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# A Whole Genome Association Study to Detect Single Nucleotide Polymorphisms for Body Conformation Traits in a Hanwoo Population

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**ABSTRACT :** A whole genome association (WGA) study was conducted to identify quantitative trait loci (QTL) for body conformation traits in Hanwoo cattle. The phenotypes of 497 steers were recorded from the Hanwoo Improvement Center of National Agricultural Cooperative Federation, Seosan, Korea, and analyzed using the Illumina Bovine 50 k SNP chip. A set of 35,987 SNPs that were available in the Hanwoo population was selected from the chip. After adjustments for the effects of year-season of birth, region and sire, phenotypes were regressed on each SNP using a linear regression model. Three hundred nineteen SNPs were detected for the ten conformation traits ($p<0.003$). For the significant SNPs, stepwise regression procedures were applied to determine best sets of markers. A total of 72 SNPs were selected ($p<0.001$), for which the sets of 5, 9, 10, 9, 8, 11, 4, 6, 3 and 7 SNPs were determined for height at withers, rump height, body length, chest depth, chest width, rump length, hip width, thurl width, pinbone width and heart girth, respectively. About 7-26% of the total phenotypic variation was explained by the set of SNPs for each trait. QTL for the conformation traits were harbored on most bovine chromosomes (BTAs). Four SNPs with pleiotropic effects on height at withers and rump height were detected on BTAs 3, 4, 6 and 16. A SNP with pleiotropic effects on chest width and rump length was also detected on BTA10. Two QTL regions, *i.e.* between 87 and 97 Mb in BTA3 and between 41 and 44 Mb in BTA7, were found, in which SNPs were detected for the five and three conformation traits, respectively. The detected SNPs need to be validated in other Hanwoo populations for commercial application to the genetic improvement of conformation characteristics in Hanwoo via marker-assisted selection (MAS). (**Key Words :** Whole Genome Association, Body Conformation, SNP, Hanwoo, QTL)

## INTRODUCTION

The mapping of QTL is the first step towards identification of the genes and causal polymorphisms responsible for traits of economic importance in farm animals (Seaton et al., 2002). Since 1990s, conventional approaches, *i.e.* linkage analysis, have been implemented with the aid of microsatellite or SNP markers to detect QTL for economically important traits. So far, more than two thousand QTLs have been reported in cattle (www.animalgenome.org). However, the next step towards utilizing the QTL information in commercial populations through marker-assisted selection (MAS) were ineffective, partly because of limited map density (lack of the amount of genetic markers), causing inefficient identification of causal mutations (Sellner et al., 2007; van Eenennaam et al., 2007). Recently, whole genome association (WGA) mapping is practiced to identify QTLs in human, plant and animals, due to the advanced sequencing technologies, which allows millions of SNPs to be available in the WGA study.

Following the first major WGA study in human by Sladek et al. (2007), the whole genome sequencing for livestock opened a new dimension on genomics study, especially due to next generation sequencing technologies that are available from 454 Life Sciences, Illumina and Applied Biosystems. For *Bos taurus* or Herford cattle breed, the Bovine Genome Sequencing and Analysis Consortium et al. (2009) and Zimin et al. (2009) sequenced the whole bovine genome, and some other cattle breeds such as

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(Holstein, Angus, Limousin etc.) are in progress (Eck et al., 2009). Gibbs et al. (2009) found more than two million SNPs in Herford, indicating a vast resource of DNA variations, which will expedite the development of high density SNP chips and thus the identification of causal mutations for the genes underlying quantitative traits (Sellner et al., 2007; van Tassell et al., 2008; Sherman et al., 2010).

Most QTL studies that have been conducted in livestock species are mainly related to production, functional or carcass traits of cattle (Keele et al., 1999; Stone et al., 1999; Casas et al., 2000, 2003, 2004; Biochard et al., 2003; Kim et al., 2003; Schnabel et al., 2005; Abe et al., 2008). On the contrary, a few QTL studies were focused on body conformation traits in daily cattle (Hiendleder et al., 2003; Ashwell et al., 2005; Malau-Aduli et al., 2005, 2007; Kolbehdari et al., 2008). However, there were no reports on body conformation QTL in beef cattle. Herein, we first report on detection of SNPs that are associated with body conformations in Hanwoo, a Korean native beef cattle, using a high-throughput SNP assay.

