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Genome-wide association analysis of body size and growth traits in Guanling cattle and mining of key candidate genes

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Abstract

Background

Genome-wide association studies (GWAS) are effective for dissecting the genetic basis of complex quantitative traits in livestock. Body conformation and growth traits in Guanling cattle are economically important, but the underlying genetic architecture remains largely unexplored.

Results

In this study, nine body conformation and growth-related traits—including withers height (WH), hip height (HH), body length (BL), chest girth (CG), abdominal girth (AG), cannon bone circumference (CBC), chest width (CW), pin bone width (PBW), and body weight (BW)—were measured in 69 Guanling cattle. Whole-genome resequencing and quality control yielded 16,417,194 high-quality variants for GWAS. Using a mixed linear model accounting for population structure and relatedness, we identified 15 significant single nucleotide polymorphisms (SNPs) annotated to 19 candidate genes. Major association signals were detected for WH, AG, CBC, and PBW. Notably, INSC, ANO3, LPL, ITPR2, PLXNA2, and IPMK were highlighted as biologically meaningful candidates involved in cell polarity, ion transport, lipid metabolism, calcium signaling, and tissue morphogenesis.

Conclusions

These findings indicate that body conformation traits in Guanling cattle are complex quantitative traits influenced by multiple genes and pathways. The identified candidate loci provide a valuable resource for future marker-assisted selection and genetic improvement of this local breed.

1. Background

China is one of the world's major beef-producing countries and possesses abundant indigenous cattle genetic resources. Over the long course of adaptation to diverse ecological environments and management conditions, these local breeds have developed heterogeneous genetic backgrounds and distinctive economic traits. In beef cattle production, meat yield and meat quality have always been the primary targets of breeding and management. Body size traits, such as body weight, body height, body length, chest girth, abdominal girth, and hip width, are closely associated with body conformation, growth and developmental rate, carcass composition, and subsequent productive performance. Therefore, they are widely used as indicators of growth and production potential in beef cattle [1–4]. In recent years, genome-wide association studies (GWAS), by integrating high-density genotypic data with phenotypic measurements, have enabled the identification of genetic variants significantly associated with target traits across the whole genome, followed by the annotation of candidate genes. As such, GWAS has become an important tool for dissecting the genetic basis of complex economic traits in

livestock [5–8]. GWAS has been widely applied to the study of body conformation, udder structure, limb and hoof traits, growth, body weight, and carcass traits in both dairy and beef cattle, and has identified a large number of candidate genes associated with skeletal development, lipid metabolism, cell proliferation, ion transport, and signaling pathway regulation [9–12]. Previous studies have shown that body size traits not only reflect the development of the skeletal framework and body tissues, but are also broadly associated with feed efficiency, fattening capacity, reproductive performance, and health status. Therefore, systematic investigation of the genetic basis of body conformation traits is of great significance for livestock production and molecular breeding [13–16]. Guanling cattle are one of the five major local yellow cattle breeds in Guizhou Province. They possess strong adaptability to mountainous terrain and good resource utilization potential, making them an important genetic resource for local cattle breeds in Southwest China. However, due to their small size, slow growth rate, and insufficient development of their growth trait genetic potential, they still lag significantly behind commercially available breeds. To further select superior populations with larger individuals and faster growth rates, we conducted GWAS analysis to identify significant loci associated with body size and growth rate, aiming to improve the growth performance of their offspring.

