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Identification of genomic regions that exhibit sexual dimorphism for size and muscularity in cattle¹

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ABSTRACT:

Sexual dimorphism, the phenomenon whereby males and females of the same species are distinctive in some aspect of appearance or size, has previously been documented in cattle for traits such as growth rate and carcass merit using a quantitative genetics approach. No previous study in cattle has attempted to document sexual dimorphism at a genome level; therefore, the objective of the present study was to determine if genomic regions associated with size and muscularity in cattle exhibited signs of sexual dimorphism. Analyses were undertaken on 10 linear type traits that describe the muscular and skeletal characteristics of both males and females of 5 beef cattle breeds; 1,444 Angus (AA), 6,433 Charolais (CH), 1,129 Hereford (HE), 8,745 Limousin (LM), and 1,698 Simmental (SI). Genome wide association analyses were undertaken using imputed whole-genome sequence data for each sex separately by breed. For each SNP that was segregating in both sexes, the difference between the allele substitution effect sizes for each sex, in each breed separately, was calculated. Suggestively ($p \leq 1 \times 10^{-5}$) sexually dimorphic SNPs that were segregating in both males and females were detected for all traits in all breeds, although the location of these SNPs differed by both trait and breed. Significantly ($p \leq 1 \times 10^{-8}$) dimorphic SNPs were detected in just three traits in the AA, seven traits in the CH and three traits in the LM. The vast majority of all segregating autosomal SNPs (86% in AA to 94% in LM) had the same minor allele in both males and females. Differences ($p \leq 0.05$) in allele frequencies between the sexes were observed for between 36% (LM) and 66% (AA) of the total autosomal SNPs that were segregating in both sexes. Dimorphic SNPs were located within a number of genes related to muscularity and/or size including the *NAB1*, *COL5A2*, and *IWS1* genes on BTA2 that are located close to, and thought to be co-inherited with, the *MSTN* gene. Overall, sexual dimorphism exists in cattle at the genome level, but it is not consistent by either trait or breed.

Keywords: beef cattle, genomics, GWAS, sexual antagonism, sexual dimorphism,

LIST OF ABBREVIATIONS

AA, Angus

BL, back length

BTA, *Bos Taurus* autosome

CD, chest depth

CH, Charolais

CW, chest width

DHQ, development of the hind quarter

DIT, development of inner thigh

DL, development of loin

GRM, genomic relationship matrix

GWAS, genome wide association study

HD, high density

HE, Hereford

HW, hip width

LM, Limousin

MAF, minor allele frequency

PAR, pseudo autosomal region

QTL, quantitative trait loci

SI, Simmental

SNP, single nucleotide polymorphism

TW, thigh width

WH, wither height

WOW, wither width

WGS, whole genome sequence

INTRODUCTION

Sexual dimorphism is the phenomenon whereby males and females of the same species are distinctive in behaviour, size, or appearance (Berns, 2013). This is attributable to the combination of sex-specific genes on sex chromosomes, sex-specific expression of genes, and other regulatory mechanisms that are not yet widely understood (Pointer et al., 2013). Sex-dependent differences have been documented for a whole range of traits in different species ranging from colour, ornamentation, mating behaviour, and size (McPherson and Chenoweth, 2012; Berns, 2013; van der Heide et al., 2016). An individual's sex is also known to have an influence on the growth of body tissues and could, therefore, affect carcass composition and weight distribution within the body tissue (Berg and Butterfield, 1976). Sexual size dimorphism is likely to have originated in mammals during evolution due to competition among males for access to females; males would fight one another to gain access to females and the winner, generally the bigger, stronger animal would mate with more females (Kirkpatrick, 1987; Katz, 2008). In selective breeding systems, breeding males are selected on numerous desirable traits and consequently competition for mates has been diminished in domesticated animals. Nonetheless, evidence of sexual dimorphism based on quantitative genetics approaches have been reported for several economically important traits in cattle, including growth rate (Koch and Clark, 1955; Marlowe and Gaines, 1958; van der Heide et al., 2016) and carcass traits (Crews Jr and Kemp, 2001; Bittante et al., 2018).

Linear type traits describing the muscular and skeletal characteristics of an animal are scored globally in both dairy (Veerkamp and Brotherstone, 1997; Berry et al., 2004) and beef (Mc Hugh et al., 2012; Mazza et al., 2014) cattle. These traits are typically considered as being genetically the same in both males and females; estimated genetic correlations of near unity between the same linear type trait in different sexes of cattle substantiate this assumption (Doyle et al., 2018). Genetic correlations, however, are a manifestation of the

cumulative effect of both linkage and pleiotropy across the entire genome and it is possible that the control of such traits by sex may differ in specific genomic locations. The objective, therefore, of the present study was to determine if genomic regions associated with size and muscularity in cattle exhibited signs of sexual dimorphism. This knowledge will be useful in informing breeding programmes of the potential improvement in accuracy achievable by evaluating males and females separately.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for the present study as data were obtained from the existing Irish Cattle Breeding Federation (ICBF) national database (<http://www.icbf.com>).

Phenotypic data

Linear type traits are routinely scored in both registered and commercial beef herds by trained classifiers from the ICBF as part of the Irish national beef breeding programme (Mc Hugh et al., 2012; Berry and Evans, 2014). The type traits used in the present study describe the muscular and skeletal development of the animal and include development of the hind quarter (DHQ), inner thigh (DIT), and loin (DL), thigh width (TW), wither width (WOW), wither height (WH), back length (BL), hip width (HW), and chest width (CW) and depth (CD). The five muscular traits were scored (Supplementary Table S1) on a scale of 1 (narrow) to 15 (wide) while the five skeletal traits (Supplementary Table S1) were scored on a scale of 1 (short or narrow) to 10 (long/tall or wide). Data on these 10 traits were available on 147,704

purebred Angus, Charolais, Hereford, Limousin, and Simmental beef cattle scored between 6 and 16 months of age between the years 2000 and 2016.

Data editing procedures and the justification for such edits are outlined in detail by Doyle et al. (2019, 2020a, 2020b). Animals were discarded from the dataset if the sire, dam, herd, or classifier was unknown, or the parity of the dam was not recorded. Parity of the dam was subsequently recoded into 1, 2, 3, 4, and ≥ 5 . Contemporary group was defined as herd-by-scoring date generated separately within each breed; each contemporary group had to have at least five records. Each of the 10 traits were separately standardized to a common variance within classifier-by-year as described in detail by Brotherstone (1994). Following edits, data were available on 81,200 animals (Supplementary Table S2) consisting of 3,356 Angus (AA), 31,049 Charolais (CH), 3,004 Hereford (HE), 35,159 Limousin (LM) and 8,632 Simmental (SI).

Generation of adjusted phenotypes

Prior to inclusion in the genome wide association analysis, all phenotypes were adjusted within breed in ASREML (Gilmour et al., 2009) using the model:

$$y_{ijkl} = \mu + \text{HSD}_i + \text{AM}_j + \text{DP}_k + \text{Animal}_l + e_{ijkl}$$

where y_{ijkl} is the linear type trait, μ is the overall mean, HSD_i is the fixed effect of herd-by-scoring date ($i=11,130$ levels), AM_j is the fixed effect of the age in months of the animal ($j=11$ classes from 6 to 16 months), DP_k is the fixed effect of the parity of the dam ($k=1, 2, 3, 4$ and ≥ 5), Animal_l is the random additive genetic effect of the animal where $N(0, \mathbf{A}\sigma_a^2)$, and e is the random residual effect where $N(0, \mathbf{I}\sigma_e^2)$; σ_a^2 is the additive genetic variance, σ_e^2 is the residual variance, $\mathbf{A}$ is the numerator relationship matrix and $\mathbf{I}$ is an identity matrix. The

adjusted phenotype used in the subsequent analysis was the raw phenotype less the fixed effect solutions of HSD, AM and DP. This approach of pre-adjustment of phenotypes was undertaken (as opposed to fitting directly in the association analysis) so as to generate a better estimate of especially the contemporary group effect which would have contained non-genotyped animals.

Genotype data

Of the phenotypic dataset of 81,200 animals, 19,449 animals from the five beef breeds (Supplementary Table S2) were imputed to whole genome sequence as part of a larger dataset of 638,662 multi-breed genotyped animals (Purfield et al., 2019). These 638,662 animals were genotyped using one of 7 different genotype panels as described previously by Doyle et al. (2020a, 2020b). The reference population used for imputation contained 90% male animals and 8% female animals; 2% of the reference population were of unknown sex. Each animal had to have a call rate $\geq 90\%$ and only SNPs with a known chromosome and position on UMD 3.1, and SNPs with a call rate $\geq 90\%$ within the panel were retained for imputation. While the imputation

All autosomes of genotyped animals were imputed to whole genome sequence (WGS) following the steps outlined in Doyle et al. (2020a, 2020b). Imputation of the pseudo-autosomal region (PAR) and non-PAR regions of the X chromosome was undertaken separately. The non-PAR region was imputed for males and females separately. The PAR region of the X chromosome was defined from 143,861,798 to 148,823,899 bp (Mao et al., 2016). Regions of poor WGS imputation accuracy were discarded as described by Purfield et al. (2019). Furthermore, within each breed and each sex, all SNPs with a minor allele

frequency (MAF) ≤ 0.002 were not considered further (Supplementary Table S2). The number of SNPs remaining for each sex in each breed is outlined in Supplementary Table S2.

Genome-wide association

Whole genome association analyses were performed within each sex in each breed separately using a mixed linear model association analysis in GCTA (Yang et al., 2011). Autosomal SNPs from the original high density (HD) panel (i.e., 734,159 SNPs) were used to construct the genomic relationship matrix (GRM) for each sex within each breed as per Doyle et al. (2020a, 2020b) who used the data from the present study but in a combined analysis of both sexes. In the association analyses of the X chromosome, all males were coded as homozygous for the genotyped allele for SNPs in the non-PAR region while heterozygous SNPs were accepted in the PAR region. The model used for the within-sex and within-breed analysis was

$$\mathbf{y} = \mu + \mathbf{x}\mathbf{b} + \mathbf{u} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of preadjusted phenotypes, μ is the overall mean, $\mathbf{x}$ is the vector of imputed genotypes, $\mathbf{b}$ is the vector of additive fixed effects of the candidate SNP to be tested for association, $\mathbf{u} \sim N(0, \mathbf{G}\sigma_u^2)$ is the vector of additive genetic effects, where $\mathbf{G}$ is the genomic relationship matrix calculated from the HD SNP genotypes, and σ_u^2 is the additive genetic variance, and $\mathbf{e} \sim N(0, \mathbf{I}\sigma_e^2)$ is the vector of random residual effects, where $\mathbf{I}$ is the identity matrix and σ_e^2 is the residual variance.

