shape, conformation, Japanese Black, QTL mapping

INTRODUCTION

Body shape and conformation measurements are useful selection traits in beef cattle because of their positive correlation with liveweight changes and growth (Varade and Ali 2001). In dairy cows, body size measurements are very useful in estimating body weight and productivity as demonstrated by the reports of Heinrichs et al. (1992), Enevoldsen and Kristensen (1997), Kertz et al. (1997) and Koenen and Groen (1998). In beef cattle, similar research has been conducted and reported by Gilbert et al. (1993), Vargas et al. (2000) and Magnabosco et al. (2002). Similar information in Japanese Black cattle is scanty and where available, is limited to performance test and field carcass traits only (Mukai et al. 1995, Mukai et al. 2000, Karnuah et al. 2001, Smith et al. 2001 and Sosa et al. 2002). There is an abundance of published work on breed, age and sex differences in body measurements in cattle (Cestnik 2001; Tozser et al. 2001; Rodriguez et al. 2001; Roy et al. 2001; Maiwashe et al. 2002; Afolayan et al. 2002a, 2002b). However, to our knowledge, apart from the work of Napolitano et al. (2001) with Italian Chianina x Piemontese crossbred cattle and Ashwell et al. (1998) with US Holsteins, there is no published information on the detection of quantitative trait loci (QTL) for body measurements related to shape and conformation traits in any other cattle breed. This justifies the need for the present study by our research group with Japanese Black beef cattle.

The mapping of QTL is the first step towards the identification of genes and causal polymorphisms for traits of importance in agriculture (Seaton et al., 2002). The detection of quantitative trait loci influencing body shape and conformation traits would be useful in the implementation of marker-assisted selection in the Japanese Black beef cattle. Comparative mammalian genomics reveal that bovine chromosome 1 (BTA1) is equivalent to the human chromosome 3 (http://bos.cvm.tamu.edu/htmls/rhbov1.html) which has been demonstrated to harbour growth-regulating genes such as growth hormone secretagogue receptor also known as ghrelin (Hosoda et al. 2003, Shuto et al. 2002), glycogenin (Mu et al. 2001) and Pit-1 (Ohta et al. 1992, Hendriks-Stegeman et al. 2001). It is therefore justifiable to focus on BTA 1 in the scan for

body conformation and growth-related QTL in Japanese Black cattle. Preliminary genome-wide scanning in our laboratory using only 30 animals (unpublished data) had suggested Bos taurus autosomes (BTA) 1, 2 and 5 as chromosomes containing segregating QTL significantly influencing growth traits in Japanese Black cattle. Therefore, in this confirmatory study with a larger data set of genotyped animals, we report for the first time, the association between microsatellite DNA markers and QTL on BTA1 influencing 15 body shape and conformation measurements at weaning of Japanese Black cattle.

MATERIALS AND METHODS

Animals and management: One hundred and thirty-two paternal half-sib progeny of five Japanese Black sires produced by artificial insemination at the Department of Livestock and Grassland Science, National Agricultural Research Centre for Western Region, Oda, Shimane Prefecture, Japan, were genotyped for this study. Sires 1 and 2 belonged to the line selected for increasing average daily gain while Sires 3, 4 and 5 belonged to the line selected for high beef marbling score. Routine management of the animals involved recording of weight at birth and monthly thereafter, until 18 months of age. Body shape and conformation measurements on withers height, hip height, hip width, body length, chest width, chest depth, shoulder width, lumbar width, thurl width, pin bone width, rump length, cannon circumference, chest girth, abdominal width and abdominal girth were also taken monthly. Calves were allowed to suckle their dams in addition to being fed 1.5 kg/day/head of concentrate and 1 kg/day/head of corn silage until 5 months of age when they were weaned. After weaning, they were moved to the grower's barn and still raised on concentrates (37% corn grain, 39% rice bran, 17% soybean meal, 7% minerals) and corn silage until 10 months of age. Between 10 and 18 months of age, they were moved to another barn and fed intensively. The proportions of the ration on dry matter basis were: 61% corn grain, 34% soybean and corn glutein meal, 2% bran and 3% mineral. For every 20kg bag, this ration provided an estimated 21% crude protein, 3.5% crude

fat, 5% crude fibre, 7% ash, 0.6% calcium, 0.40% phosph ate and a total digestible nutrient of 77%. From 18 to 24 months of age, breeding females were returned to the calving barn while steers were moved to the fattening barn and raised primarily on “Mosa meal” a specially formulated fattening ration containing 77% corn and rye grain, 10.5% wheat and rice bran, 9% soybean oil meal and 3.5% mineral supplement. At all ages, routine veterinary vaccinations and health checks were observed.

