Genome-wide association studies (GWAS) are employed to identify genomic regions and candidate genes associated with several traits. The aim of this study was to perform a GWAS to identify causative variants and genes associated with milk yield, frame, and udder conformation traits in Gir dairy cattle. Body conformation traits were classified as “frame,” and “udder” traits for this study. After genotyping imputation and quality control, 42,105 polymorphisms were available for analyses, and 24,489 cows with pedigree information had phenotypes. First, $P$-value was calculated based on the variance of the prediction error of the SNP-effects on the first iteration. After that, 2 more iterations were performed to carry out the weighted single-step genome-wide association methodology, performed using genomic moving windows defined based on linkage disequilibrium. The significant SNPs and top 10 windows explaining the highest percentage of additive genetic variance were selected and used for QTL and gene annotation. The variants identified in our work overlapped with QTLs from the animal QTL database on chromosomes 1 to 23, except for chromosome 4. The Gir breed is less studied than the Holstein breed, and as such, the animal QTL database is biased to Holstein results. Hence it is noteworthy that our GWAS had similarities with previously described QTLs. These previously known QTLs were related to milk yield, body height, rump angle, udder width, and udder depth. In total, 5 genes were annotated. Of these genes, FAM13A and CMSS1 had been previously related to bone and carcass weight in cattle.

INTRODUCTION

Body conformation or type traits in dairy cattle are often used in breeding programs. Producers use these traits as indicators of a cow’s performance, productivity, and ability to stay in the herd. In other words, body conformation traits are related to economically important traits, such as milk yield, overall health, and longevity. For example, udder conformation traits were related to cow’s health (Dube et al., 2009). Frame conformation traits, such as stature and heart girth were associated with feed efficiency and energy balance (Søndergaard et al., 2002). Conformation traits such as rump angle and udder depth were associated with longevity (Lund et al., 1994, Vollema et al., 2000). Additionally, body conformation traits have been genetically correlated with milk yield in Holstein dairy cattle (Short and Lawlor, 1992, De Haas et al., 2007). Therefore, studies on the genetics of body conformation traits are of benefit to dairy cattle breeding and the milk industry.

Gir dairy cattle (Bos taurus indicus) are an important genetic resource for tropical dairy industries. Gir cattle are capable of milk production in pasture-based systems and have lower nutritional requirements, and higher resilience to heat and parasites when compared with Holstein cattle (Santana Jr et al., 2014). The genetics of Holstein cattle have been far more studied than the genetics of Gir cattle, especially in terms of applying genomics to identify variants and genes or QTL (quantitative trait loci) that affect production traits. Employing a genome-wide association approach (GWAS) within the Gir breed, some studies have identified and annotated potential candidate genes associated with milk yield (Toro-Ospina et al., 2023) as well as reproductive traits (Rocha et al., 2023). Recently Braga et al. (2023) identified high confidence...
copy number variation regions potentially affecting genes related to complex traits, such as production, health, and reproduction in Gir cattle. Despite these recent efforts, GWAS for body conformation traits in the Gir breed have not been reported yet.

The Holstein breed is probably the most studied breed of dairy cattle. Many genome-wide association studies have documented QTL, variants and genes associated to body conformation traits (Schnabel et al., 2005, Wu et al., 2013, Wang et al., 2022), as well as milk production traits (Bennewitz et al., 2004, Cole et al., 2011, Ning et al., 2018). In short, the heritability and the underpinning genetics of Holstein phenotypes have been reported. This knowledge may or may not apply to other dairy cattle breeds. Some QTLs are breed specific, as studies in beef cattle reported (Hawken et al., 2012, Fortes et al., 2020). Therefore, it is important to investigate these traits genetics within the Gir breed to verify which variants are relevant in Bos taurus indicus dairy cattle. The objective of this study was to perform GWAS to identify causative variants and genes associated to milk yield, frame and udder conformation traits in Gir dairy cattle.

MATERIALS AND METHODS

Traits and heritability estimates

The traits used to perform GWAS are a subset of traits from our previous study (Dominguez-Castaño et al., 2024). In our previous paper, univariate animal models were used to estimate variance components by the Bayesian approach for milk yield and 9 body conformation traits using pedigree and genotype files (Dominguez-Castaño et al., 2024). The body conformation traits selected were 4 traits associated with the udder: rear udder width (RU), udder depth (UD), teat diameter (TD), and teat length (TL); and 3 conformations traits related to the frame: hip height (HH), heart girth (HG), and rump angle (RA). The data set consists of ~1050 individuals measured for conformation traits, according definitions set by the Brazilian Dairy Gir National Breeding Program (Panetto et al., 2022). We also had 38,996 records of 305-d cumulative milk yield (MY) from 24,489 Gir cows born between 1969 and 2020. The heritability estimates of each trait and their corresponding standard error, number of records, and descriptive statistic are provided in Table 1.