In recent years, substantial progress has been made in genomic studies of body size and conformation traits in cattle. A study in Qinchuan cattle, based on 254 individuals and 14 conformation traits, identified 250 suggestive loci and annotated 37 candidate genes, providing an important reference for research on body conformation traits in Chinese indigenous yellow cattle [1]. In Chinese Holstein populations, single-trait and multi-trait GWAS have detected 63 significant SNPs across 17 conformation traits and annotated 66 candidate genes, indicating that multi-trait analysis has clear advantages in improving detection efficiency [3, 5]. At the same time, studies in Chinese Holstein, Gyr dairy cattle, Xinjiang Brown cattle, Wenshan cattle, Xiannan cattle, and other cattle populations have identified multiple QTLs and functional genes with potential breeding value for body conformation, body size, or body weight traits. These studies have increasingly incorporated fine mapping, transcriptomic analysis, and functional validation to strengthen the biological interpretation of the results [10, 11, 14, 17, 18]. In addition, studies focusing on economically important traits such as meat quality, carcass characteristics, and growth performance have continuously enriched our understanding of the genetic basis of complex quantitative traits in cattle, and have provided important references for the biological interpretation of candidate genes associated with body size traits [19–23]. These studies indicate that the genetic architecture of body size traits shows both shared patterns across breeds and clear population specificity. Therefore, independent GWAS analyses in indigenous cattle populations are needed.

However, comprehensive studies on growth-related traits in Guanling cattle remain limited. Therefore, based on GWAS results, the present study systematically investigated the genetic basis of body size and growth-related traits in this breed, with the aim of identifying candidate loci and functional genes significantly associated with key conformation traits. This work is expected to further enrich the molecular genetic research on body size traits in Chinese indigenous yellow cattle and to provide a theoretical foundation for subsequent marker-assisted selection, core breeding population development, and genetic improvement of Guanling cattle.

2. Materials and Methods

2.1 Experimental materials

A total of 69 healthy Guanling cattle aged 2–3 years were selected for this study. All experimental animals were raised under the same environmental conditions and were obtained from the Guanling Cattle Conservation Farm in Guanling County, Guizhou Province, China. Approximately 5 mL of jugular venous blood was collected from each animal and transferred into tubes containing EDTA as an anticoagulant. The samples were transported to the laboratory in an ice box at 4°C and then stored at −20°C until further use. All animal experimental procedures were approved by the Animal Welfare and Ethics Committee of the Guizhou Institute of Animal Husbandry and Veterinary Science.

Nine key growth traits were measured using standard measurement tools in accordance with the standards of Livestock Breeding [24]. WH: Vertical distance from the highest point of the withers to the ground, measured with the animal standing on a level surface. HH: The vertical distance from the cruciate vertebra (the front of the sacrum/the highest point of the hip) to the ground when the cow is standing naturally, measured with a measuring ruler. BL: The oblique vertical distance from the shoulder end (the front edge of the shoulder joint or acromion) to the ischial end (ischial tuberosity) when the cow is standing naturally, measured with a soft measuring tape. CG: Use a soft measuring tape to measure around the chest along the back edge of the scapula (behind the front of the chest), keeping the tape close to the body but not pressing, and record the chest circumference. AG: Use a soft measuring tape to measure around the body along the most bulging part of the abdomen (usually behind the last rib), and record the abdominal circumference. CBC: Use a soft measuring tape to measure the circumference at the narrowest part of the middle of the bones of the forelimb or hindlimb. CW: Measure the horizontal distance between the two shoulder joints (or the outer edge of the scapula) with calipers or a ruler and record the chest width. PBW: Measure the horizontal distance between the two ischial tuberosities with calipers and record the width; BW: Weigh the child on the same weighbridge (minimum weighing capacity 5 kg) before feeding in the morning and record the weight.

2.2 Descriptive statistics and normality tests of phenotypic data

Descriptive statistical analyses of the nine traits were performed using R software. The sample size, mean, standard deviation, minimum, maximum, and coefficient of variation were calculated to comprehensively evaluate the degree of dispersion and distributional characteristics of each trait. To reduce the potential influence of extreme values on subsequent association analyses, outliers were screened using boxplots in combination with standardized residuals. Records exceeding the mean ± 3 standard deviations, or those confirmed to involve measurement errors after verification, were excluded or corrected accordingly.