Extractions of genomic DNA: Following the method of Sambrook et al. (1989) and described in detail elsewhere (Malau-Aduli et al. 2003), genomic DNA was extracted and prepared from blood leucocytes and sperm.

Polymerase chain reaction (PCR): PCR pre-mix (13 µl) that comprised of: 10.55 µl of distilled water, 1.04 µl of 2.5 mM dNTP Mixture (Takara, Shiga, Japan), 1.3 µl of 10 x buffer containing 15 mM $MgCl_2$ and 0.11 µl of 25 mM of $MgCl_2$ was prepared. A primer (12.5 pmol/ µl) of microsatellite DNA markers each of which was labelled with one of three fluorescent dyes FAM, HEX and TET supplied by the Shirakawa Institute of Animal Genetics, Fukushima, Japan, based on the bovine genetic map at the U.S. Meat Animal Research Centre (Kappes et al., 1997; http://sol.marc.usda.gov) was added to the PCR pre-mix. Genomic DNA (1 µl) (conc of 20ng/µl) was added followed by 0.5 µl of Taq polymerase enzyme (conc of 0.75 units/µl) containing 50% glycerol (Takara, Japan). The PCR plates were hotplate-sealed and subjected to PCR in a DNA thermal cycler. The annealing temperature settings were: 50ºC, 55º C and 60ºC.

Genotyping: Prior to genotyping, the PCR products were mixed with markers which could be genotyped simultaneously in combinations of 4 µl of HEX, 1 µl of FAM and 1 µl of TET for multiplex genotyping. Then 0.8 µl of the mixed PCR products was added to 4.5 µl of DNA size

marker, centrifuged for 1 min at 1000 rpm and denatured using the PCR machine at a denaturing temperature of 94ºC for 9 mins. The denatured products were subjected to electrophoresis and genotyping in an automated ABI 377 DNA Sequencer. The number of informative microsatellite DNA markers utilized for the genotyping in each family is portrayed in Table 2.

Traits analyzed: Offspring of the five sires born between 1997 and 2002 were evaluated for the following body shape and conformation measurements at weaning (5 months of age): withers height, hip height, hip width, body length, chest width, chest depth, shoulder width, lumbar width, thurl width, pin bone width, rump length, cannon circumference, chest girth, abdominal width and abdominal girth.

QTL analysis: We adopted the methods of Knott et al. (1996), Haley and Knott (1992) and de Koning et al. (1998, 2001) for the detection and mapping of QTL in half-sib populations using least squares simple regression. We used the QTL Express computer program with a web-based user interface (http://qtl.cap.ed.ac.uk/) developed by Seaton et al. (2002) and based on the methods of the researchers mentioned above for the QTL analysis. The half-sib model of QTL Express run within and across sires, implemented the analysis in a two-step procedure: Firstly, microsatellite DNA marker data on progeny and their common parent (sire) were combined in a multi-point approach to calculate the probabilities of inheriting allele 1 or 2 from the sire at specific chromosomal intervals. These probabilities were combined into coefficients with values between 0.0 and 1.0. Secondly, the phenotypic data on progeny were regressed on these probability coefficients in a within-common-parent regression analysis. A linear model containing the fixed effects of sire, sex, parity and season of birth as well as age as a covariate, was fitted to the coefficients and phenotypic data. Appropriate F-statistic thresholds for a $P<0.05$ chromosome-wise type 1 error rate were generated by permutation test of 10,000 iterations as described by

Churchill and Doerge (1994), Doerge and Churchill (1996) (and applied to other half -sib studies by Spelman et al. 1996 and Vilkki et al.1997). In determining significant thresholds, the QTL Express software (Seaton et al. 2002) computed both the F-statistics and the F-threshold at P<0.05 chromosome-wise level. QTL were classified as significant when the F-statistic exceeded the F-threshold indicating a marker-trait association.