Genotypes, imputation, and quality control

A total of 1,593 animals of both sexes were genotyped using 6 different commercial SNPs panels (Table S1). Genotypes were imputed to the moderate density panel known as 50K, with approx. 50 thousand DNA markers. A genotyping quality control (QC) on 50K genotypes was performed in accordance with the following exclusion criteria: a minor allele frequency (MAF) less than 0.01, call rate lower than 0.9 (for animals or individual SNPs), and maximum difference between observed and expected allele frequency for Hardy Weinberg Equilibrium of 0.15 and no pedigree conflicts. In total, 51,675 SNPs from the 50K panel distributed over the 29 autosomes passed all QC criteria and were used for the imputation of the target population. These same QC criteria were applied to the other genotype panels. All raw genotypes were mapped to the ARS-UCD1.2 reference genome.

Genotype imputation was performed with the FImpute program (Sargolzaei et al., 2014) by using the pedigree file. First, SNPs in the HD panel that were not in common with the reference panel (50K) were eliminated. Next, low-density genotypes and HD common SNPs to the reference panel were imputed to the 50K. After imputation, an additional QC was performed on imputed genotypes by using the PREGSF90 software (Aguilar et al., 2010). The filters applied were the same as used in the previous QC, with the difference that the MAF criteria was < 0.05.

Table 1. Descriptive statistic for 305-d cumulative milk yield and body conformation traits related to the udder and frame in Gir dairy cattle

<table>
<thead>
<tr>
<th>Trait</th>
<th>Units/Ideal Score</th>
<th>N</th>
<th>N_GP</th>
<th>Mean ± SD</th>
<th>Min</th>
<th>Max</th>
<th>h² ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Production</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Milk yield kg</td>
<td></td>
<td>38,996</td>
<td>979</td>
<td>3,566.5 ± 1,975.5</td>
<td>209</td>
<td>15,355</td>
<td>0.23 ± 0.01</td>
</tr>
<tr>
<td><strong>Frame</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hip height cm</td>
<td>cm</td>
<td>1,062</td>
<td>851</td>
<td>134.1 ± 7.1</td>
<td>103</td>
<td>180</td>
<td>0.33 ± 0.08</td>
</tr>
<tr>
<td>Heart girth cm</td>
<td>cm</td>
<td>1,055</td>
<td>844</td>
<td>176.6 ± 9.7</td>
<td>134</td>
<td>210</td>
<td>0.26 ± 0.08</td>
</tr>
<tr>
<td>Rump angle ≤5</td>
<td>cm</td>
<td>1,062</td>
<td>851</td>
<td>6*</td>
<td>2</td>
<td>9</td>
<td>0.23 ± 0.07</td>
</tr>
<tr>
<td>Udder</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rear udder width</td>
<td>9</td>
<td>916</td>
<td>724</td>
<td>5*</td>
<td>2</td>
<td>9</td>
<td>0.35 ± 0.07</td>
</tr>
<tr>
<td>Udder depth 5</td>
<td>5</td>
<td>1,043</td>
<td>850</td>
<td>5*</td>
<td>1</td>
<td>8</td>
<td>0.30 ± 0.06</td>
</tr>
<tr>
<td>Teat length ≤5</td>
<td>cm</td>
<td>1,044</td>
<td>851</td>
<td>5*</td>
<td>1</td>
<td>9</td>
<td>0.27 ± 0.06</td>
</tr>
<tr>
<td>Teat diameter 5</td>
<td>cm</td>
<td>1,043</td>
<td>850</td>
<td>5*</td>
<td>2</td>
<td>9</td>
<td>0.25 ± 0.06</td>
</tr>
</tbody>
</table>

Units: Units of measurement; N: number of records; N_GP: number of animals with genotype and phenotype; Min: minimum value for the evaluated trait; Max: maximum value for the evaluated trait; Mean: mean value for the evaluation trait; SD: mean standard deviation by trait; h²: heritability estimate; SE: heritability standard error. *Mode. 1Ideal score according to (Panetto et al., 2022).
After data trimming, 42,105 SNPs and 1,593 animals were kept for further analysis.