## MATERIALS AND METHODS

### Animals and phenotypes

The animals (N = 497) for phenotype data were chosen among the steers of candidate bulls for progeny testing in the Hanwoo Improvement Center of National Agricultural Cooperative Federation in Seosan, Chungnam province, Korea. The sample comprised paternal half-sib pedigrees from 63 Korean proven sires. The steers were born between spring of 2005 and fall of 2007, weaned at 5 or 6 months of age, and each group of 10 steers were raised in a pen. The feeding program was divided into early, middle, and late stage, each with six months of interval. In the early and middle stages, the steers were fed with concentrates with the amount of 1.8% of the body weight and ad labium in the late stage. The concentrates were composed of 15%, 13%, and 11% of crude protein, and 71%, 72%, and 73% totally digestible nutrients (TDN), in the respective feeding stages. Roughages with 4.5% crude protein and 37.5 TDN were offered ad labium with other additives such as vitamin and minerals. Traits related to body conformations in the experiment were height at withers (HgtWithers), rump height (HgtRump), body length (BodyLen), chest depth (ChestDep), chest width (ChestWdt), rump length (RumpLen), hip width (HipWdt), thurl width (ThurlWdt), and pinbone width (PinWdt) and heart girth (HeartGrt). All the traits were measured at about 16 (±6) months of age, according to the protocol of Korea Animal Improvement Association. A summary of the collected phenotypes is described in Table 1.

### Molecular data

Following a standard protocol, the DNA samples were extracted from blood of 497 steers, and the DNA concentration was adjusted to 50 ng/μl. The Illumina bovine 50K SNP bead chips (55,074 SNPs) (Matukumalli et al., 2008; van Tassell et al., 2008) were used for WGA tests. Approximately 200 ng of genomic DNA was used to genotype each sample on the chip. Detailed procedures were described in Lee at al. (2010).

Every SNP from the chip data was screened for the availability of GWA tests. At first, all SNPs found in 29 autosomes were considered primarily and those SNPs having the following three criteria, such as i) the number of genotype group is one or none (*e.g.* only AA genotypes and no AB or BB), ii) having a minor allele frequency less than 0.05, and iii) with a proportion of genotyped individuals less than 90% was subsequently removed from the WGA tests.

### Statistical analysis

Phenotypes were preadjusted using SAS GLM procedure of SAS version 9.1 (SAS Inst., Inc., Cary, NC) before WGA tests. Two factors, *i.e.* year and season of birth

**Table 1.** Summary statistics for observations on body conformation traits in Hanwoo population

| Trait | Average | Std Dev[a] | Minimum | Maximum | CV[b] |
|---|---|---|---|---|---|
| Height at wither, cm | 133.3 | 6.5 | 95 | 149 | 4.9 |
| Rump height, cm | 134.7 | 6.4 | 98 | 152 | 4.7 |
| Body length, cm | 152.6 | 10.4 | 94 | 178 | 6.8 |
| Chest depth, cm | 73.7 | 5.2 | 48 | 82 | 7.0 |
| Chest width, cm | 48.6 | 5.4 | 27 | 59 | 11.1 |
| Rump length, cm | 49.8 | 3.5 | 33 | 68 | 7.0 |
| Hip width, cm | 47.8 | 5.7 | 25 | 63 | 11.9 |
| Thurl width, cm | 45.4 | 4.3 | 27 | 58 | 9.5 |
| Pinbone width, cm | 24.9 | 3.0 | 16 | 32 | 12.0 |
| Heart girth, cm | 204.6 | 17.6 | 125 | 245 | 8.6 |

[a] Standard deviation. [b] Coefficient of variation (%).

and region, were fitted as fixed effects and another factor, sire as a random effect in the model for all of the ten conformation traits. The residuals were regressed on each SNP using a simple linear regression model. The SNP genotype values for BB, BA and AA were assigned as -1, 0, and 1, such that allele substitution effect replacing 'B' with 'A' allele was estimated. For significance threshold, 0.3% point-wise p value from *F* distribution was applied for each SNP test.

Among the significant SNPs, the best set of SNP markers were selected for each trait using a stepwise regression procedure (Neter et al., 1990). Because, some of the significant SNPs would yield redundant information in implementing MAS program due to the relationships of closely linked SNPs, also termed as linkage disequilibrium (LD), *i.e.* a non-random association between alleles of different SNPs. Inclusion and exclusion of each SNP out of the model was determined at the $p<0.001$ level.