Dimorphism

For each SNP that was analysed in both sexes (i.e., segregating in both sexes), the difference between the allele substitution effect sizes for each sex, in each breed separately, was calculated using a t-test:

$$t = \frac{b_m - b_f}{\sqrt{\frac{SE_m^2 + SE_f^2}{n_m + n_f}}}$$

where b_x is the allele substitution effect in males (m) and females (f), SE is the estimated standard error of the allele effect, and n is the respective sample size. The presence of dimorphism was determined at each SNP based on the calculated p-value from the t-test statistic. A SNP with a p-value $\leq 1 \times 10^{-5}$ was assumed to have a suggestively different allele effect in the two sexes while a SNP with a p-value $\leq 1 \times 10^{-8}$ was assumed to have a significantly different allele substitution effect in the two sexes. These levels of significance are generally consistent with recommended levels (Pe'er et al., 2008). Nonetheless, an additional test was undertaken in the CH and LM breeds where two populations were generated: the first population included half the males and half the females combined with the second population consisting of the remainder. Association analyses were undertaken in each population and the allele effects compared statistically to mimic the approach used in the present study to detect dimorphism. The significance of the difference in allele substitution effect was not $< 1 \times 10^{-8}$, thus providing confidence in this threshold used in this study.

QTL detection

To identify QTL regions that were dimorphic in more than one trait or more than one breed, each chromosome was split into 1kb genomic windows and windows containing at least one suggestive ($p \leq 1 \times 10^{-5}$) or significant ($p \leq 1 \times 10^{-8}$) SNP were compared across the traits and breeds.

RESULTS

The scale of measurement, mean, and standard deviation of the linear type traits in each sex in each breed is in Supplementary Table S1. Single nucleotide polymorphisms with evidence of significant ($p \leq 1 \times 10^{-8}$) dimorphism were detected for some traits, while suggestively ($p \leq 1 \times 10^{-5}$) dimorphic SNP were detected for all of the traits in all 5 breeds; however, these SNPs differed both by trait and by breed.

Angus

A total of 16,541,913 SNPs were segregating in the 1,044 males and 15,402,160 SNPs were segregating in the 400 females. Of these totals, 15,008,408 SNPs were segregating in both the male and female populations (Supplementary Table S2). Significant dimorphism ($p \leq 1 \times 10^{-8}$) was evident for a total of 7 SNPs across just three traits (HW, TW, and DIT; Table 1) while suggestive dimorphism ($p \leq 1 \times 10^{-5}$) was evident for between 31 (DHQ) and 1,254 (HW) SNPs depending on the trait (Table 1). In general, the allele substitution effects of the dimorphic SNPs tended to be in opposite directions in each sex (i.e., if the allele effect in the male population was negative, then the allele effect of the same allele in the female population was positive or vice versa; Table 2 and 4). The allele effects in the male

population also tended to be closer to zero than those in the female population (Table 2 and 4) and the most significantly dimorphic traits tended to have a very low MAF in the female population. Of the muscular traits investigated, the most significantly dimorphic SNP was an intronic SNP ($p = 3.45 \times 10^{-9}$) located within the *ADGRA3* gene on BTA6 and was associated with DIT (Table 2); this SNP had an allele effect of +0.12 (SE = 0.13) and a MAF of 0.026 in males but an allele effect of -3.68 (SE 0.63) and a MAF of 0.003 in females. Of the skeletal traits, the most significantly dimorphic SNP was an intergenic SNP, rs208222963 ($p = 9.86 \times 10^{-10}$), located on BTA8 that was associated with HW (Table 3); this SNP had an allele substitution effect of -0.23 (SE = 0.10) in males but +2.29 (SE = 0.40) in females with a MAF of 0.025 in the males and 0.005 in the females.

Of the 1kb windows containing at least one suggestively associated dimorphic SNP, there was little overlap between the muscular and skeletal groups of traits. The only overlap in windows between the muscular and skeletal traits was between HW, DL and WOW (two windows on each of BTA23 located at 14.555Mb and 51.713Mb), between HW and TW (one window on BTA8 located at 66.264Mb), and between HW and DL (two windows on BTA27 at 18.141Mb and 18.403Mb). Only one 1kb genomic window was suggestively associated with three skeletal traits (WH, BL, and HW; Supplementary Fig. S1a) and this was located between 66.386Mb and 66.387Mb on BTA8, within the *ENSBTAG00000006446* gene. The greatest overlap across traits in AA was between WH and HW where a total of 12 1kb windows across 5 chromosomes suggestively exhibited sexual dimorphism (Supplementary Fig. S1a). Similar to the skeletal traits, only one 1kb window was common to more than two muscular traits (DL, DIT, and TW) and this was located between 59.524Mb and 59.525Mb on BTA24 (Supplementary Fig. S2a). The largest overlap across all skeletal traits was between DL and TW where 7 1kb windows exhibited suggestive dimorphism. Minimal overlap was detected among the remaining skeletal traits

Charolais

A total of 18,054,274 SNPs were segregating in the 4,641 CH males and 17,448,948 SNPs were segregating in the 1,792 CH females. Of these, 17,227,625 SNPs were segregating in both the male and female animals. Evidence of suggestive dimorphism ($p \leq 1 \times 10^{-5}$) existed for between 51 (DIT) and 3,051 (CW) SNPs depending on the trait (Table 1), while evidence of significant dimorphism ($p \leq 1 \times 10^{-8}$) was evident in all but three traits (i.e., DIT, HW and WH). Of the muscular traits, the most significantly dimorphic SNP was rs110487743 ($p = 1.36 \times 10^{-10}$), an intronic SNP located within the *NAB1* gene on BTA2 which exhibited dimorphic associations for DL (Table 4). Of the skeletal traits, the most significantly dimorphic SNP was for CW and was an intergenic SNP, rs446294174 ($p = 4.44 \times 10^{-16}$; Table 5) that had an allele effect of -0.03 (SE = 0.18) in males but -3.34 (SE = 0.36) in females with a MAF of 0.015 in males and 0.008 in females.

Of the 1kb windows containing at least one dimorphic SNP, no windows were shared between the skeletal and muscular trait groups. Despite the lack of overlap between the skeletal and muscular traits in the CH, considerable dimorphism was detected across the muscular traits. Across trait dimorphism was detected in four of the five muscular traits (i.e., DHQ, DL, TW, and WOW; Supplementary Fig. S2b) where 8 1kb windows in common between 5.54Mb and 5.60Mb on BTA2 contained a suggestively associated dimorphic SNP; only one gene, *NAB1*, was located within this region. An additional 22 1kb windows on BTA2 were also deemed to exhibit across trait dimorphism for the muscular traits (Supplementary Fig. S2b). Compared to the muscular traits, fewer windows containing a suggestive SNP were common among the skeletal traits. Seven 1kb windows were common to CW and CD (Supplementary Fig. S1b), one window on each of BTA4, BTA5, BTA12, and

BTAX and three windows on BTA13 that contained the *BTBD3* gene. A single window on BTA15 at 72.31Mb was common to both WH and BL.

Hereford

A total of 17,241,152 SNPs were segregating in the 727 HE males and 16,494,904 SNPs were segregating in the 402 HE females. Of these, 15,991,751 SNPs were segregating in both the male and female animals. In comparison to the AA and CH, evidence of suggestive dimorphism ($p \leq 1 \times 10^{-5}$) was evident for fewer SNPs in all of the traits, ranging from 39 (DIT) to 256 (CW) SNPs depending on the trait; there was no evidence of significant dimorphism ($p \leq 1 \times 10^{-8}$; Table 1). Similar to the AA, the allele substitution effect of the dimorphic SNPs in the males tended to be in the opposite direction to the allele effect of the same SNP in the females (Table 6 and 8). The most significantly dimorphic SNP in the muscular traits was rs798960299 ($p = 6.30 \times 10^{-8}$), an intronic variant located within the *NR5A2* gene on BTA16 with an allele effect of +0.42 (SE = 0.13) in males but -0.61 (SE = 0.14) in females (Table 6). Of the skeletal traits, the most significantly dimorphic SNP was rs381085044, an intergenic SNP on BTA1 that had a dimorphic association with CW represented by an allele effect of -0.22 (SE = 0.06) in males but +0.32 (SE = 0.08) in females (Table 7).

No 1kb window that contained at least one dimorphic SNP was common to more than two traits. Limited dimorphism was found between CW and HW, where three windows between 40.75Mb and 40.78Mb on BTA24 containing the *PTPRM* gene were suggestively associated with both traits (Supplementary Fig. S1c). Chest width also had two separate windows exhibiting dimorphism on BTA13 between 27.46Mb and 27.47Mb in common with CD, and one window on BTA14 at 45.485Mb in common with WH. Two adjacent 1kb windows on BTA8 at 25.965Mb were common to both WH and BL. For the muscular traits,

WOW had one window in common with each of DL (BTA10 at 48.327Mb), TW (BTA10 at 50.420Mb) and DHQ (BTA9 at 83.332Mb). One 1kb window was also common to both TW and DHQ (BTA16 at 68.580Mb; Supplementary Fig. S2c).

Limousin

A total of 18,056,913 SNPs were segregating in the LM males and 17,767,237 SNPs were segregating in the LM females. Of these, 17,482,131 SNPs were segregating in both the male and female animals. Between 46 (TW) and 1,105 (CW) SNPs were suggestively dimorphic ($p \leq 1 \times 10^{-5}$) while 3 traits (i.e., CW, CD, and DHQ) had evidence of significant dimorphism ($p \leq 1 \times 10^{-8}$; Table 1). Of the muscular traits, the most significantly dimorphic SNP was rs42425148 ($p = 1.85 \times 10^{-9}$), an intergenic SNP located on BTA1 that had a dimorphic association with DHQ (Table 8) represented by an allele effect of -0.01 (SE = 0.15) in males but -1.64 (SE = 0.23) in females. The most significantly dimorphic SNP for the skeletal traits was also an intergenic SNP, rs478688690 ($p = 3.63 \times 10^{-11}$), located on BTA11, that had a dimorphic association with CW (Table 9) with an allele effect of +0.03 (SE = 0.29) in males and -3.86 (SE = 0.51) in females; this SNP had a MAF of 0.005 in males and 0.003 in females. Similar to the AA and CH, SNPs with a higher MAF tended to have an allele effect that was closer to zero. An intergenic SNP with dimorphic associations in HW ($p = 5.71 \times 10^{-7}$) had a MAF of 0.493 in males and 0.486 in females but the allele substitution effects were just -0.07 (SE = 0.01) in males and +0.06 (SE = 0.02) in females.