**Genome-wide association study**

The variance of estimated SNP-effects used in the GWAS were calculated with the POSTGSF90 software (Misztal et al., 2018). The P-value was calculated based on the variance of the prediction error of the SNP-effects, according to Aguilar et al. (2019). Adjusted Bonferroni correction (P < 0.05/total SNPs) was applied to correct for multiple testing. Thus, the significant threshold for all traits at 5% was 0.05/42,105, which is equivalent to 5.9 on the -log10 scale.

In addition, we calculated the proportion of genetic variance explained by the moving windows of adjacent SNPs using the weighted single-step genomic approach (WssGBLUP; Wang et al., 2012), where the $A$ inverse is replaced by the $H$ inverse (Aguilar et al., 2010), which is a relationship matrix that combines both pedigree ($A$) and genomic relationships ($G$). The WssGBLUP is an iterative process that involves: (i) initializing $D$ equal to an identity matrix ($I$); (ii) constructing $G$, as $G = ZDZ'$, in which $Z$ is an incidence matrix adjusted for allele frequencies, where $D$ is a diagonal matrix of weights for SNP variances, $M$ is the number of markers, and $p_i$ represents the MAF of the $i^{th}$ SNP; (iii) calculating genomic breeding values (GEBV); (iv) converting DGV into SNP effects by $\hat{u} = \lambda DM'G^{-1}DGV$, in which $\hat{u}$ is a vector of estimated SNP effects, $\lambda$ is the ratio of SNP variance to genetic variance and DGV is the direct genomic value; (v) calculating SNP weights for the next iteration by a nonlinear procedure according to VanRaden’s classic paper (VanRaden, 2008),

$$d_i = 1.125 \frac{1}{\sigma_u^2} \left( 1 - \frac{1}{M} \right) \sum_{i=1}^{M} 2p_i (1 - p_i),$$

where 1.125 is a constant that describes the deviation of the SNP effect from a normal distribution, $\sigma_u$ is the absolute estimated SNP effect for marker $i$, and $\sigma(\hat{u})$ is the standard deviation of the vector of the estimated SNP effects; (vi) normalizing $D$ to maintain a constant total genetic variance; (vii) iterating from step (ii) (Lourenco et al., 2017).

We used results from each of 2 iterations of WssGBLUP, because 2 iterations of weights are reported as enough to maximize genomic accuracy and to correctly identify major SNP (Zhang et al., 2016). The WssGBLUP was conducted using the BLUPF90 software family (Miszta et al., 2018), and the GWAS results were reported as the percentage of genetic variance explained by a moving window of 0.11-megabase, in which the window size was determined by the calculating of linkage disequilibrium by chromosome (Figure 1S) using the PREGSF90 software (Misztal et al., 2018). In this study, the use of a 0.11-megabase window size allowed us to achieve an $r^2$ value above 0.3 for linkage disequilibrium. This level of linkage disequilibrium among markers proved to be highly effective in GWAS (Ardlie et al., 2002). Manhattan plots were created using ‘CMplot’ package (Yin et al., 2021) in R software (R, 2022).

**Causative variants and QTL regions**

QTL annotation was carried out based on the position of significant SNP effects. For traits where no significant variants were found, the top 10 windows explaining the highest percentage of additive genetic variance (Vargas et al., 2018, Otto et al., 2020, Rocha et al., 2023) were selected to perform QTL annotation, based on the initial and final coordinates of each window. The identification of genes associated with variants was carried out based on the position of significant SNP effect, using 0.05-megabase upstream and downstream (distance determined based on population linkage disequilibrium). QTL and gene annotations were performed using the ARS-UCD1.2 assembly of the bovine genome with the GALLO package (Fonseca et al., 2020) in the software R (R, 2022). Which uses the databases Animal QTLdb (https://www.animalgenome.org/QTLdb) and Ensemble (http://www.ensembl.org/), for QTL annotations and gene search, respectively.

**RESULTS AND DISCUSSION**

Identify causative variants influencing traits of economic interest holds the potential to enhance the genomic prediction (Jang et al., 2023) and, consequently, animal selection strategies for dairy cattle. Breed specific QTLs may be present and so it is important to study each dairy breed and confirm (or reject) known QTLs from other studies. This study focus on the Gir breed, which is a Bos taurus taurus breed and confirm (or reject) known QTLs from other studies. This study focus on the Gir breed, which is a Bos taurus indicus breed and therefore genetically distant from the Holstein Bos taurus taurus cattle that is often studied (Decker et al., 2014).