The variation explained by each SNP ($S^2_{SNP}$) was calculated as $\sum_{i=1}^{3} \alpha_i^2 f_i - \mu^2$, where i denotes each genotype, $\alpha_i$ is allele substitution effect (=- â, 0, and +â for BB, AB, and AA, respectively, in which â is estimated from the simple regression analysis for the SNP), $f_i$ is the frequency of $i^{th}$ genotype, μ is the population mean that can be expressed as $(f_{AA}-f_{BB})$â (Falconer and Mackay, 1996). Proportion of phenotypic variance due to the SNP was then estimated as $S^2_{SNP}/S^2_P$, in which $S^2_P$, phenotypic variance, was obtained from residual values of the trait after adjusting the fixed and random effects. Therefore, the estimate of the proportion of phenotype variance due to all of the significant SNPs was $\sum S^2_{SNPi}/S^2_P$.

## RESULTS AND DISCUSSION

The coefficients of variation (CV) for the ten conformation traits are, in general, low, *i.e.* less than 10% (Table 1). These low variability indexes indicates smaller variability in body conformations than in growth and carcass quality traits in Hanwoo cattle (Lee et al., 2010).

A total of 35,987 SNPs were selected from the 55,074 SNPs in the bovine Illumina SNP chip. The physical map of the available SNPs spanned about 2,543 Mbps with an average distance of 70.4±67.8 Kb between adjacent SNPs. The number of available SNPs was slightly greater and the average distance between flanking SNPs was shorter, compared to our previous report (Lee et al., 2010), in which a fewer number of steers (N = 289) was used.

A total of 319 SNPs were detected ($p<0.003$), and the numbers of significant SNPs were 30, 20, 41, 40, 29, 48, 18, 29, 29 and 35 SNPs for HgtWithers, HgtRump, BodyLen, ChestDep, ChestWdt, RumpLen, HipWdt, ThurlWdt, PinWdt, and HeartGrt, respectively. Among the 319 significant SNPs, 72 SNPs were determined as the best set of SNPs by the stepwise regression procedures that considered LD between closely linked SNPs (Table 2). A set of SNPs for each trait explained about 7-26% of total phenotypic variance, with the maximum value estimated for RumpLen and the minimum for PinWdt. The detected SNPs individually explained a very small portion (1.8-4.9%) of the phenotypic variance with the highest value estimated for BTA-61748-no-rs SNP on BTA28 for ChestDep.

In general, the detected SNPs for each trait were distributed in different chromosomes. The SNPs that were detected on the same chromosomes were located at a far distance, *e.g.* 92 Mbp away for the two HgtRump SNPs on BTA4 (Table 2). These results were not surprising, because the stepwise regression procedures were applied, which excluded the closely linked SNPs that were located near the significant one. Figure 1(a-f) displays profiles of the test statistics on several chromosomes for the five conformation traits.

Many SNPs for conformation traits were not found by the WGA tests in this study, compared with other reports (Ashwell et al., 2005; Kolbehdari et al., 2008). This may be partly due to the genetic background of Hanwoo breed and the sample size used (N = 497). Lee et al. (2010) found that LDs between closely located markers were low in Hanwoo, compared with other western breeds such as Angus Hereford or Holstein, because intensive selections on Hanwoo were implemented only about three decades ago. Further, the SNP contents that were assayed in the Illumina bovine SNP chip were based on Hereford or Holstein breeds, such that only about 65% of SNPs in the bovine chip were available in Hanwoo, which caused the average distance between two flanking SNPs to be much longer (70.4 kb), than using all the available SNPS in the chip. This suggests the possibility that many QTL are missed, unless those QTL are closely located to the available SNPs on the Illumina 50K SNP chip. Hence, it is needed to use a better chip, *i.e.* with a much greater number of available SNPs and thus a higher map density, which would allow the detection of greater numbers of SNPs that are associated with the traits in this study. In addition, more phenotypes and genotypes are needed to acquire greater power to detect QTL and higher accuracy for the estimates of SNP effects.

We did not apply chromosome- or genome-wise threshold values that were taken multiple tests into account in the detection of significant SNPs for the conformation traits. Because more than 30,000 tests were performed for each trait with the small sample size (N = 497). Further, the threshold values that were obtained by permutation tests or false discovery rate methods (Churchill and Doerge, 1994; Benjamini and Hochberg, 1995) were so high that almost none of the statistical tests for the WGA analyses reached the stringent threshold values (results not shown).