2.3 Quality control of genotype data and statistical analysis of locus distribution

A total of 69 Guanling cattle samples underwent 10x whole-genome resequencing, which was performed by Beijing Compson Agricultural Technology Co., Ltd. (Tianjin, China). All samples underwent whole-genome sequencing using the BGI Genomics T7 sequencer, with a sequencing length of 150 bp, including steps such as DNA extraction, detection, fragment purification, and library construction. Before subsequent analysis, the raw data was filtered according to the following conditions: reads containing adapter sequences were removed; reads with an N content exceeding 10% of the total number of bases in the sequencing reads were removed; and reads with a low-quality ($Q \leq 5$) base count exceeding 50% of the total number of bases in the reads were removed. The original genotype data contained a total of 49,187,509 variant sites, of which 1,219,128 were non-chromosomal sites. After multiple rounds of screening, 16,417,194 high-quality sites were ultimately retained for subsequent analysis.

2.4 Comparison and Variation Detection

After data filtering, an index was built based on the provided reference genome. Then, Clean reads were aligned to the reference genome using BWA-MEM (v0.7.17) [25] software. Samtools (v1.7) was used to sort and build the index. The Bam file was deduplicated using the built-in module of GATK (v4.1.8.0) [26] software. Then, based on the Bam file, the sequencing depth, genome coverage and other information of each sample were statistically analyzed to prepare for subsequent variant detection. SNPs (single nucleotide polymorphisms)/insertions/deletions (less than 50 bp) were identified using the GATK (v4.1.8.0) software to call SNPs based on the alignment results of Clean Reads with the reference genome, followed by rigorous filtering using the Variant Filtration module.

2.5 Group Structure and Kinship Analysis

To reduce the interference of population stratification and inter-individual kinship on GWAS results, the genetic structure of the Guanling cattle population was systematically assessed before genome-wide association analysis. First, the quality-controlled genotype data were converted into a software format suitable for subsequent analysis, and a genetic relationship matrix was constructed based on high-quality SNP markers. Principal component analysis (PCA) was used to extract the top principal components with the largest explanatory variance to describe the genetic differentiation and population stratification among samples. Two-dimensional scatter plots of the first two principal components and three-dimensional visualizations of the first three principal components are provided to observe whether there is a clear clustering trend in the samples. In terms of kinship analysis, a kinship matrix between individuals was further constructed, and the degree of genetic correlation between samples was displayed in the form of a heatmap. Meanwhile, a phylogenetic tree was constructed based on genetic distance to assess the clustering relationships and genetic distances among different individuals. Considering that linkage disequilibrium (LD) level has a significant impact on GWAS resolution, an LD decay map was plotted to assess the characteristic that LD decreases with increasing physical distance in the population. In addition, the proportion of ancestral components under different K values was compared by Admixture [27] analysis, and the optimal number of clusters was determined by combining CV error, so as to further reveal the potential structure of the population. The above-mentioned population structure analysis and kinship assessment results together provide a basis for the setting of

covariates and model calibration in subsequent GWAS, which helps to reduce false positive signals and improve the credibility of association analysis.

2.6 Genome-wide association analysis

Genome-wide association analysis was performed using a mixed linear model (MLM) [28]. The first two principal components were included as fixed effect covariates in the model to control for subtle population structure, while the genomic relationship matrix was included as a random effect to account for residual relatedness among individuals. The output was provided in the form of P-values, effect sizes, minor allele frequencies, and phenotypic variance explained (PVE) for each variant, with statistical analyses conducted separately for each trait. For the significance threshold, the Bonferroni correction based on the total number of effective loci was applied. The mixed linear model, first published by Yu et al. [28] in Nature Genetics, has been widely adopted for GWAS analyses due to its ability to effectively correct for population structure and complex relatedness within populations.

$$Y=X\beta + Z\gamma + \xi + e$$

y is the phenotypic vector, Xβ is the fixed effect (population structure, sex), Zγ is the marker effect to be tested, ξ ~ N (0,Kσa2) is the polygenic effect, and e ~ N (0,Iσe2) is the residual effect.