Genomic regions that exhibited sexual dimorphism across traits in the LM were limited; 8 1kb windows were found to be suggestively associated with three of the skeletal traits (WH, BL, HW; Supplementary Fig. S1d) whereas only 3 windows were common between TW and WOW of the muscular traits (Supplementary Fig. S2d). All 8 windows associated with WH, BL and HW were on BTA6 but no obvious candidate gene was located

in the vicinity. The 40 windows suggestively associated with both CW and CD (Supplementary Fig. S1d) were located on 15 different autosomes, BTA5, BTA6, BTA8, BTA9, BTA10, BTA11, BTA13, BTA16, BTA17, BTA18, BTA20, BTA22, BTA24, BTA26, BTA29, and BTAX.

Simmental

A total of 18,257,175 SNPs were segregating in the SI males and 17,814,297 SNPs were segregating in the SI females, while 17,319,250 of these SNPs were segregating in both the males and females. Between 87 (BL) to 679 (CD) SNPs were suggestively dimorphic ($p \leq 1 \times 10^{-5}$) while no SNP was significantly dimorphic ($p \leq 1 \times 10^{-8}$; Table 1). Once again, the most significantly dimorphic SNPs tended to have a low MAF and a large allele effect size. The most significantly dimorphic SNP associated with any of the muscular traits was rs110995439 ($p = 1.40 \times 10^{-8}$), an intron variant located within the *GPC5* gene on BTA12 that had a dimorphic association with DIT; the allele substitution effect in the males was -0.85 (SE = 0.34) while the allele substitution effect in the females was +1.76 (SE = 0.30; Table 10). Of the skeletal traits, the most significantly dimorphic SNP was an intergenic SNP, rs437227524 ($p = 1.98 \times 10^{-8}$), that had a dimorphic association with CD (Table 11) and had an allele substitution effect of -0.08 (SE = 0.24) in the male population but -2.64 (SE = 0.42) in the female population with a MAF of 0.004 in the males and 0.002 in the females. An intronic SNP, rs133629874 ($p = 2.20 \times 10^{-7}$), located within the *MMRN1* that had a dimorphic association with CW had a MAF of 0.439 in males and 0.472 in females with an effect size of +0.14 (SE = 0.03) in males and -0.13 (SE = 0.04) in females.

Few 1kb windows containing a suggestive SNP overlapped among the muscular and skeletal traits. A single 1kb window on BTA2, approximately 0.1Mb from the *IWS1* gene, contained suggestively dimorphic SNPs for all of DIT, DL, and CW. Of the skeletal traits, no

genomic windows exhibited suggestive associated dimorphism (Supplementary Fig. S1e) and no window was suggestively associated with three or more muscular traits (Supplementary Fig. S2e). Three 1kb windows, all located on BTA18 between 3.78Mb and 3.80Mb, contained dimorphic SNPs for both TW and WOW (Supplementary Fig. S2e); these windows were located approximately 0.3Mb from the *CNTNAP4* gene. One window located on BTA28 at 41.045Mb and 6 windows on the X chromosome between 114.572Mb and 114.578Mb were dimorphic for both TW and DL. A single 1kb window was common to each of DIT and TW (13.541Mb on BTA8), DHQ and WOW (102.906Mb on BTA6), and WH and BL (145.410Mb on BTAX).

Across-breed

The numerically smaller breeds of AA, HE, and SI, had approximately 1.5 times more SNPs segregating in only one sex than the numerically larger breeds of CH and LM. Of the total autosomal SNPs that were segregating in both sexes, between 86% (AA) and 94% (LM) had the same minor alleles in both sexes. However, differences ($p \leq 0.05$) in allele frequencies between the sexes were observed for between 36% (LM) and 66% (AA) of the total autosomal SNPs that were segregating in both sexes.

The vast majority of SNPs and 1kb windows associated with any one trait were breed-specific. The most windows displaying dimorphic characteristics in common for more than one breed was for CW in both the CH and LM with 9 1kb windows common to these breeds occurring on BTA2 at 89.527Mb (n=1), on BTA12 between 87.128Mb and 87.303Mb and containing the *ENSBTAG00000032038* gene (n=6), and on BTA24 between 31.661Mb and 31.671Mb (n=2). Also for CW, a single 1kb window on BTA6 approximately 0.1Mb from the *SLC34A2* gene displayed dimorphic associations in both the AA and the CH. A single 1kb window containing the *ENSBTAG00000046311* gene on BTA10 had dimorphic associations

with HW in both the AA and SI. In the CH and the SI, two common windows, one at 91.126Mb on BTA7 and one at 70.827Mb on BTA9, exhibited dimorphism with CD in both breeds.

DISCUSSION

While several studies in cattle have investigated the presence of sexual dimorphism using a quantitative genetics approach (Crews and Kemp, 2001; van der Heide et al., 2016; Bittante et al., 2018; Doyle et al., 2018), no previous study in cattle has attempted to detect evidence of sexual dimorphism at the genome level or to compare these effects across multiple breeds of cattle. From previous quantitative genetics studies, differences in genetic parameters by cattle sex have been observed for growth rate (Koch and Clark, 1955; Marlowe and Gaines, 1958), post-weaning gain (van der Heide et al., 2016), feed intake and efficiency, fleshiness scores, carcass weight and yield (Bittante et al., 2018), as well as longissimus muscle area and backfat (Crews and Kemp, 2001). In contrast, negligible differences in genetic parameters between the sexes were detected for early growth traits such as weaning weight (Koch and Clark, 1955; van der Heide et al., 2016).

A single trait measured in different environments (or different sexes) can be regarded as separate traits which are genetically correlated (Falconer, 1952). In many situations, the genetic correlations of the same trait taken in different environments are less than unity, indicating that selection occurring in one environment may not be optimal for performance in the other environment (Mulder and Bijma, 2005). This represents a genotype-by-environment interaction although Robertson (1959) postulated that the genetic correlation between environments would need to be weaker than 0.80 to be considered of importance for breeding purposes. In quantitative genetics studies on dimorphism, it is not necessarily the environment that is causing the genetic correlations to differ from unity, but possibly the

effect of dimorphism (which is often cofounded with environment). Weaker than unity genetic correlations between the sexes may be indicative of many factors including the alleles having a different substitution effect in each sex; these differences may be due to inter-sex differences in effect sizes or the sign of the allele substitution effect differing by sex.

Bittante et al. (2018), while investigating the effects of sexual dimorphism on the fattening performance and muscling of young Belgian Blue and Piedmontese dairy cross bulls and heifers, noticed that the effects of dimorphism were greater in the Belgian Blues than the Piedmontese suggesting that the effects of sexual dimorphism may actually differ by breed. Because linear type traits which describe the skeletal and muscular conformation of an animal are related to many performance traits such as animal live weight (Mc Hugh et al., 2012), carcass merit (Mukai et al., 1995; Conroy et al., 2010), primal cut yields (Berry et al., 2019), and feed intake (Veerkamp and Brotherstone, 1997; Crowley et al., 2011), it is plausible that the underlying variome of animals contributing to differences in their skeletal or muscular characteristics may also exhibit sexual dimorphism; it is also plausible that these regions exhibiting dimorphism may differ by breed. The data set used in the present study was particularly useful to test this hypothesis in that all linear type traits were assessed in all breeds and sexes using the same scale by the same classifiers and, therefore, a direct comparison of sex effects as well as commonalities of detected regions across breeds was possible.

Using a dataset of 32,725 males and 30,887 females of the CH and LM breeds, Doyle et al. (2018) estimated variance components for 18 type traits in both sexes separately; the type traits included in the present study were those represented in that study and included functional, skeletal and muscular subjective measures. Numerical differences in variance estimates were detected between both sexes in each breed while inter-sex differences in heritability estimates were only significant ($p < 0.05$) for BL, WH, and DHQ in the CH, with

no differences observed in the LM (Doyle et al., 2018). Within trait genetic correlations between each of the 18 type traits in each sex were all stronger than 0.90 (Doyle et al., 2018); because Robertson (1959) concluded that genetic correlations had to be weaker than 0.80 to be impactful, Doyle et al. (2018) concluded a lack of dimorphism in their study. Nonetheless, genetic correlations are derived from the entire genome and therefore may not capture the granularity achieved by investigation of specific regions of the genome, as undertaken in the present study. This is especially true when only a few regions exhibit dimorphism and the extent of dimorphism in these regions may be small. Indeed the results from the present study indicate that, in fact, only a few regions exhibit dimorphism and the effects are small. Moreover, while the analyses conducted in the present study only considered SNPs segregating in both sexes, the existence of SNPs that were monomorphic in one sex may also be indicative of dimorphism.

The X chromosome

The X chromosome is the second largest chromosome in the bovine genome and accounts for over 6% of the total physical genome (148,823,899 bp; Zimin et al., 2009); it is, however, regularly discarded from genome-based studies in cattle due the inheritance of the X chromosome being different to the autosomes. Males are heterogametic (XY) and the females are homogametic (XX; Fernando and Grossman, 1990); therefore, male offspring inherit their X chromosome from their dam only, while female offspring inherit one copy of the X chromosome from their dam and the other from their sire. Furthermore, a small region of the X chromosome, known as the pseudo-autosomal region (PAR), is homologous to the Y chromosome and is inherited like an autosome with some recombination occurring during meiosis (Van Leare, et al., 2008; Su et al., 2014).