**Table 2.** Identities, positions, and effects of the SNPs associated with body conformation traits in a Hanwoo population

| Trait/SNP Marker[a] | SNP[b] | BTA | Kbp[c] | MAF[d] | -$Log_{10}P$[e] | Estimate[f] | SE[g] | $\%\sigma_P^2$ [h] |
|---|---|---|---|---|---|---|---|---|
| Height at withers (HgtWithers) | | | | | | | | 11.7 |
| BTA-68507-no-rs | G/T | 3 | 87,616 | 0.11 | 3.28 | -1.20 | 0.35 | 2.4 |
| ARS-BFGL-NGS-73518 | A/G | 3 | 97,485 | 0.35 | 2.82 | 0.72 | 0.23 | 2.0 |
| BTA-72175-no-rs | A/T | 4 | 106,128 | 0.28 | 3.79 | 0.91 | 0.24 | 2.8 |
| Hapmap52018-BTA-75646 | A/G | 6 | 29,803 | 0.25 | 2.75 | -0.81 | 0.26 | 1.9 |
| BTA-88802-no-rs | G/T | 16 | 22,887 | 0.46 | 3.45 | 0.79 | 0.22 | 2.5 |
| Rump height (HgtRump) | | | | | | | | 23.2 |
| BTA-68507-no-rs | G/T | 3 | 87,616 | 0.11 | 3.50 | -1.25 | 0.35 | 2.6 |
| ARS-BFGL-NGS-68531 | A/C | 4 | 13,434 | 0.38 | 2.77 | -0.70 | 0.22 | 2.0 |
| BTA-72175-no-rs | A/T | 4 | 106,128 | 0.28 | 4.11 | 0.95 | 0.24 | 3.1 |
| Hapmap52018-BTA-75646 | A/G | 6 | 29,803 | 0.25 | 3.59 | -0.95 | 0.26 | 2.7 |
| Hapmap28019-BTC-054809 | C/T | 6 | 44,190 | 0.26 | 3.71 | -0.94 | 0.25 | 2.8 |
| BTA-88802-no-rs | G/T | 16 | 22,887 | 0.46 | 3.11 | 0.74 | 0.22 | 2.2 |
| Hapmap50009-BTA-50200 | A/G | 20 | 29,599 | 0.09 | 3.38 | 1.34 | 0.38 | 2.5 |
| ARS-BFGL-NGS-13436 | C/T | 22 | 7,472 | 0.18 | 3.36 | -1.02 | 0.29 | 2.5 |
| ARS-BFGL-NGS-34801 | A/G | 25 | 16,923 | 0.22 | 3.88 | -1.03 | 0.27 | 2.9 |
| Body length (BodyLen) | | | | | | | | 23.3 |
| ARS-BFGL-NGS-81865 | A/G | 2 | 7,441 | 0.30 | 4.11 | -1.49 | 0.37 | 3.1 |
| BTA-80221-no-rs | A/G | 7 | 95,708 | 0.07 | 4.39 | 2.66 | 0.64 | 3.3 |
| Hapmap43147-BTA-108562 | C/T | 12 | 48,755 | 0.16 | 2.88 | 1.45 | 0.45 | 2.1 |
| BTB-01666402 | A/G | 13 | 6,784 | 0.14 | 3.05 | 1.68 | 0.50 | 2.2 |