RESULTS

The means and standard deviations of body conformation measurements at weaning in the five Japanese Black families are shown in Table 1. It was evident that in all families, almost all of the body conformation measurements within traits were similar. The only clearly visible sign of significant differences between families was in chest girth (CHESTGTH) measurements in which Families 1 and 2 (125.9 and 127.2 cm respectively) were higher than in Families 3, 4 and 5 (121.7, 123.4 and 120.2 cm respectively). Portrayed in Table 2 are the microsatellite DNA markers and their relative positions on the BTA1 map that were utilized in genotyping the sires and half-sib progeny. The table shows that 18, 23, 11, 19 and 17 markers were informative for families 1, 2, 3, 4 and 5 respectively.

The estimates of allele substitution of sire QTL effects and locations obtained at a peak of F-statistics and thresholds of chromosome-wide 5% significant levels for body shape and conformation traits in the five Japanese Black families are shown in Table 3, while the plot of F-statistics in groups of 5 body conformation measurements is shown in Figure 1. A significant QTL for chest width (CHESTWD) at 91cM was detected in Family 3.

DISCUSSION

Animal improvement has been achieved by selection based on either phenotype or predicted additive genetic merit of superior animals for production traits. Molecular biology techniques allow the identification of genetic variation at specific loci and the association between QTL and

production traits. The final goal is to use marker assisted selection to improve the genetic gain achieved by selection as a result of higher accuracy on the estimation of an animal's genetic value (Tambasco et al. 2003). Microsatellites are referred to be the best genome markers and useful ones can be included in marker-assisted selection programmes to increase the rate of genetic progress (Georges et al. 1993). Napolitano et al. (1996) reported the localization of three microsatellites IDVGA-2, IDVGA-3 and IDVGA-46 on bovine chromosomes 2, 11 and 19 respectively, and their association with beef performance traits in F_1 Piemontese x Chianina crossbred cows. Of the three microsatellites, IDVGA-46 was reported to be the best marker for most beef conformation traits in this crossbred population, and that animals homozygous for allele 205 gave the best results in terms of linkage with segregating QTL for beef conformation (Napolitano et al. 2001). Their study examined only seven body conformation measurements – Withers height, body length, chest width, chest depth, chest girth, rump length and pelvis width. In our present study, we examined 15 body conformation measurements and detected a significant QTL for chest width located at 91 cM. The implication is that the microsatellite markers BMS119 and BMS4019 flanking this interval can be used in marker-assisted selection to introduce or retain the beneficial QTL allele. The phenomenon of genetic linkage means that each marker can be used to follow the inheritance of a section of the linked chromosome. However, markers have to be very closely linked to the causative mutation in the trait gene if they are to remain associated with specific QTL alleles through several generations of selection and therefore be useful in practical breeding programmes. If a genetic marker and a trait are significantly linked as portrayed in our study, there is a tendency for such associations to be maintained at a population level. This phenomenon of linkage disequilibrium could be exploited to locate the trait genes using single nucleotide polymorphisms (SNPs), that is where two DNA sequences differ by a single base. On-going work in our laboratory to confirm or dispute the presence of significant QTL for body conformation and growth on BTA2 and BTA5 are still in

progress. It is our goal to utilize positional cloning using the candidate gene approach in the future to identify the underlying mutation linked to the detected QTL in this study.

There were significant differences between families in chest girth (CHESTG TH) measurements in which Families 1 and 2 were higher than in Families 3, 4 and 5. This was not entirely surprising because Sires 1 and 2 had been selected for average daily gain (daily gain line) while Sires 3, 4 and 5 belonged to the beef marbling score (BMS) line. Chest girth is an important body conformation measurement that has been reported in Japanese Black cattle. For instance, Mukai et al. (1995) studied the genetic relationships between body measurements, growth and field carcass performance trai ts and reported highly significant and positive genetic correlations between chest girth and carcass weight at the beginning, middle and end of performance testing of 0.64, 0.77 and 0.79 respectively. They concluded that it was possible to improve total me rit of the carcass by introducing chest girth into performance testing of Japanese Black cattle. Other studies (Oyama et al. 1996; Kitamura et al. 1999) on genetic relationships among recorded body measurement traits, reproductive traits of breeding female s and carcass traits in Japanese Black cattle buttress the finding of Mukai et al. (1995) that there is an unfavourable or low correlation between chest girth and beef marbling score (-0.07, 0.28 and 0.21 at the beginning, middle and end of performance tes ting respectively). It is this low correlation that has been observed in this present study with the BMS line families having lower chest girth measurements than the daily gain line families. Other body conformation measurements like chest depth, thurl wid th and withers height were also found to be genetically correlated with field carcass weight ranging from 0.64 to 0.90 (Mukai et al. 1995), indicating that body conformation measurements can be valuable in selection for meat quality as well. Unpublished data from our group portray a significant and positive relationship between body conformation measurements and average daily gain to weaning and yearling age. Thus, the identification of a significant QTL for chest width in the present study holds hope for t he