Ignoring the X chromosome could lead to important biological functions being missed and could also impact the accuracy of genomic evaluations (Lyons et al., 2014; Su et al., 2014; Mao et al., 2016). A previous study on the role of the sex chromosomes in dimorphism (Rice, 1984) revealed that while sex chromosomes were not required for the evolution of sexual dimorphism, they facilitated the evolution of sexual dimorphism for a wider range of traits than would have occurred without them and that X-linked genes in particular had a large role in the evolution of sexually dimorphic traits. In the present study, only 406 SNPs located on the X chromosome expressed sexual dimorphism in at least one breed or trait. The low number of dimorphic SNPs on the X chromosome may be a function of possible allelic content variation where females have two copies of an allele and males only have one, thus interfering with the detection of dimorphic SNPs on the X chromosome. However, previous studies have discovered that in most cases, sex chromosomes are only required to initiate sexual dimorphism and the corresponding genes are mostly located on the autosomes (Saifi and Chandra, 1999; Fairbairn and Roff, 2006).

Previous studies have linked mutations on the X chromosome to andrological and growth traits in beef cattle (Lyons et al., 2014) as well as the length of productive life in dairy cattle (Saowaphak et al., 2017). In the present study, all sexually dimorphic SNPs located on the X chromosome for any trait in any of the breeds had a greater effect size in females than in males; this is in agreement with a previous study on sexual dimorphic gene expression in cattle using RNA-seq which stated that all X-chromosomal sexually dimorphic genes had a greater effect in females than males (Seo et al., 2016). In other species, such as *Drosophila melanogaster*, it has been proven that an X-linked recessive mutation that benefits males will accumulate faster as expression in males is hemizygous and there will be no masking by dominance (Gibson et al., 2002); however, the male-biased expression of these alleles

reduces as the allele becomes more frequent in the population which enables counter-selection in the females to halt the spread of this male-biased allele.

Allele frequencies

The number of SNPs included in each of the analyses in the present study differed by both sex and breed due solely to the SNP not always segregating in each sub-population. While the vast majority of SNPs in the present study had the same minor allele in both sexes, differences between sexes in allele frequencies still exist. In humans, it has been hypothesised that inter-sex differences in allele frequencies occur during the initial evolution of sexual dimorphism due to males and females having different fitness optima for a phenotype (Rice, 1984; Lucotte et al., 2016). In cattle, differences in allele frequencies between the sexes may also have arisen due to these differential fitness optima for males and females where selection occurred at a given locus in one sex but not the other, or due to different selection pressures at that locus in each sex (Lucotte et al., 2016); for example, selection for a female trait could have very different effects on genetically correlated traits in females compared to those traits in males (Bittante et al., 2018).

Inter-sex differences in the frequency of a given allele may also be due to inter-sex differences in recombination rates; up to 75% of species that undergo recombination in their genome have different recombination rates per sex (Burt et al., 1991; Wyman and Wyman, 2013). In the majority of species, the male recombination rate is generally lower than in females (Poissant et al., 2010; Wyman and Wyman, 2013). It is thought that this lower recombination rate is advantageous to males as it maintains combinations of beneficial genes that have undergone sexual selection (Trivers, 1988); however, studies in both cattle (Ma et al., 2015) and sheep (Maddox and Cockett, 2007) reported that the male recombination rate in these species is actually higher than the females.

Across breed

Based on a series of within-breed genome-wide associations undertaken across both sexes combined using the data from the present study, Doyle et al. (2020a; 2020b) detected little to no commonality in the genomic regions associated with each type trait across breeds. This indicates that the underlying genetic basis of the same trait in each breed is quite different; therefore it was somewhat expected that the regions exhibiting dimorphism may also differ by breed. In general, the British breeds (AA and HE) had fewer suggestively or significantly dimorphic SNPs than the continental breeds but the British breeds had a greater percentage of SNPs exhibiting significant differences in allele frequencies between the sexes than the continental breeds. The location of the most significantly dimorphic SNPs also differed across the breeds. The differences observed between the breeds may be due to actual differences in the genetic basis of sexual dimorphism among the breeds, as previously observed between the Belgian Blue and Piemontese cattle breeds (Bittante et al., 2018), or may be simply due to differences in the statistical power to detect QTL due to the differences in breed-specific population sizes (Doyle et al., 2020a). Actual differences in the genetics underlying each trait may be attributable to different mutations affecting specific genes in each breed, such as the breed-specific *MSTN* mutations, or may, more likely be attributable to different QTL being affected by different selection pressures within each breed (Bittante et al., 2018).

Genes exhibiting dimorphism

Single nucleotide polymorphisms exhibiting sexually dimorphism were located within, or close to a number of different genes that have previously been associated with muscularity and/or size in cattle (Doyle et al., 2020a; 2020b). Three genes on BTA2 (*NAB1*, *COL5A2* and *IWS1*) containing dimorphic SNPs associated with multiple traits are thought to either be in

strong linkage disequilibrium with *MSTN* (Grade et al., 2009) or have been previously identified as being located within a QTL also containing *MSTN* that was associated with muscularity in beef cattle (Doyle et al., 2020a). The *MSTN* gene has already been documented as being responsible for muscular hypertrophy in cattle (Grobet et al., 1997; McPherron and Lee, 1997) and is widely known as the causal variant for many muscularity and carcass traits in cattle (Casas et al., 2000; Allais et al., 2010; Purfield et al., 2019). Another candidate gene for muscularity that exhibited evidence of sexual dimorphism was the *PDHX* gene on BTA15 that contained dimorphic SNPs for 3 of the muscularity traits in CH and has previously been associated with carcass quality traits in beef cattle (Karisa et al., 2013).

CONCLUSION

While many significantly and suggestively sexually dimorphic SNPs associated with the muscular and skeletal type traits were identified in the present study, the location and effect sizes of these tended to be both trait-specific and breed-specific. Both the allele substitution effect sizes and the allele frequencies of the dimorphic SNPs also differed by sex. This indicates that while sexual dimorphism exists in cattle at a genome level, it occurs at a low frequency but also differs both by trait and by breed.

DISCLOSURES

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Table 1: The number of suggestively dimorphic ($p \leq 1 \times 10^{-5}$) and significantly dimorphic ($p \leq 1 \times 10^{-8}$; in parenthesis) SNPs for each trait in each breed. Where there is no parenthesis, no significantly dimorphic SNP was detected.

	Angus	Charolais	Hereford	Limousin	Simmental
Chest depth	259	1,439 (84)	148	699 (5)	679
Chest width	259	3,051 (172)	256	1,105 (27)	136
Back length	34	176 (1)	241	229	87
Hip width	1,254 (1)	272	264	107	178
Wither height	155	62	122	95	115
Development of hind quarter	31	341 (28)	82	433 (3)	115
Development of inner thigh	329 (5)	51	39	241	91
Development of loin	274	101 (9)	97	74	233
Thigh width	128 (1)	216 (9)	62	46	160
Wither width	42	125 (9)	67	268	92

Table 2: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the muscular traits in the Angus.

Trait	Chr	Start	End	No. of dimorphic SNPs	Location of most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Development of hind quarter	10	101970186	102988802	4	102482010 ^a	101424768	0.017	-0.25 (0.14)	0.008	1.53 (0.37)	6.64x10 ⁻⁶
	12	61322071	62452555	6	61890529 ^a	61531778	0.118	-0.12 (0.06)	0.118	0.41 (0.10)	3.60x10 ⁻⁶
	14	33610209	34610573	2	34110209 ^b	32047165	0.122	0.10 (0.06)	0.140	-0.37 (0.09)	5.32x10 ⁻⁶
	20	15474737	16474737	1	15974737 ^a	15988960	0.034	-0.41 (0.10)	0.056	0.10 (0.14)	1.30x10 ⁻⁶
	21	53862500	54867369	5	54367218 ^a	53876946	0.020	0.39 (0.13)	0.015	-0.90 (0.25)	4.16x10 ⁻⁶
Development of inner thigh	5	10273554	11452988	5	10773554 ^b	10714008	0.004	0.50 (0.31)	0.003	-3.28 (0.63)	7.04x10 ⁻⁸
	6	42909192	44746796	7	43497285 ^b	42045392	0.026	0.12 (0.13)	0.003	-3.68 (0.63)	3.45x10 ⁻⁹
	14	33610209	35958833	69	34110209 ^b	32047165	0.122	0.12 (0.06)	0.140	-0.49 (0.10)	8.22x10 ⁻⁸
	20	15474737	17005863	10	15974737 ^a	15988960	0.034	-0.39 (0.12)	0.056	0.58 (0.14)	1.50x10 ⁻⁷
	26	17899058	19802025	5	18537518 ^{bc}	18672598	0.005	0.88 (0.30)	0.003	-4.42 (0.89)	1.44x10 ⁻⁸
Development of loin	2	101653384	102770408	4	102270408 ^a	101752093	0.005	-0.45 (0.27)	0.004	2.60 (0.56)	9.12x10 ⁻⁷
	5	99020985	100028321	3	99527732 ^a	99094471	0.025	0.30 (0.12)	0.039	-0.70 (0.15)	3.75x10 ⁻⁷
	6	117849749	118880939	4	118349749 ^d	113543086	0.007	-0.59 (0.24)	0.004	2.46 (0.55)	4.29x10 ⁻⁷
	11	76054540	77056745	11	76556745 ^a	76492699	0.207	0.07 (0.05)	0.133	-0.46 (0.09)	2.36x10 ⁻⁷
	21	53940632	55017766	6	54450845 ^a	53960572	0.011	0.40 (0.18)	0.014	-1.28 (0.27)	4.06x10 ⁻⁷
Thigh width	8	65764830	67442321	23	66797263 ^a	66310487	0.004	-1.25 (0.31)	0.003	2.78 (0.70)	1.53x10 ⁻⁷
	9	29472999	30503566	6	29977509 ^a	29598390	0.039	-0.36 (0.11)	0.086	0.39 (0.12)	5.43x10 ⁻⁶
	10	54322355	55487705	8	54835748 ^b	54777779	0.008	-0.66 (0.24)	0.004	2.35 (0.57)	1.21x10 ⁻⁶
	12	49908375	50963553	5	50408375 ^a	50050440	0.010	-0.71 (0.22)	0.003	2.78 (0.70)	1.95x10 ⁻⁶
	24	59024887	60257758	24	59524887 ^a	59018608	0.008	0.77 (0.23)	0.011	-1.49 (0.30)	3.90x10 ⁻⁹
Width of withers	2	34064457	35064503	2	34564503 ^b	34459316	0.329	0.12 (0.05)	0.386	-0.32 (0.07)	6.09x10 ⁻⁷
	3	2519849	3522479	2	3019849 ^a	2958782	0.009	0.69 (0.23)	0.008	-1.71 (0.43)	1.03x10 ⁻⁶
	9	2753165	3753801	6	3253165 ^a	3188640	0.015	-0.20 (0.17)	0.011	1.44 (0.31)	3.22x10 ⁻⁶
	11	76054540	77056745	11	76556745 ^a	76492699	0.207	0.13 (0.06)	0.133	-0.45 (0.11)	1.27x10 ⁻⁶
	23	14054921	15055421	3	14554921 ^a	14546664	0.018	-0.55 (0.17)	0.008	1.58 (0.43)	5.12x10 ⁻⁶

^aintergenic variant, ^bintron variant, ^cdownstream gene variant, ^dupstream gene variant

Table 3: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the skeletal traits in the Angus.