| Hapmap57858-rs29019930 | C/T | 13 | 72,530 | 0.14 | 3.77 | -1.80 | 0.48 | 2.8 |
| BTB-01280026 | C/T | 14 | 25,171 | 0.07 | 3.22 | 2.23 | 0.65 | 2.3 |
| BFGL-NGS-114922 | C/T | 15 | 26,968 | 0.29 | 2.80 | -1.19 | 0.38 | 2.0 |
| ARS-BFGL-NGS-45350 | C/T | 19 | 14,422 | 0.27 | 2.57 | 1.10 | 0.37 | 1.8 |
| Hapmap24768-BTC-058762 | C/T | 25 | 43,365 | 0.38 | 2.56 | 1.04 | 0.35 | 1.8 |
| ARS-BFGL-NGS-100421 | A/G | 28 | 12,314 | 0.12 | 2.64 | 1.57 | 0.51 | 1.9 |
| Chest depth (ChestDep) | | | | | | | | 24.3 |
| BFGL-NGS-118771 | A/G | 3 | 37,201 | 0.25 | 3.03 | 0.80 | 0.24 | 2.2 |
| ARS-BFGL-NGS-36707 | A/G | 6 | 87,371 | 0.18 | 3.46 | -0.99 | 0.28 | 2.5 |
| ARS-BFGL-NGS-64956 | C/T | 7 | 43,515 | 0.10 | 3.16 | 1.23 | 0.36 | 2.3 |
| BTB-00586906 | A/G | 15 | 22,728 | 0.08 | 4.56 | -1.71 | 0.40 | 3.5 |
| ARS-BFGL-NGS-49089 | C/G | 16 | 73,329 | 0.05 | 2.86 | -1.58 | 0.49 | 2.0 |
| Hapmap56365-rs29022398 | C/G | 17 | 56,371 | 0.07 | 3.50 | -1.47 | 0.41 | 2.5 |
| ARS-BFGL-NGS-14017 | C/G | 18 | 24,121 | 0.12 | 3.34 | 1.16 | 0.33 | 2.5 |
| ARS-BFGL-NGS-101622 | A/G | 23 | 20,436 | 0.21 | 2.66 | -0.81 | 0.26 | 1.9 |
| BTA-61748-no-rs | A/G | 28 | 21,958 | 0.05 | 6.25 | -2.29 | 0.45 | 4.9 |
| Chest width (ChestWdt) | | | | | | | | 17.5 |
| ARS-BFGL-NGS-100563 | A/C | 5 | 105,907 | 0.43 | 3.13 | 0.62 | 0.18 | 2.3 |
| ARS-BFGL-NGS-40198 | C/T | 10 | 2,149 | 0.32 | 2.74 | -0.63 | 0.20 | 1.9 |
| ARS-BFGL-NGS-10310 | A/G | 10 | 45,585 | 0.17 | 2.64 | -0.73 | 0.24 | 1.9 |
| BTB-00467445 | C/T | 11 | 25,535 | 0.19 | 2.87 | 0.72 | 0.22 | 2.0 |
| ARS-BFGL-NGS-108568 | C/T | 13 | 39,735 | 0.47 | 3.51 | -0.63 | 0.17 | 2.6 |
| UA-IFASA-8264 | A/G | 23 | 43,488 | 0.16 | 2.79 | 0.78 | 0.25 | 2.0 |
| ARS-BFGL-NGS-25894 | C/T | 26 | 25,234 | 0.13 | 3.81 | 0.96 | 0.25 | 2.8 |
| BTA-88213-no-rs | C/G | 27 | 10,328 | 0.23 | 2.72 | 0.66 | 0.21 | 1.9 |