2.7 Visualization of Association Results and Location of Candidate Intervals

To visually represent the GWAS analysis results, QQ plots and Manhattan plots were created for each trait. QQ plots are used to compare the consistency between observed P-value distributions and theoretical P-value distributions, thereby assessing whether the model effectively controls population structure and systematic bias; Manhattan plots are used to display the significance level distribution of each SNP locus on different chromosomes, so as to quickly identify significant association peaks and potential candidate regions. GWAS QQ plots and Manhattan plots have been generated for the nine traits, providing a visual basis for subsequent candidate site selection and result interpretation. For the detected significant association signals, this study further located the candidate intervals by combining the physical location of the sites. Multiple significant SNPs clustered within the same chromosomal region can be considered potential association peak regions and serve as important references for subsequent candidate gene searches. Furthermore, if multiple closely linked significant sites exist within a region, local region statistics and functional annotation can be used to screen for key genes most likely to influence trait formation.

2.8 Candidate gene annotation and functional enrichment analysis

To further analyze the potential biological functions of significant SNPs, gene annotation was performed on the significant loci, and candidate genes were searched within a 100 kb window upstream and downstream of each significant SNP. The annotation results were mainly derived from the functional

annotation file of the significant loci and the exonic annotation file. The annotation of significant loci for each trait showed that the WH-related loci were primarily located in the INSC gene and its adjacent regions, while the AG-related loci were mainly associated with ANO3 and ZNF214. The CBC-related signals were primarily located near LPL and SLC18A1, and the PBW-related loci involved multiple candidate genes, including PARD3B, ITPR2, EPHA5, NKAIN2, NALF1, PLXNA2, and IPMK. Subsequently, Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) enrichment analyses were conducted to systematically evaluate the functional characteristics of these candidate genes and their potential regulatory pathways. GO enrichment results showed that the relevant candidate genes are mainly involved in functions such as cell division regulation, ion channel activity, ion transmembrane transport, calcium ion signaling, and membrane receptor activity; KEGG pathway analysis showed that some candidate genes are involved in biological networks such as lipid metabolism, inositol phosphate signaling system, axonal guidance, and neural signaling pathways. The above results suggest that the genetic regulation of body size traits in Guanling cattle is not only related to classical skeletal development and growth metabolism, but may also be influenced by cell development regulation, ion homeostasis, and signal transduction pathways. Candidate gene annotation and functional enrichment analysis provide important basis for subsequent key gene validation, molecular mechanism analysis and marker-assisted selection.

3. Results

3.1 Phenotype and Genotype

A total of 69 cattle were measured for body conformation traits, and the descriptive statistics of the phenotypic data are presented in Table 1. The mean and standard deviation for body weight (BW) and the other nine body traits (WH, HH, BL, CG, AG, CBC, CW, and PBW) were as follows: 385.94 ± 33.49, 127.70 ± 3.96, 132.45 ± 3.84, 145.50 ± 6.44, 171.94 ± 7.68, 203.67 ± 10.51, 19.30 ± 1.68, 35.63 ± 2.76, and 25.59 ± 3.37, respectively. PBW exhibited the highest coefficient of variation (CV) at 13.17%, while HH had the lowest CV at 2.90%. The CVs for the other traits ranged from 3.10% to 8.70%. The phenotypic data followed a normal distribution and were suitable for subsequent analyses (Fig. 1). In this study, 10x whole-genome sequencing (WGS) was performed on the 69 cattle, identifying a total of 49,187,509 SNPs. After quality control, 16,417,194 high-quality SNPs were retained for GWAS analysis. These SNPs were roughly evenly distributed across the 29 chromosomes (Fig. 2).