Trait	Chr	Start	End	No. of dimorphic SNPs	Location of most significantly dimorphic SNP (UMD 3.1)	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Wither height	5	110840144	111861436	4	111346952 ^b	110829906	0.010	-0.25 (0.17)	0.006	1.63 (0.33)	4.3x10 ⁻⁷
	8	60455638	62004178	27	61312774 ^a	60912522	0.084	-0.20 (0.06)	0.014	1.07 (0.24)	2.45x10 ⁻⁷
	10	31872810	32902266	7	32402196 ^b	32316973	0.091	-0.12 (0.06)	0.036	0.61 (0.14)	7.23x10 ⁻⁷
	18	6104766	7113421	4	6613421 ^a	6584541	0.276	0.09 (0.04)	0.01	-0.32 (0.07)	8.69x10 ⁻⁷
	29	48236260	49251635	2	48751635 ^a	48087103	0.011	-0.21 (0.16)	0.006	1.63 (0.33)	4.25x10 ⁻⁷
Back length	1	70204850	71422791	16	70835180 ^b	70223171	0.259	0.11 (0.04)	0.224	-0.30 (0.07)	2.45x10 ⁻⁷
	2	28943486	30056216	3	29556216 ^a	29476541	0.009	0.68 (0.18)	0.026	-0.46 (0.17)	3.28x10 ⁻⁶
	6	26975924	27975924	1	27475924 ^b	26065467	0.067	-0.11 (0.07)	0.033	0.70 (0.15)	1.19x10 ⁻⁶
	8	65886591	67412672	3	66912672 ^a	66423762	0.019	-0.35 (0.13)	0.006	1.46 (0.36)	2.12x10 ⁻⁶
	23	23943976	24943976	1	24443976 ^b	24699576	0.008	-0.30 (0.18)	0.006	1.60 (0.35)	1.30x10 ⁻⁶
Hip width	1	62250123	63302205	6	62787935 ^a	62183938	0.023	-0.10 (0.10)	0.009	1.58 (0.30)	9.27x10 ⁻⁸
	8	57066889	67412672	77	66296263 ^a	65817557	0.025	-0.23 (0.10)	0.005	2.29 (0.40)	9.86x10 ⁻¹⁰
	10	81021198	83021473	3	81521198 ^c	81172739	0.011	-0.25 (0.14)	0.003	2.84 (0.55)	5.48x10 ⁻⁸
	11	30092116	31173851	16	30670702 ^d	30824114	0.022	-0.20 (0.12)	0.003	2.84 (0.55)	6.34x10 ⁻⁸
	13	6530211	7544606	3	7030211 ^b	6887666	0.007	-0.46 (0.19)	0.003	2.87 (0.56)	1.72x10 ⁻⁸
Chest width	2	12527638	14665457	29	16317185 ^a	16287817	0.008	0.48 (0.18)	0.003	-2.24 (0.52)	6.46x10 ⁻⁷
	6	42435811	43438281	2	42938281 ^b	41487714	0.497	-0.05 (0.03)	0.424	0.27 (0.06)	9.43x10 ⁻⁷
	6	46088094	47172011	47	46597538 ^a	45051418	0.200	-0.10 (0.04)	0.140	0.32 (0.08)	1.08x10 ⁻⁶
	15	74696711	75749423	10	75205777 ^b	74292869	0.085	-0.07 (0.06)	0.034	0.75 (0.15)	2.27x10 ⁻⁷
	28	23985323	24991309	3	24485323 ^a	24334640	0.080	0.11 (0.06)	0.068	-0.47 (0.10)	4.54x10 ⁻⁷
Chest depth	3	87713085	88819263	2	88213085 ^a	87638290	0.018	-0.29 (0.12)	0.015	0.82 (0.19)	8.77x10 ⁻⁷
	6	76026228	77061527	89	76542923 ^a	74889187	0.287	-0.10 (0.03)	0.228	0.22 (0.06)	7.15x10 ⁻⁷
	11	48278616	49764300	31	48778616 ^a	48908041	0.165	0.11 (0.04)	0.196	-0.26 (0.06)	2.11x10 ⁻⁷
	23	3078545	4088215	44	3581168 ^b	3660670	0.044	-0.13 (0.07)	0.008	1.28 (0.28)	9.81x10 ⁻⁷
	27	16617773	17634805	3	17128718 ^a	18055239	0.499	0.09 (0.03)	0.433	-0.17 (0.05)	1.21x10 ⁻⁶

^aintergenic variant, ^bintron variant, ^cmissense variant, ^d3' UTR variant

Table 4: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the muscular traits in the Charolais.

Trait	Chr	Start	End	No. of dimorphic SNPs	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Development of hind quarter	1	103824917	105170930	25	104363453 ^a	103548640	0.215	-0.04 (0.03)	0.208	0.21 (0.04)	3.86x10 ⁻⁷
	2	1255471	9445764	113	5302042 ^a	5369735	0.497	-0.21 (0.02)	0.496	0.12 (0.03)	1.55x10 ⁻¹⁵
	12	45346059	48106494	85	47588546 ^a	47283052	0.107	-0.08 (0.03)	0.085	0.25 (0.06)	6.02x10 ⁻⁷
	15	60710700	61831852	4	61210700 ^a	60427864	0.005	0.60 (0.16)	0.003	-0.89 (0.26)	1.29x10 ⁻⁶
	16	70153655	71221659	3	70653655 ^b	69141596	0.004	-0.45 (0.17)	0.004	1.05 (0.23)	1.45x10 ⁻⁷
Development of inner thigh	1	117119798	118119961	2	117619798 ^b	116726201	0.204	0.47 (0.14)	0.219	-0.86 (0.23)	7.34x10 ⁻⁷
	2	37440689	38440693	2	37940693 ^a	37839039	0.033	0.69 (0.32)	0.038	-2.01 (0.46)	1.46x10 ⁻⁶
	19	8575554	9576597	2	9076597 ^a	8844572	0.482	0.35 (0.13)	0.492	-0.80 (0.20)	1.46x10 ⁻⁶
	26	45221800	46222229	4	45721883 ^b	45385940	0.486	0.18 (0.12)	0.462	-0.94 (0.19)	8.10x10 ⁻⁷
	X	107228339	108242126	8	107728339 ^a	102268740	0.499	0.18 (0.08)	0.498	-0.80 (0.20)	6.48x10 ⁻⁶
Development of loin	1	84531371	85539275	3	85034032 ^a	84419934	0.003	-0.12 (0.19)	0.003	1.75 (0.31)	2.74x10 ⁻⁷
	2	0	648674	11	148674 ^a	225688	0.482	-0.08 (0.03)	0.470	0.14 (0.04)	4.37x10 ⁻⁷
	2	4801997	6104335	12	5587046 ^b	5654486	0.487	0.15 (0.03)	0.467	-0.13 (0.04)	1.36x10 ⁻¹⁰
	3	51686577	52703486	2	52186577 ^a	52028651	0.020	-0.09 (0.08)	0.022	0.56 (0.11)	1.33x10 ⁻⁶
	15	26121639	27171054	3	26671054 ^b	26249705	0.034	-0.16 (0.07)	0.017	0.60 (0.13)	3.89x10 ⁻⁷
Thigh width	2	4801997	6104335	13	5587046 ^b	5654486	0.487	0.17 (0.03)	0.467	-0.16 (0.04)	8.62x10 ⁻¹³
	5	51522594	52583478	5	52022594 ^b	51784070	0.016	0.15 (0.10)	0.012	-0.78 (0.16)	8.37x10 ⁻⁷
	6	100685822	102462671	3	101962671 ^a	100182435	0.236	-0.12 (0.03)	0.250	0.12 (0.04)	1.64x10 ⁻⁶
	21	37454121	39897176	100	37969433 ^a	37571983	0.420	0.05 (0.03)	0.425	-0.17 (0.04)	8.68x10 ⁻⁷
	27	39790937	40817098	7	40317098 ^a	40462706	0.295	-0.06 (0.03)	0.320	0.17 (0.04)	9.75x10 ⁻⁷
Width of withers	1	25066241	26077136	3	25577136 ^a	26076126	0.095	0.09 (0.04)	0.126	-0.24 (0.05)	4.07x10 ⁻⁷
	2	5064592	6104335	9	5587046 ^b	5654486	0.487	0.15 (0.03)	0.467	-0.12 (0.04)	1.66x10 ⁻⁹
	4	26737341	27961476	2	27461476 ^b	27487938	0.002	-1.17 (0.25)	0.003	0.73 (0.29)	5.38x10 ⁻⁷
	9	60485268	61503827	4	60993475 ^a	60117188	0.005	-0.73 (0.16)	0.003	1.04 (0.32)	9.89x10 ⁻⁷
	21	39307646	40307667	4	39807694 ^a	39393236	0.006	0.37 (0.15)	0.008	-0.80 (0.18)	7.25x10 ⁻⁷

^aintergenic variant, ^bintron variant, ^cdownstream gene variant

Table 5: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the skeletal traits in the Charolais.