**Table 2.** Identities, positions, and effects of the SNPs associated with body conformation traits in a Hanwoo population (Continued)

| Trait/SNP Marker[a] | SNP[b] | BTA | Kbp[c] | MAF[d] | -$Log_{10}P$[e] | Estimate[f] | SE[g] | $\%\sigma_P^2$ [h] |
|---|---|---|---|---|---|---|---|---|
| Rump length (RumpLen) | | | | | | | | 25.7 |
| BTB-00027056 | A/G | 1 | 65,560 | 0.41 | 2.70 | 0.48 | 0.16 | 1.9 |
| BTB-01771876 | C/T | 3 | 87,577 | 0.08 | 3.17 | 0.94 | 0.27 | 2.3 |
| BTA-69346-no-rs | A/G | 3 | 113,664 | 0.28 | 2.69 | -0.51 | 0.17 | 1.9 |
| Hapmap53668-rs29025196 | C/T | 8 | 111,188 | 0.21 | 3.17 | -0.59 | 0.17 | 2.3 |
| ARS-BFGL-NGS-40198 | C/T | 10 | 2,149 | 0.32 | 3.52 | -0.60 | 0.17 | 2.6 |
| ARS-BFGL-NGS-19364 | A/C | 13 | 9,653 | 0.42 | 3.36 | -0.52 | 0.15 | 2.5 |
| Hapmap46352-BTA-122434 | A/T | 14 | 57,994 | 0.46 | 2.61 | -0.46 | 0.15 | 1.8 |
| ARS-BFGL-NGS-17643 | A/G | 17 | 51,723 | 0.14 | 3.47 | 0.76 | 0.21 | 2.6 |
| BTB-00775883 | A/G | 20 | 20,681 | 0.33 | 3.49 | -0.56 | 0.16 | 2.6 |
| BTA-63833-no-rs | A/G | 28 | 25,547 | 0.20 | 4.34 | 0.76 | 0.19 | 3.3 |
| ARS-BFGL-NGS-57882 | C/T | 29 | 45,743 | 0.29 | 2.79 | 0.51 | 0.16 | 2.0 |
| Hip width (HipWdt) | | | | | | | | 8.5 |
| Hapmap58211-rs29015635 | C/T | 6 | 81,959 | 0.48 | 2.95 | -0.49 | 0.15 | 2.1 |
| BTB-01207246 | A/G | 7 | 40,831 | 0.18 | 3.31 | -0.67 | 0.19 | 2.4 |
| BTB-01250664 | A/G | 7 | 82,951 | 0.34 | 2.57 | 0.50 | 0.17 | 1.8 |
| BTB-01249515 | C/T | 9 | 38,626 | 0.39 | 3.03 | -0.51 | 0.15 | 2.2 |
| Thurl width (ThurlWdt) | | | | | | | | 15.7 |
| Hapmap27565-BTA-101823 | A/G | 2 | 93,963 | 0.44 | 3.20 | 0.55 | 0.16 | 2.3 |
| ARS-BFGL-NGS-32644 | A/G | 5 | 80,481 | 0.16 | 3.08 | 0.67 | 0.20 | 2.2 |
| ARS-BFGL-NGS-54516 | A/G | 8 | 97,628 | 0.26 | 3.8 | 0.65 | 0.17 | 2.8 |
| BTA-92485-no-rs | A/G | 9 | 59,455 | 0.42 | 3.32 | -0.52 | 0.15 | 2.4 |
| BTA-84365-no-rs | A/T | 9 | 82,321 | 0.35 | 3.38 | -0.57 | 0.16 | 2.5 |
| BTB-00400339 | C/T | 9 | 84,609 | 0.08 | 4.52 | 1.12 | 0.27 | 3.4 |
| Pinbone width (PinWdt) | | | | | | | | 7.2 |
| Hapmap35504-SCAFFOLD52046_3051 | C/T | 2 | 27,274 | 0.07 | 3.66 | 0.72 | 0.19 | 2.7 |
| ARS-BFGL-BAC-11798 | C/T | 12 | 12,723 | 0.26 | 2.58 | 0.34 | 0.11 | 1.8 |
| ARS-BFGL-NGS-57983 | A/G | 23 | 49,264 | 0.15 | 3.64 | 0.52 | 0.14 | 2.7 |
| Heart girth (HeartGrt) | | | | | | | | 16.9 |
| BTB-00901868 | A/G | 1 | 33,983 | 0.05 | 2.72 | 2.87 | 0.92 | 1.9 |
| Hapmap44539-BTA-37518 | C/T | 1 | 82,378 | 0.41 | 3.64 | 1.48 | 0.40 | 2.7 |
| ARS-BFGL-NGS-52663 | A/G | 1 | 141,654 | 0.11 | 3.07 | 2.19 | 0.65 | 2.2 |
| BTB-00139072 | C/T | 3 | 86,548 | 0.19 | 3.86 | -1.96 | 0.51 | 2.9 |
| BTB-01207097 | A/G | 7 | 40,797 | 0.14 | 2.83 | 1.77 | 0.56 | 2.0 |
| Hapmap42167-BTA-28651 | A/G | 18 | 51,323 | 0.16 | 3.34 | -1.94 | 0.55 | 2.4 |
| ARS-BFGL-NGS-23411 | C/T | 22 | 5,075 | 0.15 | 3.7 | -2.09 | 0.56 | 2.7 |

[a,c] SNP marker annotations and their positions were based on the bovine reference genome (btau4.0).
[b] Nucleotides of substitution. [d] Minor allele frequency.
[e] Negative logarithm of the comparison-wise p-value of the test statistic against the null hypothesis of no SNP effect at the SNP position.
[f] Estimate is for allele substitution effect replacing the latter with the former allele (nucleotide) in the SNP column.
[g] Standard error.
[h] Proportion of phenotypic variance explained by the SNP. The values on the rows of trait names are the sum of the $\%\sigma^2_p$ values across all SNPs for the trait.

For height at withers (HgtWithers), five significant QTLs were detected on BTAs 3, 4, 6 and 16 (Table 2). Two QTL on BTA3 were positioned at 88 and 97 Mb, respectively. Abe et al. (2008) found a QTL for the trait on BTA5 in an F2 cross population between Japanese Black and Limousin, while we could not find any SNP on the chromosome. Malau-Aduli et al. (2007) reported a QTL for HgtWithers on BTA2, while no QTL was detected on that chromosome in Japanese Black cattle. These inconsistent results may be partly due to different genetic background effects between breeds.

For Rump height (HgtRump), nine QTL were detected on BTAs, 3 (88 Mb), BTA4 (13 and 106 Mb), BTA6 (30 and 44 Mb), BTA16 (23 Mb), BTA20 (30 Mb), BTA22 (7