Table 1
Descriptive statistics of phenotypes

Trait	Number	Mean	SD	Min	Max	CV
BW, kg	69	385.94	33.49	334.00	453.00	8.68%
WH, cm	69	127.70	3.96	118.00	135.50	3.10%
HH, cm	69	132.45	3.84	121.00	143.00	2.90%
BL, cm	69	145.50	6.44	131.00	163.00	4.43%
CG, cm	69	171.94	7.68	153.00	193.00	4.47%
AG, cm	69	203.67	10.51	180.20	235.00	5.16%
CBC, cm	69	19.30	1.68	16.00	22.80	8.70%
CW, cm	69	35.63	2.76	30.00	44.00	7.75%
PBW, cm	69	25.59	3.37	15.00	32.50	13.17%

SD, standard deviation. Abbreviations: BW, body weight; WH, withers height; HH, hip height; BL, body length; CG, chest girth; AG, abdominal girth; CBC, cannon bone circumference; CW, chest width; PBW, pin bone width; CV, coefficient of variation (SD/Mean).

3.2 Principal Component Analysis and Kinship Analysis

Principal component analysis (PCA) was performed on the samples using GCTA software v1.94.1, and the first two principal components were visualized using R software. The results showed that the individuals were widely distributed, with no distinct stratification or independent clustering, indicating that there was no significant genetic differentiation within the population (Fig. 3A). Further analysis of the 3D visualization in Fig. 3B revealed a similarly even distribution of individuals in three-dimensional space, with no obvious clustering trends, which further confirmed the consistency of the genetic background within the population, consistent with the results presented in Figs. 3C and 3D. Therefore, only routine principal component correction was needed in the subsequent GWAS analysis to effectively control for the impact of population structure. As shown in Fig. 3E, there was a slight deepening of color in some local regions, but no significant large-scale clustering was observed, indicating that there were no highly related individuals or inbred groups within the population. Overall, the population displayed a relatively distant genetic relationship with high genetic diversity. As shown in Fig. 3F, the population exhibited a relatively fast LD decay rate with low levels of linkage disequilibrium, reflecting a high genomic recombination rate and abundant genetic diversity. This characteristic is consistent with the genetic traits of indigenous cattle breeds that have not undergone intense artificial selection, and also suggests that the current SNP density is sufficient for GWAS analysis. Combined with the results from PCA, kinship analysis, NJ tree, and LD analysis, The results indicate that the population has a stable genetic structure, with no significant stratification, low inbreeding, and high genetic diversity. These characteristics provide an ideal population foundation for conducting genome-wide association studies.

3.3 Application of Genome-wide Association Studies in Body Shape Characteristics

Figure 4 displays the Manhattan plots of the genome-wide association analysis for each trait. A total of 15 significant SNPs were identified and used for the GWAS of nine body conformation traits in 69 cattle, and these SNPs were annotated to 19 candidate genes (Table 2). For WH, one SNP was found on chromosomes 10 and 15, annotated to three genes (Fig. 4B), including FLRH2, TRNAC-ACA-107, and INSC. For AG, one SNP was identified on chromosome 15, annotated to two genes, ZNF214 and ANO3 (Fig. 4F). For CBC, one SNP was found on chromosome 8, annotated to two genes, LPL and SLC18A1 (Fig. 4G). For PBW, eight SNPs were found on six different chromosomes (2, 5, 6, 9, 12, and 16), annotated to 12 candidate genes, including PARD3B, ITPR2, EPHA5, CENPC, NKAIN2, NOX3, ARID1B, NALF1, TRNAW-CCA-93, PLXNA2, IPMK, and LOC100295832 (Fig. 4I). For BW, HH, BL, CG, and CW, no SNPs or candidate genes were annotated. Overall, eight SNPs located on chromosomes 9, 10, and 15 warrant further attention.