Trait	Chr	Start	End	No. of dimorphic SNPS	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Wither height	7	96716729	97718351	3	97483338 ^b	94984764	0.213	-0.08 (0.02)	0.254	0.09 (0.02)	1.50x10 ⁻⁶
	10	75208550	77306612	5	75708579 ^a	75395884	0.029	-0.13 (0.05)	0.028	0.28 (0.07)	5.89x10 ⁻⁶
	17	34267907	35272234	15	34770503 ^a	34374526	0.120	-0.09 (0.03)	0.113	0.14 (0.04)	1.64x10 ⁻⁶
	19	33223631	34225743	6	33723631 ^b	33122406	0.451	0.03 (0.02)	0.499	-0.11 (0.03)	5.95x10 ⁻⁶
	29	29284867	30316330	11	29807810 ^a	29436465	0.246	0.03 (0.02)	0.170	-0.16 (0.03)	1.46x10 ⁻⁶
Back length	1	60942796	62141649	4	61529004 ^a	60977668	0.020	0.08 (0.06)	0.008	-0.76 (0.14)	5.31x10 ⁻⁸
	8	65823397	67021631	17	66520586 ^{bc}	66036297	0.014	0.24 (0.07)	0.014	-0.39 (0.11)	7.09x10 ⁻⁷
	11	67394139	68443814	13	67936368 ^b	67962565	0.039	0.11 (0.04)	0.033	-0.29 (0.07)	1.18x10 ⁻⁶
	12	66787629	68105969	3	67354072 ^a	66817243	0.005	0.19 (0.11)	0.003	-1.24 (0.22)	6.64x10 ⁻⁹
	26	16741492	17746984	6	17242026 ^b	17376909	0.198	-0.06 (0.02)	0.196	0.14 (0.03)	2.43x10 ⁻⁷
Hip width	1	71113538	72230151	34	71680557 ^a	71071338	0.007	-0.18 (0.09)	0.003	1.09 (0.24)	7.09x10 ⁻⁷
	1	150460935	151629392	5	150960935 ^c	*	0.031	0.11 (0.05)	0.046	-0.29 (0.06)	1.96x10 ⁻⁷
	7	78851675	79854739	3	79352226 ^a	77071480	0.027	-0.09 (0.05)	0.013	0.49 (0.11)	9.91x10 ⁻⁷
	19	41254273	42757991	23	42257563 ^c	41624383	0.127	-0.09 (0.02)	0.116	0.14 (0.04)	1.32x10 ⁻⁶
	23	40292666	41337462	14	40792666 ^d	41014434	0.044	0.13 (0.04)	0.052	-0.21 (0.06)	1.49x10 ⁻⁶
Chest width	2	39826441	43069032	11	42375687 ^d	*	0.003	0.46 (0.38)	0.002	-5.30 (0.71)	1.01x10 ⁻¹²
	8	24830532	26713234	9	29877151 ^a	29907983	0.015	-0.03 (0.18)	0.008	-3.34 (0.36)	4.44x10 ⁻¹⁶
	9	21416858	24598647	19	21916858 ^a	21654494	0.007	0.21 (0.26)	0.003	-4.10 (0.52)	1.66x10 ⁻¹³
	14	5222811	6612129	22	6528804 ^a	5500130	0.010	0.50 (0.23)	0.006	-3.14 (0.43)	4.49x10 ⁻¹⁴
	28	0	865080	17	365080 ^a	1347377	0.006	0.62 (0.28)	0.003	-4.79 (0.63)	6.66x10 ⁻¹⁵
Chest depth	2	78501288	79652702	7	79001288 ^a	78633046	0.005	0.29 (0.27)	0.002	-3.88 (0.56)	2.50x10 ⁻¹¹
	6	22501427	30700058	17	29804490 ^a	28380999	0.006	0.17 (0.28)	0.003	-4.13 (0.57)	1.55x10 ⁻¹¹
	17	20292176	22351653	28	20871130 ^a	20556557	0.016	0.01 (0.18)	0.008	-2.36 (0.30)	1.22x10 ⁻¹¹
	19	5471820	6722162	11	6222162 ^a	6015594	0.013	0.15 (0.19)	0.008	-2.41 (0.33)	1.32x10 ⁻¹¹
	20	68770623	70729278	50	70127722 ^a	*	0.002	0.23 (0.46)	0.002	-5.16 (0.57)	2.42x10 ⁻¹³

^aintergenic variant, ^bintron variant, ^cdownstream gene variant, ^dupstream gene variant

*SNP has not been mapped on the latest build

Table 6: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the muscular traits in the Hereford.

Trait	Chr	Start	End	No. of dimorphic SNPs	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Development of hind quarter	1	47475388	48477830	9	47975875 ^a	47609095	0.440	-0.14 (0.05)	0.460	0.20 (0.06)	5.34x10 ⁻⁶
	7	38157809	39157899	3	38657899 ^a	37308156	0.307	-0.20 (0.05)	0.291	0.17 (0.06)	1.58x10 ⁻⁶
	12	33106286	34154759	5	33654759 ^b	33414723	0.008	-0.84 (0.24)	0.002	1.90 (0.56)	6.14x10 ⁻⁶
	16	79654320	81344038	20	80834643 ^b	78911900	0.032	0.42 (0.13)	0.041	-0.61 (0.14)	6.30x10 ⁻⁸
	29	48954403	49974227	13	49471817 ^a	*	0.080	0.29 (0.09)	0.092	-0.31 (0.09)	4.83x10 ⁻⁶
Development of inner thigh	1	139386569	140386569	1	139886569 ^b	138390445	0.131	-0.24 (0.07)	0.098	0.31 (0.09)	3.36x10 ⁻⁶
	6	104110238	105116799	3	104610238 ^b	102834429	0.030	0.46 (0.14)	0.021	-0.59 (0.18)	4.31x10 ⁻⁶
	13	42113572	43125008	4	42613572 ^a	42236685	0.003	-1.57 (0.41)	0.005	1.22 (0.4)	1.09x10 ⁻⁶
	19	48026847	49047485	15	48526847 ^b	47877987	0.078	-0.23 (0.09)	0.095	0.33 (0.09)	6.22x10 ⁻⁶
	20	45699238	46731354	6	46213822 ^a	46189379	0.169	-0.18 (0.06)	0.193	0.32 (0.07)	1.21x10 ⁻⁷
Development of loin	3	89108056	90628279	9	90128279 ^d	89550331	0.072	0.14 (0.09)	0.040	-0.82 (0.16)	1.76x10 ⁻⁷
	16	16872687	17885604	2	17372687 ^a	16732806	0.211	0.19 (0.06)	0.183	-0.29 (0.08)	9.83x10 ⁻⁷
	21	57418522	58508022	5	57972000 ^b	57385760	0.018	0.44 (0.18)	0.019	-1.06 (0.23)	2.06x10 ⁻⁷
	23	44376366	45381654	9	44876460 ^b	45012825	0.433	-0.18 (0.05)	0.445	0.19 (0.06)	2.30x10 ⁻⁶
	26	24760894	25969246	11	25358414 ^d	25093228	0.052	0.06 (0.10)	0.016	-1.32 (0.25)	2.54x10 ⁻⁷
Thigh width	4	30981541	31996449	3	31481541 ^a	31358361	0.052	-0.24 (0.11)	0.050	0.61 (0.15)	2.84x10 ⁻⁶
	11	34683559	35683570	2	35183559 ^a	35342330	0.210	-0.17 (0.06)	0.249	0.28 (0.07)	1.98x10 ⁻⁶
	15	48172990	49186437	10	48675268 ^c	48028112	0.010	-0.59 (0.25)	0.016	1.07 (0.25)	3.00x10 ⁻⁶
	27	37804950	38804962	3	38304950 ^a	*	0.004	-1.24 (0.38)	0.010	1.25 (0.32)	3.96x10 ⁻⁷
	29	32341813	33341891	5	32841813 ^a	32298517	0.010	-0.24 (0.26)	0.005	2.33 (0.45)	6.10x10 ⁻⁷
Width of withers	1	23635565	24635601	2	24135565 ^a	24617417	0.044	0.19 (0.12)	0.027	-0.87 (0.20)	6.32x10 ⁻⁶
	11	88551389	89554029	5	89052894 ^a	89077280	0.263	-0.11 (0.06)	0.195	0.34 (0.08)	4.63x10 ⁻⁶
	16	16859305	17861510	3	17361510 ^a	16721630	0.297	0.21 (0.06)	0.320	-0.22 (0.07)	9.32x10 ⁻⁷
	23	28067269	29080639	4	28580639 ^c	28787480	0.023	-0.66 (0.18)	0.035	0.58 (0.17)	7.84x10 ⁻⁷
	29	3021804	4053998	21	3553943 ^a	3466707	0.483	0.14 (0.05)	0.469	-0.28 (0.06)	6.82x10 ⁻⁷

^aintergenic variant, ^bintron variant, ^cdownstream gene variant, ^dupstream gene variant

*SNP has not been mapped on the latest build

Table 7: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the skeletal traits in the Hereford.