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Table 1. Means ± S.D. of the body conformation measurements (cm) in the progeny of 5 Japanese Black sires at weaning.

Trait/Acronym	Family 1	Family 2	Family 3	Family 4	Family 5
WHT Withers height	99.5 ± 3.9	100.9 ± 3.5	98.5 ± 3.5	97.5 ± 2.7	97.6 ± 4.0
HIPHT Hip height	103.1 ± 3.9	103.0 ± 3.0	101.0 ± 3.8	101.1 ± 3.8	98.7 ± 4.1
BL Body length	106.5 ± 5.9	108.1 ± 5.0	103.2 ± 7.5	103.2 ± 4.5	101.9 ± 5.3
CHESTWD Chest width	28.1 ± 2.2	29.5 ± 2.3	27.7 ± 2.6	26.9 ± 2.2	27.2 ± 1.6
SHOUWD Shoulder width	31.2 ± 2.6	31.4 ± 2.1	28.4 ± 2.2	28.6 ± 2.0	27.4 ± 2.3
CHESTDP Chest depth	46.3 ± 1.8	46.6 ± 1.5	44.7 ± 1.8	45.5 ± 1.4	43.8 ± 2.2
HIPWDT Hip width	28.3 ± 1.8	29.0 ± 1.3	26.3 ± 2.1	28.1 ± 1.4	27.4 ± 1.5
LUMBARWD Lumbar width	22.7 ± 1.5	23.1 ± 1.0	21.1 ± 2.1	22.6 ± 1.3	22.0 ± 1.3
THURLWD Thurl width	33.0 ± 2.2	33.6 ± 1.7	31.0 ± 1.6	31.3 ± 1.9	31.0 ± 2.0
PINBWD Pin bone width	20.5 ± 2.1	20.6 ± 1.3	18.6 ± 1.9	18.9 ± 1.0	18.1 ± 1.4
RUMPL Rump length	35.2 ± 2.1	35.8 ± 1.8	34.6 ± 1.7	35.3 ± 1.4	34.4 ± 1.7
CANNONCIR Cannon circumference	14.4 ± 0.9	14.7 ± 0.9	13.8 ± 1.0	13.5 ± 0.8	13.4 ± 0.9
CHESTGTH Chest girth	125.9 ± 5.2[a]	127.2 ± 4.3[a]	121.7 ± 4.9[b]	123.4 ± 3.8[b]	120.2 ± 5.9[b]
ABDWD Abdominal width	37.0 ± 2.5	37.7 ± 2.5	35.4 ± 2.9	36.5 ± 2.2	35.5 ± 1.9
ABDGTH Abdominal girth	144.0 ± 7.0	143.5 ± 6.1	138.5 ± 7.4	140.6 ± 6.0	138.0 ± 7.2
No. of progeny	40	36	19	17	20

Means in rows bearing different superscripts significantly differ between families.

Table 2. Microsatellite DNA markers used for genotyping in the 5 Japanese Black cattle families and their relative positions on the map (cM)*