3.4 GO enrichment analysis and KEGG pathway analysis

GO and KEGG enrichment analyses of candidate genes within 100 kb upstream and downstream of significant SNPs revealed that genes associated with different traits exhibited significant functional differentiation. In Fig. 5A, WH-related genes are mainly enriched in items such as establishment of spindle orientation, spindle localization, and regulation of cell division, suggesting that they may affect body height development by regulating the establishment of cell polarity and the direction of mitosis. In Fig. 5B, AG-related genes are mainly enriched in chloride channel activity and chloride transmembrane transport. Combined with the efferocytosis pathway in the AG-KEGG diagram, this suggests that AG formation may be related to the maintenance of ion homeostasis and the regulation of tissue metabolism. Figure 5C shows that CBC-related genes are mainly enriched in triacylglycerol lipase activity, and their CBC-KEGG map is further enriched in cholesterol metabolism, glycerolipid metabolism, and PPAR signaling pathway, indicating that CBC variations may be closely related to lipid metabolism and energy distribution. For PBW, Fig. 5D shows that it is mainly enriched in calcium channel activity, calcium ion transmembrane transporter activity, and semaphorin receptor activity. At the same time, PBW-KEGG plots show significant enrichment in phosphatidylinositol signaling system and axon guidance, suggesting that PBW may be jointly regulated by calcium signal transduction and tissue morphogenesis. Overall, the body size trait of Guanling cattle is a typical complex quantitative trait, which is influenced by cell division, ion transport, lipid metabolism and developmental signaling networks.

4. Discussion

Body weight and body conformation are among the most fundamental and economically valuable traits in beef cattle production. They reflect the individual’s growth and developmental status and are closely

associated with feed conversion efficiency, fattening performance, carcass yield, and overall breeding profitability. Conformational traits, including withers height, body length, chest girth, abdominal girth, hip width, and cannon circumference, serve not only as critical phenotypic indicators of body development but are also widely used in early selection and molecular breeding programs [8, 29–31]. Previous studies have shown that these traits are typical complex quantitative traits, influenced jointly by multiple minor-effect genes and environmental factors [35–38]. Compared to traditional phenotypic selection, genome-wide association study (GWAS) provides an effective strategy for analyzing the genetic architecture of quantitative traits and offers valuable information for the discovery of molecular markers, candidate gene identification, and subsequent genomic selection [13, 14, 38, 41]. In this study, GWAS was conducted for nine body size and growth-related traits in 69 Guanling cattle, and after genotype quality control, 16,417,194 high-quality variant sites were retained. The candidate gene annotation results revealed that three genes were associated with withers height (WH), two with abdominal girth (AG), two with cannon bone circumference (CBC), and twelve with pin bone width (PBW), with the most concentrated association signals observed for PBW. GO and KEGG enrichment analyses further indicated that the WH-associated genes were mainly involved in spindle localization and regulation of cell division, while the AG-associated genes were primarily related to chloride channel activity and ion transmembrane transport. The CBC-associated genes were mainly involved in triglyceride lipase activity, cholesterol metabolism, glycerolipid metabolism, and the PPAR signaling pathway, whereas the PBW-associated genes were enriched in calcium ion transport, receptor activity, phosphatidylinositol signaling pathways, and axon guidance-related pathways. Taken together, these results suggest that body conformation traits in Guanling cattle may be influenced by multiple biological processes, including cell proliferation and polarity establishment, ion transport and calcium signaling, lipid metabolism, and tissue morphogenesis [13, 14, 34–38, 41–44].

Among the candidate genes associated with WH, FLRH2, TRNAC-ACA-107, and INSC were identified. Compared to the first two gene loci, INSC appears to have stronger biological plausibility. GO enrichment analysis suggested that INSC may be involved in spindle orientation, spindle localization, and regulation of cell division, indicating that it could potentially promote the proliferation and differentiation of skeletal-related cells through its known roles in cell polarity establishment and mitotic orientation regulation. Previous studies have shown that spindle orientation and cell polarity play important roles in epithelial morphogenesis and organ growth [39]. Additionally, height is closely associated with the proliferation of growth plate chondrocytes, osteogenic differentiation, and endocrine regulation, and the insulin-like growth factor system has been recognized as an important molecular basis for linear growth [32]. Therefore, INSC may represent a potential candidate gene for WH in Guanling cattle, although its specific role in skeletal growth still requires experimental validation. For abdominal girth (AG), the candidate genes mainly include ZNF214 and ANO3, with ANO3 appearing to be more strongly supported by association evidence, as it corresponds to two significant loci and is enriched in GO terms related to chloride channel activity and chloride ion transmembrane transport. Abdominal girth is a complex trait that reflects not only skeletal structure but also abdominal wall musculature, visceral development, digestive tract capacity, and fat deposition [29, 33]. It is known that chloride channels play an important