Trait	Chr	Start	End	No. of dimorphic SNPs	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Wither height	1	1925823	2922535	2	2422535 ^b	3142926	0.010	0.63 (0.20)	0.009	-0.99 (0.27)	1.22x10 ⁻⁶
	10	49372889	50457497	10	49872889 ^b	49812963	0.004	-1.27 (0.30)	0.006	0.83 (0.31)	1.18x10 ⁻⁶
	10	68414747	69451655	11	68933579 ^b	68686530	0.107	0.27 (0.06)	0.137	-0.20 (0.07)	5.97x10 ⁻⁷
	16	916164	1945553	12	1441711 ^c	1624685	0.025	-0.36 (0.13)	0.016	0.78 (0.20)	1.05x10 ⁻⁶
	24	10954731	11969624	6	11461076 ^a	11159461	0.096	-0.27 (0.06)	0.067	0.29 (0.09)	2.65x10 ⁻⁷
Back length	4	12086873	13087742	3	12587742 ^a	12740501	0.008	-0.90 (0.24)	0.005	1.22 (0.39)	3.37x10 ⁻⁶
	8	25464831	26824440	23	25966773 ^a	25943096	0.110	0.32 (0.07)	0.132	-0.23 (0.08)	3.56x10 ⁻⁷
	14	30747311	31768991	12	31247311 ^a	29553248	0.461	0.14 (0.04)	0.471	-0.20 (0.06)	1.38x10 ⁻⁶
	25	13061095	14195964	4	13561095 ^b	*	0.003	-1.27 (0.36)	0.012	0.75 (0.24)	3.63x10 ⁻⁶
	28	32468295	34072536	3	33572536 ^b	33371736	0.146	-0.10 (0.06)	0.148	0.37 (0.09)	3.18x10 ⁻⁶
Hip width	5	75173455	76244035	40	75719616 ^a	75344242	0.006	-0.73 (0.28)	0.004	1.85 (0.44)	8.46x10 ⁻⁷
	11	88093610	89599089	7	89005217 ^a	89030779	0.263	-0.13 (0.06)	0.195	0.40 (0.09)	8.95x10 ⁻⁷
	12	82288642	83293488	3	82793488 ^a	78806868	0.155	-0.17 (0.06)	0.208	0.29 (0.07)	3.07x10 ⁻⁷
	23	51480640	52527183	5	52013801 ^b	52167774	0.089	-0.16 (0.08)	0.091	0.46 (0.10)	3.27x10 ⁻⁷
	27	8148686	10276462	17	8648686 ^a	9657276	0.107	-0.24 (0.06)	0.106	0.30 (0.09)	5.65x10 ⁻⁷
Chest width	1	62368829	63399292	5	62868829 ^a	62264629	0.082	-0.22 (0.06)	0.108	0.32 (0.08)	5.58x10 ⁻⁸
	5	49311974	50341913	23	49822014 ^b	49592445	0.428	-0.17 (0.04)	0.384	0.13 (0.05)	5.20x10 ⁻⁷
	6	41424236	42580067	9	42029809 ^b	40571631	0.003	1.31 (0.31)	0.005	-1.13 (0.33)	7.10x10 ⁻⁸
	9	31485678	32498136	4	31985678 ^a	31570153	0.010	0.42 (0.19)	0.004	-1.78 (0.38)	2.34x10 ⁻⁷
	13	2019339	3201947	16	2522257 ^d	2613918	0.066	0.10 (0.07)	0.030	-0.67 (0.13)	1.94x10 ⁻⁷
Chest depth	10	2981982	4121382	3	3621377 ^a	3672531	0.008	0.11 (0.19)	0.002	2.49 (0.48)	3.42x10 ⁻⁶
	11	67322056	68784534	4	68278582 ^d	68305651	0.003	-0.87 (0.32)	0.002	2.05 (0.48)	4.15x10 ⁻⁷
	16	9638392	10667968	6	10150979 ^a	9550179	0.044	-0.24 (0.08)	0.040	0.46 (0.13)	3.62x10 ⁻⁶
	19	42220630	43244434	32	42738845 ^d	42096896	0.349	0.11 (0.03)	0.322	-0.20 (0.06)	2.67x10 ⁻⁶
	22	25263617	26332810	15	25767332 ^a	25654951	0.054	-0.15 (0.07)	0.050	0.49 (0.11)	7.27x10 ⁻⁷

^aintergenic variant, ^bintron variant, ^cdownstream gene variant, ^dupstream gene variant

*SNP has not been mapped on the latest build

Table 8: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the muscular traits in the Limousin.

Trait	Chr	Start	End	No. of dimorphic SNPS	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Development of hind quarter	10	87342478	88342595	3	87842478 ^a	86838930	0.004	-0.01 (0.15)	0.003	-1.64 (0.23)	1.85x10 ⁻⁹
	12	88313474	89356176	25	88814730 ^a	84800697	0.011	0.16 (0.08)	0.005	-0.84 (0.17)	1.96x10 ⁻⁷
	14	80691409	81691453	2	81191409 ^a	78818851	0.002	0.10 (0.19)	0.002	-1.46 (0.24)	4.02x10 ⁻⁷
	16	7877931	9577924	42	8703762 ^a	8116291	0.003	0.12 (0.16)	0.002	-1.50 (0.24)	2.53x10 ⁻⁸
	18	53678352	54842543	90	54323356 ^a	53885291	0.003	0.36 (0.17)	0.002	-1.28 (0.25)	1.03x10 ⁻⁷
Development of inner thigh	1	134576003	135674198	26	135111581 ^a	*	0.024	-1.21 (0.31)	0.035	1.27 (0.38)	4.64x10 ⁻⁷
	7	94624535	94624535	9	95351376 ^a	92825575	0.021	1.27 (0.31)	0.082	-0.92 (0.26)	9.29x10 ⁻⁸
	8	83362119	84373117	16	83862344 ^a	82440029	0.026	-0.71 (0.29)	0.029	1.77 (0.43)	2.06x10 ⁻⁶
	14	12997796	14065940	91	13497889 ^a	12381763	0.351	-0.39 (0.11)	0.373	0.60 (0.16)	3.15x10 ⁻⁷
	20	15771955	16909647	12	16366926 ^a	16380235	0.003	3.16 (0.79)	0.005	-2.93 (0.93)	6.26x10 ⁻⁷
Development of loin	2	90388815	91414365	6	90901181 ^a	90485467	0.170	-0.09 (0.03)	0.168	0.12 (0.03)	1.37x10 ⁻⁶
	6	95583095	96694369	5	96194369 ^a	94427267	0.004	-0.43 (0.15)	0.002	1.00 (0.27)	4.45x10 ⁻⁶
	15	81201476	82201561	2	81701476 ^a	80411671	0.149	0.07 (0.03)	0.171	-0.14 (0.03)	1.04x10 ⁻⁶
	25	3582865	4590247	3	4090247 ^{bc}	4072335	0.492	0.09 (0.02)	0.460	-0.07 (0.03)	5.72x10 ⁻⁷
	X	33834595	34867127	35	34354746 ^a	34130068	0.376	-0.03 (0.01)	0.404	0.11 (0.03)	5.35x10 ⁻⁶
Thigh width	2	19380958	20380975	3	19880958 ^a	19838410	0.014	0.27 (0.09)	0.011	-0.38 (0.11)	6.57x10 ⁻⁶
	2	20700909	21720973	6	21217950 ^a	21181655	0.100	0.06 (0.03)	0.090	-0.19 (0.05)	7.05x10 ⁻⁶
	14	6060940	7069392	3	6569392 ^a	5540717	0.004	-0.36 (0.16)	0.003	0.87 (0.21)	3.45x10 ⁻⁶
	23	40690020	41776379	6	41276379 ^b	41595913	0.009	-0.15 (0.10)	0.003	0.94 (0.20)	1.11x10 ⁻⁶
	X	16962347	17966732	2	17466732 ^b	17527360	0.415	-0.02 (0.01)	0.445	0.12 (0.03)	3.38x10 ⁻⁶
Width of withers	1	51070933	52117339	12	51577476 ^a	51177783	0.289	0.07 (0.02)	0.294	-0.10 (0.03)	1.96x10 ⁻⁶
	2	85735779	86812555	7	86265284 ^a	85863432	0.019	-0.18 (0.08)	0.032	0.31 (0.07)	2.80x10 ⁻⁶
	10	28209680	29266690	175	28742392 ^b	28681684	0.378	-0.07 (0.02)	0.353	0.10 (0.03)	2.53x10 ⁻⁶
	12	66608973	67613368	3	67108973 ^b	66572583	0.011	-0.20 (0.10)	0.009	0.60 (0.13)	9.62x10 ⁻⁷
	19	7961956	8967691	5	8466831 ^b	8237090	0.003	-0.95 (0.19)	0.002	0.61 (0.27)	1.69x10 ⁻⁶

^aintergenic variant, ^bintron variant, ^cupstream gene variant

*SNP has not been mapped on the latest build

Table 9: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the skeletal traits in the Limousin.

Trait	Chr	Start	End	No. of dimorphic SNPs	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							MAF	Allele Effect (SE)	MAF	Allele Effect (SE)	
Wither height	3	9818384	10820240	2	10318384 ^a	*	0.022	-0.20 (0.05)	0.013	0.26 (0.08)	1.08x10 ⁻⁶
	6	36963566	40499953	40	39760256 ^a	38319979	0.484	-0.07 (0.02)	0.487	0.09 (0.02)	1.07x10 ⁻⁸
	11	48105352	49267580	9	48766334 ^a	48896156	0.006	0.26 (0.09)	0.006	-0.49 (0.13)	3.40x10 ⁻⁶
	19	30754934	31762424	2	31254934 ^a	30619941	0.257	-0.06 (0.02)	0.248	0.09 (0.02)	1.94x10 ⁻⁷
	X	16956607	17966732	6	17462347 ^b	17522975	0.428	-0.01 (0.01)	0.454	0.11 (0.02)	1.19x10 ⁻⁶
Back length	2	19533709	20573649	21	20065919 ^a	20029900	0.096	-0.06 (0.02)	0.089	0.16 (0.04)	1.02x10 ⁻⁶
	15	7167859	8174094	3	7674094 ^b	7433522	0.143	-0.05 (0.02)	0.118	0.13 (0.03)	3.14x10 ⁻⁶
	16	64732311	65827907	8	65324669 ^a	63842035	0.003	0.39 (0.14)	0.003	-0.74 (0.19)	1.47x10 ⁻⁶
	21	10874079	11978348	2	11374079 ^a	11140251	0.009	-0.12 (0.07)	0.006	0.60 (0.14)	4.03x10 ⁻⁶
	23	19728831	20739036	5	20228831 ^b	20236461	0.005	-0.34 (0.10)	0.004	0.55 (0.16)	3.04x10 ⁻⁶
Hip width	4	1742345	2747816	5	2245736 ^a	2343834	0.018	0.15 (0.05)	0.021	-0.27 (0.07)	1.83x10 ⁻⁶
	6	39032482	40040409	8	39539558 ^a	38099446	0.493	-0.07 (0.01)	0.486	0.06 (0.02)	5.71x10 ⁻⁷
	12	5047438	6074330	3	5547438 ^a	5568301	0.020	-0.14 (0.05)	0.009	0.39 (0.10)	1.23x10 ⁻⁶
	21	23430143	24464331	28	23931207 ^a	23468504	0.237	-0.01 (0.02)	0.202	0.11 (0.03)	1.74x10 ⁻⁷
	29	13364114	14373070	4	13872420 ^a	13797973	0.011	0.21 (0.07)	0.011	-0.34 (0.09)	1.11x10 ⁻⁶
Chest width	11	15939177	16959054	3	16459054 ^a	16439125	0.005	0.03 (0.29)	0.003	-3.86 (0.51)	3.63x10 ⁻¹¹
	20	60692205	68001633	7	62047530 ^a	61941499	0.008	0.03 (0.22)	0.002	-3.67 (0.58)	2.64x10 ⁻⁹
	22	55794366	59621588	10	56329073 ^a	55689684	0.031	0.31 (0.12)	0.017	-1.26 (0.22)	2.01x10 ⁻¹⁰
	26	38382849	39632022	5	38919539 ^a	*	0.006	0.40 (0.26)	0.002	-3.51 (0.58)	8.26x10 ⁻¹⁰
	X	15184800	16185025	2	15684800 ^a	15786355	0.004	0.36 (0.21)	0.003	-3.37 (0.53)	6.15x10 ⁻¹¹
Chest depth	3	26560340	27936092	8	27203740 ^a	*	0.003	0.59 (0.39)	0.002	-3.35 (0.58)	1.52x10 ⁻⁸
	6	65184840	66194780	2	65684840 ^a	64045311	0.003	0.54 (0.39)	0.002	-4.10 (0.65)	8.70x10 ⁻¹⁰
	10	66552011	70565607	71	70065607 ^c	69820365	0.005	0.55 (0.30)	0.002	-3.16 (0.58)	1.69x10 ⁻⁸
	17	24086084	25381796	56	24844625 ^a	*	0.003	0.42 (0.26)	0.002	-2.21 (0.39)	1.95x10 ⁻⁸
	20	60681167	62562427	6	61192205 ^a	61100715	0.004	0.21 (0.35)	0.002	-3.81 (0.60)	9.40x10 ⁻⁹

^aintergenic variant, ^bintron variant, ^cdownstream gene variant

*SNP has not been mapped on the latest build

Table 10: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the muscular traits in the Simmental.