Herein, we identified significant SNP effects for HH (on BTA 6) and RA (on BTA 1). Those SNPs positions overlap with QTLs previously associated with body height and rump angle, respectively. Also, we detected QTL previously described for milk yield (on BTA 5 and 12), udder width (on BTA 14 and 20) and udder depth (on BTA 2 and 18). These QTLs overlapped with some of the top 10 windows with the highest percentage of additive genetic variance explained for MY, RU and UD. Additionally, our analysis has identified 5 genes as near to significative SNPs for HH and RA traits. Genes implicated in reproduction, milk production, carcass weight and bone weight. Notably, certain variants unveiled by...
this study have not been associated with milk yield, frame structure, or udder conformation traits before. This suggests the existence of causative variants that might be unique to Gir cattle and are yet to be fully characterized. Further exploration of *Bos taurus indicus* breeds might unveil distinct potential causative variants linked to traits of economic interest for the dairy industry.

*P*-values were obtained to identify candidate SNPs associated with analyzed traits. Significant SNPs were found on BTA 6 and BTA 1 for HH and RA traits (Figure 1), respectively. However, for the remaining traits, none of the tested SNPs were found to be significantly associated with the phenotypes (Figure 1 and 2), suggesting either the need for analysis on a larger data set or the size of the SNP chip used. In this study, the GGP_Indicus_50k_A1 (50K) chip was used as a reference. However, it is possible that a higher density chip could help pinpoint more significant SNPs.

Another potential reason for finding a small number of SNPs with significant effects on the investigated traits is the limited size of the population references used for the imputation (100 animals). The decision to use the population genotyped with a 50k chip as a reference was based on studies that showed similar gains in prediction accuracy of GEBV when comparing whole-genome sequences versus medium-density SNP arrays (Van Binsbergen et al., 2015, Heidaritabar et al., 2016, Frischknecht et al., 2018).

The literature shows that the imputation of low to medium-density SNPs chips in the Gir breed is accurate.

**Figure 1.** Circular-Manhattan plot of the -log10 (*P*-value) for rump angle, heart girth, hip height, and milk yield traits plotted from outside to inside, respectively. The dashed red line indicates the Bonferroni threshold (0.05 divided by the number of SNPs). Significant SNPs were highlighted in red. Outside numbers correspond to 29 *Bos taurus* autosomes. A rectangular-Manhattan version of the plot is shown in the Supplementary Figures.
For example, Ospina et al. (2021) using a subpopulation of the genotypes used in this study (289 genotyped animals), demonstrated high accuracy (correlation and concordance rate values of 0.95 and 0.97, respectively) imputing SNPs chips from low (9k) to medium-density (35k). Similarly, performing imputation in different scenarios Boison et al. (2015), obtained higher correlation (0.91) and concordance rate (0.92) values when genotypes were imputed from the 3K to 50K chip using 171 reference animals.

The WssGBLUP approach was performed to identify causative variants associated with phenotypes, mainly for traits where non-significant P-values were found. Weighted SNPs can be a superior prior for scenarios with smaller populations (Lourenco et al., 2017, Santana et al., 2023) or a worse fit (Santana et al., 2023), increasing the detection power for GWAS (Spencer et al., 2009). The use of weights might help elucidate features of trait architecture mainly in polygenic traits (Santana et al., 2023).

The percentage of genetic variance explained by each window of 0.11-megabase is displayed in Manhattan plots for milk production, frame, and udder conformation traits (Figure 3 and 4). As seen in the figures, there is a key region on BTA 3 that seems relevant to most of the studied traits. The additive genetic variance explained by each one of 10 top windows identified for the studied traits ranged from 2.5% (for HG) to 0.27% (for RU) (Tables 2–4). These small genetic variances confirm the common assumption that the evaluated traits are
polygenic, and that the importance of each QTL, gene or associated SNP is small. Therefore, these traits will probably benefit from whole genome approaches, such as genomic selection, and are not likely to be selected using a reduced panel of specific markers.