role in ion homeostasis, epithelial secretion, and tissue function in the digestive system [47]. Based on these observations, ANO3 may be indirectly associated with abdominal girth variation through ion transport processes and tissue physiological regulation. In contrast, ZNF214, as a zinc finger protein, may be involved in transcriptional regulation and developmental processes, but its functional relevance to abdominal girth remains unclear and requires further investigation. For cannon bone circumference (CBC), LPL and SLC18A1 were identified as particularly noteworthy candidate genes. CBC is typically considered an important indicator of limb robustness, bone mass, and structural support in beef cattle [8, 30]. However, this trait may not fully reflect skeletal development, as peripheral tissue deposition, metabolic status, and energy allocation could also contribute to phenotypic variation [36, 37]. Among the candidate genes, LPL is a known gene involved in lipid hydrolysis, fatty acid utilization, and fat deposition. In this study, LPL was enriched in triglyceride lipase activity as well as cholesterol metabolism, glycerolipid metabolism, and the PPAR signaling pathway. These results are consistent with previous studies, indicating that lipid metabolic networks are closely related to body conformation, muscle growth, and fat deposition in cattle [46, 50, 51]. In addition, studies on carcass and meat quality traits have also indicated that body conformation and energy metabolism may share overlapping genetic foundations [48, 52, 53]. Therefore, LPL may be a biologically significant candidate gene for cannon bone circumference (CBC). In contrast, SLC18A1 may have a more indirect association with this trait, possibly influencing it through neuroendocrine regulation, feeding behavior, or growth rhythms. However, this hypothesis requires further validation.

The most significant finding in this study was related to pin bone width (PBW), where a relatively large number of candidate genes were annotated, including PARD3B, ITPR2, EPHA5, CENPC, NKAIN2, NOX3, ARID1B, NALF1, PLXNA2, and IPMK. These genes have diverse functions, but some appear to be closely related to biological processes associated with tissue development and structural formation. For example, ITPR2, NALF1, and IPMK may be involved in calcium signaling and phosphatidylinositol-related pathways. Calcium signaling is widely involved in processes such as cell proliferation, differentiation, osteogenesis, cartilage development, and muscle function [40], and studies on calcium channel regulation in skeletal muscle further confirm the importance of calcium homeostasis in tissue development and function [45, 54]. Therefore, these genes may be reasonable functional candidates for PBW, although their specific effects on the pelvic morphology of Guanling cattle still need to be validated. Similarly, EPHA5 and PLXNA2 are typically associated with receptor-mediated guidance pathways, particularly Ephrin and Semaphorin signaling pathways. Although these pathways are commonly discussed in the context of neurodevelopment, they are also involved in cell migration, tissue boundary formation, and morphogenesis in broader biological contexts. Based on this, these genes may be indirectly related to pelvic structure development, although there is currently no direct functional evidence to suggest that they play such a role in Guanling cattle. Additionally, PARD3B, CENPC, and ARID1B may further support the idea that cell polarity, chromosome segregation, and chromatin remodeling are involved in developmental regulation. In summary, the genetic loci associated with PBW suggest that this trait is likely polygenic and may be influenced by multiple biological processes, rather than being controlled by a single major-effect gene. Compared to previous studies, the results from this