Trait	Chr	Start	End	No. of dimorphic SNPs	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Development of hind quarter	1	61306996	70287318	7	61948489 ^a	61358095	0.014	0.63 (0.20)	0.013	-0.75 (0.21)	1.46x10 ⁻⁶
	16	25091200	26156103	7	25645958 ^a	*	0.007	-0.81 (0.28)	0.008	1.12 (0.25)	2.47x10 ⁻⁷
	18	38816641	40478326	7	39974706 ^a	39838731	0.003	1.27 (0.40)	0.005	-1.25 (0.32)	1.05x10 ⁻⁶
	19	48915944	50012600	4	49415944 ^a	48765663	0.011	-0.40 (0.23)	0.003	2.08 (0.47)	1.86x10 ⁻⁶
	20	12847020	13908908	29	13347020 ^b	13394150	0.006	0.99 (0.30)	0.005	-1.10 (0.32)	1.50x10 ⁻⁶
Development of inner thigh	6	106083805	107083825	2	106583805 ^a	114749586	0.002	2.31 (0.55)	0.004	-0.98 (0.38)	8.40x10 ⁻⁷
	8	13016740	14043577	6	13541906 ^b	13620555	0.051	0.51 (0.12)	0.082	-0.22 (0.09)	7.91x10 ⁻⁷
	12	65403646	67717725	14	67209065 ^a	66672413	0.007	-0.85 (0.34)	0.006	1.76 (0.30)	1.40x10 ⁻⁸
	17	29020755	30121482	5	29520755 ^b	29099068	0.008	-1.06 (0.30)	0.003	1.73 (0.48)	7.74x10 ⁻⁷
	22	2823206	3890106	3	3390106 ^c	3346386	0.006	-1.65 (0.34)	0.005	0.72 (0.31)	3.22x10 ⁻⁷
Development of loin	2	127861842	128864558	2	128364558 ^a	127768904	0.025	-0.23 (0.16)	0.013	1.14 (0.22)	7.57x10 ⁻⁷
	10	89463351	90472920	2	89963351 ^c	88893256	0.006	1.09 (0.30)	0.005	-1.23 (0.36)	7.37x10 ⁻⁷
	12	84618243	85621166	2	85118243 ^a	81125408	0.087	-0.45 (0.10)	0.061	0.28 (0.11)	4.18x10 ⁻⁷
	25	35252984	36256151	4	35752984 ^a	35196894	0.078	-0.27 (0.10)	0.068	0.43 (0.10)	9.22x10 ⁻⁷
	28	3386654	4391033	2	3886654 ^a	3541484	0.003	-2.29 (0.50)	0.005	1.06 (0.36)	6.03x10 ⁻⁸
Thigh width	1	131926057	133026755	19	132524816 ^a	131446846	0.186	0.23 (0.07)	0.173	-0.24 (0.07)	7.78x10 ⁻⁷
	2	55252366	56331341	6	55802026 ^a	55583385	0.022	0.40 (0.19)	0.013	-0.96 (0.23)	3.25x10 ⁻⁶
	2	99511847	100585115	3	100011847 ^a	99572436	0.014	1.00 (0.23)	0.013	-0.52 (0.21)	1.23x10 ⁻⁶
	14	68627562	70444960	30	69137624 ^a	66845331	0.059	-0.46 (0.11)	0.037	0.32 (0.13)	2.92x10 ⁻⁶
	18	3288714	4902994	7	3802911 ^a	3762701	0.015	0.93 (0.22)	0.026	-0.35 (0.16)	2.56x10 ⁻⁶
Width of withers	3	97729943	99024542	2	98229943 ^a	*	0.015	1.04 (0.24)	0.017	-0.50 (0.22)	2.13x10 ⁻⁶
	16	13116847	14137101	55	13629940 ^a	13011210	0.446	-0.19 (0.06)	0.487	0.18 (0.05)	3.41x10 ⁻⁶
	18	3288714	4302911	3	3802911 ^a	3762701	0.015	1.15 (0.24)	0.026	-0.27 (0.17)	1.64x10 ⁻⁶
	22	5987150	6987507	3	6487150 ^a	6411683	0.062	0.23 (0.11)	0.040	-0.63 (0.14)	1.57x10 ⁻⁶
	29	46651577	47656859	2	47156859 ^a	46499562	0.027	-0.69 (0.17)	0.032	0.37 (0.15)	2.27x10 ⁻⁶

^aintergenic variant, ^bintron variant, ^cupstream gene variant

*SNP has not been mapped on the latest build

Table 11: The location of the most significantly dimorphic SNPs, limited to the top 5, which were associated with the skeletal traits in the Simmental.

Trait	Chr	Start	End	No. of dimorphic SNPs	Most significantly dimorphic SNP	Updated position of most significantly dimorphic SNP (ARS-UCD 1.2)	Male		Female		Significance of dimorphism
							Allele Frequency	Allele Effect (SE)	Allele Frequency	Allele Effect (SE)	
Wither height	10	39416014	40523072	17	39916014 ^b	39827207	0.003	-0.86 (0.32)	0.004	1.05 (0.29)	8.11x10 ⁻⁶
	15	79224399	80224427	2	79724399 ^d	78498073	0.031	-0.23 (0.09)	0.016	0.55 (0.15)	9.47x10 ⁻⁶
	21	43816205	44823203	2	44316205 ^a	43898184	0.005	-0.82 (0.25)	0.005	0.94 (0.27)	1.70x10 ⁻⁶
	23	29940021	31111779	72	30451606 ^a	30700499	0.314	-0.14 (0.04)	0.319	0.13 (0.04)	9.09x10 ⁻⁷
	X	144910600	145867274	8	145410600 ^b	134272382	0.007	-0.26 (0.19)	0.011	0.30 (0.22)	3.54x10 ⁻⁸
Back length	1	68029603	69086059	16	68580516 ^{bd}	67982646	0.476	0.11 (0.04)	0.483	-0.15 (0.04)	7.57x10 ⁻⁷
	6	12731620	13787338	4	13287338 ^a	*	0.004	1.11 (0.26)	0.009	-0.44 (0.18)	1.01x10 ⁻⁶
	9	84630969	85633807	2	85130969 ^b	84014933	0.025	-0.52 (0.12)	0.018	0.40 (0.14)	6.71x10 ⁻⁷
	26	23562542	24623399	7	24110489 ^a	23866480	0.086	-0.20 (0.06)	0.059	0.30 (0.08)	6.31x10 ⁻⁷
	28	39092226	40119176	5	39592226 ^a	39277437	0.348	-0.20 (0.04)	0.347	0.08 (0.04)	5.94x10 ⁻⁷
Hip width	7	2278460	3359162	15	2785141 ^a	2871594	0.109	0.16 (0.05)	0.071	-0.35 (0.08)	2.81x10 ⁻⁷
	7	92446667	93472476	2	92972476 ^a	90587933	0.029	-0.25 (0.10)	0.020	0.67 (0.15)	1.94x10 ⁻⁷
	8	23629760	24686981	6	24129760 ^c	24165949	0.004	-0.84 (0.27)	0.003	1.66 (0.39)	1.51x10 ⁻⁷
	21	3783435	4810305	6	4308308 ^a	4167947	0.129	-0.23 (0.05)	0.125	0.17 (0.06)	5.70x10 ⁻⁷
	X	138125669	139135827	3	138625669 ^a	138267978	0.067	0.02 (0.06)	0.060	0.29 (0.10)	5.57x10 ⁻⁷
Chest width	2	116794370	119288912	3	117931744	*	0.009	0.31 (0.18)	0.005	-1.24 (0.26)	5.88x10 ⁻⁷
	6	35397549	36711379	11	36185495 ^b	34752887	0.439	0.14 (0.03)	0.472	-0.13 (0.04)	2.20x10 ⁻⁷
	12	53187285	54432359	5	53687285 ^a	53340630	0.208	0.07 (0.04)	0.228	-0.21 (0.05)	3.91x10 ⁻⁶
	16	57116725	58168280	26	57657852 ^b	56195234	0.007	-0.82 (0.19)	0.011	0.43 (0.18)	1.85x10 ⁻⁶
	22	23885582	25123955	9	24451172 ^a	24349773	0.086	0.18 (0.06)	0.121	-0.21 (0.06)	2.41x10 ⁻⁶
Chest depth	1	8065635	9123471	237	88582433 ^a	87956643	0.004	0.08 (0.24)	0.002	-2.64 (0.42)	1.98x10 ⁻⁸
	6	117081578	119074538	2	117581578 ^a	112778288	0.008	0.54 (0.17)	0.003	-1.47 (0.34)	1.95x10 ⁻⁷
	7	90595916	91626272	3	91121080 ^a	88762617	0.004	0.54 (0.25)	0.002	-2.06 (0.42)	1.27x10 ⁻⁷
	11	56218949	59206326	7	58002539 ^a	58081253	0.002	0.36 (0.38)	0.002	-3.48 (0.60)	6.15x10 ⁻⁸
	12	5835154	6893124	2	6335154 ^a	6351298	0.004	-0.07 (0.24)	0.002	-3.48 (0.60)	1.12x10 ⁻⁷

^aintergenic variant, ^bintron variant, ^cdownstream gene variant, ^dupstream gene variant

*SNP has not been mapped on the latest build