**QTL regions**

The Gir QTLs annotated here for HH and RA are corroborated by previous literature (Table 5). Significant SNP on BTA 1 was detected for RA overlapping a QTL previously reported as associated to rum angle in French Holstein, Normande, and Montbéliarde (Boichard et al., 2003). In the same study, Boichard et al. (2003) also reported QTLs related to body height overlapping the significant SNPs identified on BTA 6 for HH. These findings suggest the relevance of these causative variants for HH and RA, despite being detected in different breeds.

QTLs discovered here for MY were previously described in the literature. A variant on BTA 5 was detected for MY, overlapping QTLs previously reported as associated to milk yield in different dairy breeds such Holstein (Bennewitz et al., 2003, Bennewitz et al., 2004), Fleckvieh (Awad et al., 2010), and Finnish Ayrshire (Viitala et al., 2003). Additionally, in the study performed by Viitala et al. (2003), they described another QTL related to milk yield on BTA 12 in the same region identified in this current study for MY (Table 6). Those QTLs for MY seem to be important across breeds. Knowing that at least some of the genetics variants for MY are relevant across breeds may encourage multi-breed, or crossbreed, selection programs. The Gir crossed Holstein ‘Girolando’ cattle is an important resource for tropical dairy industries that may benefit from this study.

Regarding udder traits, genetic variants on BTA 14 and BTA 20 associated with RU are located within QTL regions previously reported to influence udder width in Holstein cattle (Schnabel et al., 2005). Similarly, variants on BTA 2 and BTA 18 related to UD overlap with QTLs that have demonstrated a significant effect on udder depth (Ashwell et al., 2005, Leyva-Baca et al., 2007). These findings show that a proportion of the top 10 identified windows overlap with QTL regions that have been previously associated with milk yield and some of the frame and udder traits in dairy cattle. Of note, MY is one of the most studied traits, which bias any GWAS results for identifying overlapping results with QTLs for MY.

Teat traits, such as TD and TL, can impact udder health, mechanical milking and calf feeding processes. Long and thicker teats generate issues for mechanical milking and calf feeding (Fernandes et al., 2019). These problems with teat traits are often reported in *Bos taurus indicus* cattle, and not so much in *Bos taurus taurus* cattle, so there are not many reports in the literature for these traits. Our results showed that TL variants overlapped with a known QTL associated with teat placement, in a region on BTA 22. Also, TD top windows were overlapping with a QTL for udder conformations traits, on BTA 20 and BTA 21. We might consider this overlap between teat and udder QTLs as an expected result because TD is genetically correlated with udder traits, such as RU and UD (0.53 and 0.54 respectively; Dominguez-Castaño et al., 2024). The causative variants reported in this study for BTA 20 and BTA 21 should be considered in future studies investigating the genes that underpin the known genetic correlation between teat and udder traits in Gir dairy cattle.

The HG top windows discovered here did not overlap with known QTL for HG. However, several of known QTLs that overlapped with the top 10 windows for HG were QTL for body weight. This result aligns with the strong genetic correlation described between HG and body weight (Koenen and Groen, 1998, Abbasi and Ghafoori-Kesbi, 2011). Therefore, selection targeting HG trait in Gir cattle, including using markers in these variants, will lead to heavier body weights on average.

**Genes associated with significant variants**

Candidate genes were identified by examining only in the traits with significant SNPs, specifically HH and RA. A SNPs was identified near the *FAM13A* gene on BTA 6 for HH (Table 5). *FAM13A* has been associated with bone weight in beef cattle (Xia et al., 2017, Niu et al., 2021). Additionally, *NAP1L5* and *HERC3* genes were detected near significant SNPs on BTA 6 for HH. *NAP1L5* is a known imprinted gene in cattle (Zaitoun and Khaitib, 2006), and both *NAP1L5* and *HERC3* were related with significant effects for milk yield (Jiang et al., 2019).

Two genes were detected near to significant variant on BTA 1 for RA. *CMSS1* gene was found to be significantly associated with carcass weight in Hanwoo Cattle (Srikanth et al., 2020), while *TMEM30C* gene is specifically expressed in the testis of mammals, relating to male reproduction (Osada et al., 2007). No reports were found in the literature on the association of *CMSS1* and *TMEM30C* specifically with body conformation traits and so our results require confirmation and further research.