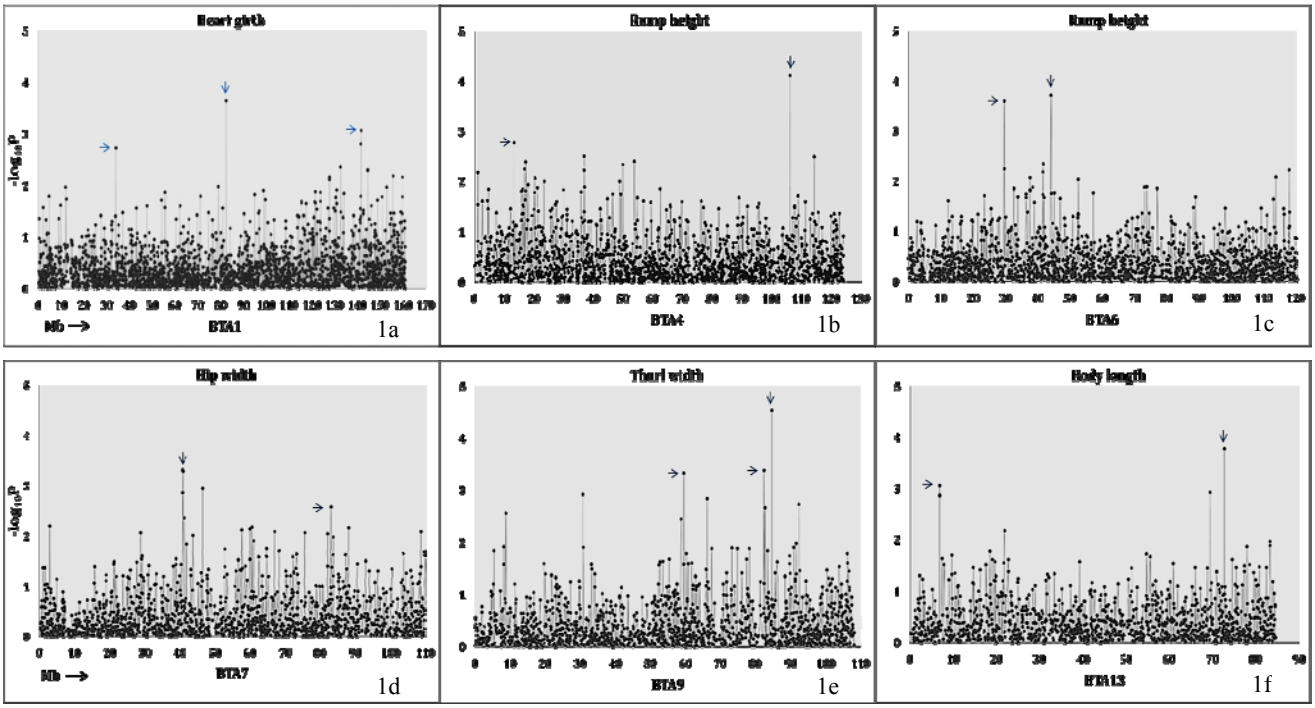


**Figure 1.** Test statistic profiles on BTA1 for heart girth (1a); BTA4, BTA6 for rump height (1b, 1c); BTA7 for hip width (1d); BTA9 for thurl width (1e); and BTA13 for body length (1f). The vertical arrows indicated the SNPs, Hapmap44539-BTA-37518 (1a), BTA-72175-no-rs (1b), Hapmap28019-BTC-054809 (1c) BTB-01207246 (1d) BTB-00400339 (1e) and, Hapmap57858-rs29019930 (1f) with the most statistical significance on the test chromosome. Other significant SNP(s) selected by the model selection (at $p<0.001$) is marked by the horizontal arrows.

Mb) and BTA25 (17 Mb) (Table 2). Kolbehdari et al. (2008) performed WGA analysis on Canadian Holstein bulls and detected QTL for stature on BTA3 (57 Mb) and BTA4 (56 Mb), along with six other SNPs on BTAs 1, 5, 7, 11, 19 and 24. Two QTLs on the BTA4 (28 cM) and BTA22 (72 cM) were found in a Holstein-Friesian population by Ashwell et al. (2005). We also detected one QTL for the trait at 13 Mb of BTA4 that was closely located to the BTA4 QTL of Kolbehdari et al. (2008). Hiendleder et al. (2003) found one QTL for HgtRump at 66 cM of BTA6, while we also detected one QTL at 44 Mb of the same BTA (Table 2).

For body length (BodyLen), ten significant SNPs were detected on BTAs 2, 7, 12, 13, 14, 15, 19, 25 and 28 (Table 2). Malau-Aduli et al. (2007) found a QTL on BTA2 at 4 cM for the trait in Japanese Black cattle, while the significant SNP on BTA2 was located at 7 Mb in this study.