Family	Marker	Position	Family	Marker	Position	Family	Marker	Position	Family	Marker	Position	Family	Marker	Position
1	BMS1928	6.9	2	BM8139	8.2	3	BMS2321	14.0	4	BMS1928	6.9	5	BM8139	8.2
1	BMS711	21.3	2	TGLA57	46.2	3	ILSTS104	28.2	4	BMS711	21.3	5	BMS2321	14.0
1	ILSTS104	28.2	2	BMS4012	51.0	3	BMS4002	47.9	4	TGLA57	46.2	5	BMS711	21.3
1	MB055	32.0	2	BMS4013	61.3	3	BMS4012	51.0	4	BMS4035	55.0	5	BMS2725	41.8
1	TGLA57	46.2	2	BMS4001	64.7	3	BMS4035	55.0	4	BMS4029	61.3	5	BMS4002	47.9
1	BMS4012	51.0	2	BM9019	67.5	3	RME36	63.0	4	BM9019	67.5	5	BMS4012	51.0
1	BMS4035	55.0	2	BL26_1	77.7	3	BM8246	76.2	4	BMS4008	71.7	5	RM326	55.6
1	RM326	55.6	2	BMS4006	79.4	3	BMS119	88.6	4	BMS4048	76.2	5	BMS4030	59.2
1	RME36	63.0	2	URB038	80.6	3	BMS4019	98.8	4	URB038	80.6	5	BMS4029	61.3
1	INRA049	67.5	2	MCM130	83.3	3	UWCA46	113.8	4	BMS4010	87.1	5	INRA119	68.7
1	BM65O6	69.2	2	BMS4010	87.1	3	BMS599	125.8	4	BM864	88.2	5	BMS4008	71.7
1	URB038	80.6	2	BM864	88.2				4	BMS1170	92.8	5	BM8246	76.2
1	BMS4052	94.6	2	BMS1170	92.8				4	BMS4019	98.8	5	BMS4006	79.4
1	BMS4028	95.6	2	BMS4028	95.6				4	BMS4011	102.1	5	BMS4010	87.1
1	BMS4040	98.8	2	BMS4019	98.8				4	BMS4049	114.3	5	BMS4019	98.8
1	BMS1789	100.9	2	BMS1789	100.9				4	BMS918	118.1	5	BMS1757	108.3
1	BMS4044	128.7	2	BMS1939	104.1				4	BMS599	125.8	5	BMS4044	128.7
1	BMS2263	135.1	2	BMS4039	108.3				4	BMS4044	128.7			
			2	BM3205	113.8				4	BMS922	135.5			
			2	BMS599	125.8									
			2	BMS4043	128.7									
			2	BMS2263	135.1									
			2	BMS4014	135.5									
Total	18			23			11			19			17	

*Based on the bovine genetic map at the U.S. Meat Animal Research Centre (Kappes et al., 1997; http://sol.marc.usda.gov)

Table 3. Allele substitution/Sire QTL effects ± standard errors (ß ± S.E.) and estimated QTL locations (cM) for body shape and conformation traits in Japanese Black cattle families.