Some QTLs and genes identified in this study had not previously been associated with milk yield, frame, or udder conformation traits (Table 2S). These inconsistencies might be due to differences in breed or particularities of the studied herd, such as the extent of LD, allelic frequencies, sample size, or discrepancy in the statistical approaches (Wang et al., 2022). This also indicated that there are many important causative variants in the bovine genome that are yet to be discovered. The study of *Bos*
CONCLUSION

The association study provided the significant causative variants for HH and RA traits in Gir dairy cattle. Some of the variants identified were located within QTL regions previously reported as related to milk yield, body height, rump angle, udder width and udder depth. Five genes were identified, of which \textit{FAM13A} and \textit{CMSS1} had been previously related to bone and carcass weight in cattle. Some of the variants were novel genomic locations that could be used to better understand the complexity of the genetic basis of the studied traits. These findings establish a foundational platform for further studies that aim to understand the biological pathways that affect milk yield, frame and udder traits in dairy cattle, particularly in Gir cattle. This research is relevant to \textit{Bos taurus indicus} cattle and the tropical industries that breed these adapted animals.

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The authors thank the breeders Adolfo de Jesus Gonzalez, Albaro Rosevelt Gonçalves, Aníbal Eugenio Vercesi, Antonio Eustaquito Alves de Souza, Alirio Barroso, Aroldo Plínio Gonçalves, Eduardo Costa Simões, Gabriel Puerta Parra, Guilherme de Melo Marci, João Guilherme Maldini Pitanguy, José Luiz Junqueira Barros, Jovelino Díaz de la Cruz, and the other breeders involved in the project.

Figure 3. Circular-Manhattan plot for the proportion of additive genetic variance (%) explained by 0.11-megabase moving windows for udder conformation traits teat diameter, teat length, udder depth, and rear udder width plotted outside to inside, respectively. Outside numbers correspond to 29 \textit{Bos taurus} autosomes. A rectangular-Manhattan version of the plot is shown in the Supplementary Figures.
Figure 4. Circular-Manhattan plot for the proportion of additive genetic variance (%) explained by 0.11-megabase moving windows for rump angle, heart girth, hip height, and milk yield plotted from outside to inside, respectively. Outside numbers correspond to 29 Bos taurus autosomes. A rectangular-Manhattan version of the plot is shown in the Supplementary Figures.

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Table 5. QTL annotation and gene identification in significant variants associated with hip height (HH) and rump angle (RA) in Gir dairy cattle

<table>
<thead>
<tr>
<th>Trait</th>
<th>BTA</th>
<th>SNP Position (bp)</th>
<th>P-value</th>
<th>QTL_Name</th>
<th>Pubmed_ID</th>
<th>Gene</th>
</tr>
</thead>
<tbody>
<tr>
<td>HH</td>
<td>6</td>
<td>36074911</td>
<td>5.976</td>
<td>Body height</td>
<td>3421</td>
<td>FAM13A</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NAP1L5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>HERC3</td>
</tr>
<tr>
<td>RA</td>
<td>1</td>
<td>4447537</td>
<td>5.981</td>
<td>Rump angle</td>
<td>3428</td>
<td>CMS51</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TMEM30C</td>
</tr>
</tbody>
</table>

BTA: Bos taurus autosome; bp: base pair; P-value on the -log10 scale.

Table 6. QTL annotation in genomic windows associated with rear udder width (RU) udder depth (UD) and milk yield (MY) in Gir dairy cattle

<table>
<thead>
<tr>
<th>Trait</th>
<th>BTA</th>
<th>Start position (bp)</th>
<th>End position (bp)</th>
<th>Var (%)</th>
<th>QTL_Name</th>
<th>Pubmed_ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>RU</td>
<td>14</td>
<td>77918152</td>
<td>78045230</td>
<td>0.27</td>
<td>Udder width</td>
<td>16167984</td>
</tr>
<tr>
<td>UD</td>
<td>20</td>
<td>22158626</td>
<td>22307782</td>
<td>0.37</td>
<td>Udder depth</td>
<td>16167984</td>
</tr>
<tr>
<td>MY</td>
<td>17</td>
<td>96709292</td>
<td>96806067</td>
<td>0.36</td>
<td>Milk yield</td>
<td>117433017</td>
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<tr>
<td></td>
<td>18</td>
<td>24230415</td>
<td>24346129</td>
<td>0.44</td>
<td>Udder depth</td>
<td>16230715</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>78689623</td>
<td>78796160</td>
<td>0.36</td>
<td>Milk yield</td>
<td>16230715</td>
</tr>
</tbody>
</table>

BTA: Bos taurus autosome; bp: base pair; Var: percentage of additive genetic variance explained by each window.


Domínguez-Castaño et al.: GWAS for milk and conformations traits in Gir cattle