Our analyses revealed nine significant SNPs for chest depth on different nine chromosomes (Table 2). Ashwell et al. (2005) found QTL for body depth, on BTAs 7, 16 and 23 in Holstein-Friesian cattle, and their 95% confidence intervals for the QTL also included the positions of the SNPs detected for the respective BTAs in this study (Table 2). Hiendleder et al. (2003) detected QTL on BTA6 for several conformation traits, *i.e.* body (trunk size) (85 cM), rump width (87 cM), which were closely located to the ChestDep QTL (87 Mb, BTA6) in this study (Table 2).

A total of eight significant SNPs affecting chest width were detected on BTAs 5, 10, 11, 13, 23, 26 and 27 (Table 2). Near the SNP on BTA10 (46 Mb), a QTL for the trait was detected at 42 cM in a Holstein-Friesian population (Ashwell et al., 2005). The WGA test in a Canadian Holstein population revealed a QTL in BTA26 (9cM) (Kolbehdari et al. (2008)), while we detected the BTA-88213-no-rs SNP for the trait at 25 Mb (Table 2). Ashwell et al. (1998) detected significant markers for dairy capacity (dairy form and strength (or chest width)) on BTA23 and BTA26, in which two SNPs for chest width were also detected in this study (Table 2).

For rump length, eleven SNPs were detected in ten chromosomes, and all of the SNPs explained about 25.7% of the phenotypic variation (Table 2). Kolbehdari et al. (2008) detected QTLs for overall rump in a Canadian Holstein population on BTA3 (17 Mb) and BTA8 (50 and 57 Mb). However, the SNPs detected on the same chromosomes in this study had inconsistent locations with Kolbehdari et al. (2008) (Table 2).

Only four SNPs for hip width were detected on BTAs 6, 7, and 9. Abe et al. (2008) performed whole genome scans to detect any significant QTL for hip-point width in a cross population of Japanese Black and Limousin. However, no QTL was reported for the trait.

Six significant SNPs were detected for thurl width on

BTAs 2, 5, 8 and 9. On BTA9, three SNPs for the trait were located at 59, 82, and 84 Mb, respectively (Table 2). Ashwell et al. (2005) and Malau-Aduli et al. (2007) found suggestive QTL on BTA2 at 2 cM and 14 cM positions, respectively. However, we found one SNP in the distal region (94 Mb) of the chromosome (Table 2).

For pinbone width, we found only three significant SNPs on BTAs 2, 12 and 23 (Table 2). Malau-Aduli et al. (2007) detected two QTLs on BTA2 at 16 and 19 cM. We detected one SNP for the trait in the similar location (27 Mb) of the chromosome (Table 2).

Seven SNPs were detected for heart girth on five chromosomes, among which three SNPs were located on BTA 1 (Table 2). Abe et al. (2008) did not find any QTL for the trait in a population of Japanese Black and Limousin cross, and Malau-Aduli et al. (2007) found only one QTL on BTA5, on which no SNP for heart girth was detected in this study (Table 2).

Some SNPs affected more than one conformation trait in this study. For example, four SNPs had significant associations with HgtWithers and HgtRump, *i.e.* BTA-68507-no-rs (BTA3, 88 Mb), BTA-72175-no-rs (BTA4, 106 Mb), Hapmap52018-BTA-75646 (BTA6, 30 Mb), and BTA-88802-no-rs (BTA16, 23 Mb). Another SNP that was located at 2 Mb of BTA10 (ARS-BFGL-NGS-40198) was associated with both ChestWdt and RumpLen traits (Table 2). For several chromosomal regions, significant SNPs influencing different traits were closely located, e.g. the SNPs in BTA3 affecting five different conformation traits were clustered between 87 to 97 Mb (Table 2). Also, in the BTA7 region flanked by 41 and 44 Mb, three SNPs for chest depth, hip width, and heart girth were detected (Table 2). These results support characteristics of gene structure and functions, *i.e.* pleiotropy and clustering of multi-gene families.

## CONCLUSION

Body conformations are positively correlated to live weight changes and growth in cattle (Varade and Ali, 2001). These traits show various ranges of heritabilities from 0.11 to 0.60 (Visscher and Goddard, 1995; Ashwell et al., 1998; Schrooten et al., 2000). Thus, care is taken in implementing breeding programs, which depends on genetic characteristics of the conformation traits of interest. We scanned the whole genome of Hanwoo steers to detect QTL for conformation traits using the Illumina 50K SNP chip, and successfully found several significant SNPs. However, additional studies are needed to further detect more SNPs and to validate the effects of the SNPs, in order to apply the SNPs into commercial Hanwoo populations via MAS programs. Additional collection of genotypes and phenotypes of the conformation measures of Hanwoo samples is on progress.

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