Trait		Family 1	Family 2	Family 3	Family 4	Family 5
WHT	' ' S.E. QTL (cM)	-3.5 ± 1.7 77cM (F=4.5/9.0) ns	2.8 ± 1.3 18cM (F=4.3/9.0) ns	5.5 ± 3.6 97cM (F=2.3/12.8) ns	2.5 ± 1.7 78cM (F=2.1/44.6) ns	-4.6 ± 1.7 58cM (F=7.5/15.1) ns
HIPHT	' ' S.E. QTL (cM)	-2.5 ± 1.6 14cM (F=2.5/9.4) ns	3.0 ± 1.1 18cM (F=7.0/9.0) ns	-2.9 ± 2.4 53cM (F=1.4/11.9) ns	-4.2 ± 1.7 16cM (F=6.1/76.0) ns	3.2 ± 1.7 0cM (F=3.7/13.0) ns
BL	' ' S.E. QTL (cM)	3.9 ± 2.4 122cM (F=2.6/8.9) ns	4.7 ± 2.0 18cM (F=5.7/9.2) ns	-7.1 ± 4.3 53cM (F=2.8/12.9) ns	-10.8 ± 6.4 132cM (F=2.8/87.5) ns	-5.4 ± 2.8 71cM (F=3.7/16.2) ns
CHESTWD	' ' S.E. QTL (cM)	-1.2 ± 0.8 109cM (F=2.0/9.3) ns	-2.0 ± 0.9 92cM (F=5.0/9.3) ns	5.3±1.5 91cM (F=12.0/10.05) sig	-7.9 ± 2.9 102cM (F=7.2/93.9) ns	-1.1 ± 0.9 5cM (F=1.2/14.8) ns
SHOUWD	' ' S.E. QTL (cM)	-2.0 ± 1.1 71cM (F=3.0/8.9) ns	1.4 ± 0.9 25cM (F=2.5/9.7) ns	2.5 ± 1.6 95cM (F=2.4/12.4) ns	-3.7 ± 3.1 0cM (F=1.4/95.4) ns	-2.0 ± 1.1 72cM (F=3.1/13.8) ns
CHESTDP	' ' S.E. QTL (cM)	-2.1 ± 0.9 81cM (F=5.3/9.4) ns	1.4 ± 0.6 18cM (F=6.0/10.2) ns	-1.5 ± 0.9 52cM (F=2.4/11.5) ns	-1.5 ± 1.6 0cM (F=0.8/74.5) ns	3.4 ± 1.7 120cM (F=3.9/13.3) ns
HIPWDT	' ' S.E. QTL (cM)	1.2 ± 1.0 36cM (F=1.6/9.8) ns	1.1 ± 0.5 18cM (F=5.7/10.3) ns	1.8 ± 0.8 10cM (F=5.5/13.2) ns	-2.0 ± 1.1 16cM (F=3.5/39.9) ns	-0.9 ± 0.6 72cM (F=2.1/10.8) ns
LUMBARWD	' ' S.E. QTL (cM)	0.8 ± 0.7 38cM (F=1.4/8.9) ns	-0.6 ± 0.4 48cM (F=2.1/9.2) ns	1.8 ± 0.7 11cM (F=6.8/12.3) ns	0.4 ± 0.5 42cM (F=0.9/49.5) ns	-0.8 ± 0.7 72cM (F=1.6/14.6) ns
THURLWD	' ' S.E. QTL (cM)	-1.4 ± 0.9 42cM (F=2.7/9.1) ns	1.9 ± 0.7 18cM(F=7.3/9.3) ns	1.2 ± 1.2 95cM (F=1.1/12.2) ns	1.0 ± 0.8 42cM (F=1.5/66.9) ns	-0.8 ± 0.7 71cM (F=1.3/15.0) ns
PINBWD	' ' S.E. QTL (cM)	1.2 ± 1.1 91cM (F=1.3/9.2) ns	0.8 ± 0.5 18cM (F=2.3/9.2) ns	2.6 ± 0.9 10cM (F=8.3/11.4) ns	1.5 ± 0.4 42cM (F=13.7/52.3) ns	-1.9 ± 1.0 101cM (F=3.8/14.9) ns
RUMPL	' ' S.E. QTL (cM)	-2.2 ± 1.0 11cM (F=4.6/8.9) ns	1.0 ± 0.6 101cM (F=3.5/9.9) ns	-1.7 ± 0.5 53cM (F=9.5/10.9) ns,	-1.8 ± 1.1 13cM (F=2.7/32.5) ns	-1.4 ± 0.6 72cM (F=5.0/12.4) ns
CANNONCIR	' ' S.E. QTL (cM)	-0.4 ± 0.3 42cM (F=2.1/9.4) ns	-0.5 ± 0.2 80cM (F=4.0/9.5) ns	1.7 ± 0.7 98cM (F=6.9/11.5) ns	0.4 ± 0.4 42cM (F=1.2/57.0) ns	-0.2 ± 0.3 53cM (F=0.4/14.3) ns
CHESTGTH	' ' S.E. QTL (cM)	-2.8 ± 2.3 14cM (F=1.5/9.1) ns	3.8 ± 1.7 24cM (F=4.9/9.9) ns	-4.2 ± 3.6 56cM (F=1.4/12.9) ns	-4.6 ± 4.7 99cM (F=1.0/69.6) ns	-3.9 ± 3.0 71cM (F=1.8/14.4) ns
ABDWD	' ' S.E. QTL (cM)	-1.9 ± 1.3 70cM (F=2.2/8.9) ns	2.2 ± 1.0 113cM (F=4.8/10.2) ns	2.8 ± 2.4 97cM (F=1.4/13.6) ns	-5.2 ± 1.4 118cM (F=14.0/60.2) ns	-1.3 ± 1.0 3cM (F=1.5/15.9) ns
ABDGTH	' ' S.E. QTL (cM)	-6.3 ± 3.4 77cM (F=3.3/9.2) ns	6.0 ± 2.5 18cM (F=6.0/9.5) ns	-5.1 ± 3.5 42cM (F=2.1/12.3) ns	-13.2 ± 6.3 115cM (F=4.3/97.6) ns	-2.4 ± 3.8 56cM (F=0.4/15.5) ns

Figures in brackets are F-statistics/F-threshold values at P<0.05 chromosome-wide level, ns=not significant