study in Guanling cattle show both population specificity and biological convergence. In Qinchuan cattle, Yu et al. [1] reported that genes such as ADAMTS17, ALDH1A3, CHSY1, MAGEL2, MEF2A, SYNM, CNTNAP5, and CTNNA3 may be associated with body conformation and growth regulation. Among these, ADAMTS17 and CHSY1 are more closely related to skeletal and connective tissue development, while MEF2A and SYNM are more related to skeletal muscle formation and muscle fiber function. In addition, Sun et al. [55] reported that the promoter methylation of MEF2A may regulate myoblast mRNA transcription and affect cellular physiological functions. Although this study did not identify the same set of candidate genes, in Guanling cattle, genes such as INSC, PARD3B, ITPR2, and PLXNA2, which are related to polarity establishment, calcium signaling, and morphogenesis, were significantly expressed. This pattern suggests that different cattle populations may harbor distinct genetic loci, but still converge on similar biological pathways associated with body size variation. Similar heterogeneity in genetic loci and pathway convergence has also been reported in Brazilian Holstein, Chinese Holstein, and North American Holstein populations [2, 14, 41]. From a breeding perspective, the primary value of this study lies in providing preliminary candidate loci and genes for subsequent validation in Guanling cattle. For indigenous yellow cattle breeds, breeding goals should not be limited to improving growth rate, but should also aim to improve body conformation and production performance in a coordinated manner while maintaining adaptability, stress resistance, and the unique characteristics of local genetic resources. Previous studies have shown that body conformation traits are not only related to growth performance and mature body size, but also to reproductive capacity, calving ease, structural soundness, and fattening potential [29, 42, 43]. In this regard, PBW, WH, CBC, and AG may have practical application value as they reflect pelvic structure, skeletal height, limb robustness, and abdominal capacity, respectively. However, the candidate genes identified in this study should still be regarded as putative candidates rather than confirmed pathogenic genes. Future research should prioritize independent population validation, haplotype analysis, tissue expression profiling, and functional experiments, with a particular focus on genes such as INSC, ANO3, LPL, ITPR2, PLXNA2, and IPMK. Integrating GWAS signals with genomic prediction models and candidate gene network analysis could further enhance the application value of these loci in the breeding of indigenous cattle [56, 57]. This study also has several limitations. First, the sample size is relatively small (n = 69), which may limit the statistical power to detect loci with low minor allele frequencies or small effects. Second, this study primarily focuses on association analysis and bioinformatic interpretation, lacking independent population validation, transcriptomic support, eQTL analysis, or functional experiments. Third, due to the polygenic nature of body conformation traits and their potential influence by developmental stages and environmental factors, the current findings should be considered preliminary rather than definitive conclusions. Therefore, future research on Guanling cattle should focus on increasing sample size, improving pedigree and generation information, integrating multi-omics data, and constructing breed-specific reference populations. If possible, research strategies combining multi-stage body size GWAS and carcass trait analyses could further improve the efficiency of candidate locus validation and breeding application [58–60].

In summary, the GWAS results for Guanling cattle indicate that the body conformation traits of this breed exhibit the typical characteristics of complex quantitative traits. The WH-associated loci may be related to cell polarity and mitotic orientation, the AG-associated loci may be involved in ion transport processes, the CBC-associated loci may reflect lipid metabolism and energy distribution, and the PBW-associated loci may be associated with calcium signaling, phosphatidylinositol signaling, and the regulation of tissue structure and morphogenesis. Overall, genes such as INSC, ANO3, LPL, ITPR2, PLXNA2, and IPMK can be considered potential candidate genes, warranting further validation to improve growth and body conformation traits in Guanling cattle. Among these, the PBW-associated loci are especially worthy of focused attention in future studies.

5. Conclusion

This study, based on the genome-wide association analysis of Guanling cattle, provides a preliminary insight into the genetic structure of body conformation and growth-related traits in this local breed. The results indicate that these traits are typical complex quantitative traits, influenced by multiple genes of small effect and multiple biological pathways, rather than being controlled by a single major-effect gene. Significant association signals were mainly detected for withers height (WH), abdominal girth (AG), cannon bone circumference (CBC), and pin bone width (PBW), and a series of candidate genes associated with these traits were identified. Among the annotated genes, INSC, ANO3, LPL, ITPR2, PLXNA2, and IPMK may represent biologically meaningful candidate genes, as their known functions are likely related to cell polarity, ion transport, lipid metabolism, calcium signaling, and tissue morphogenesis. These findings suggest that different body conformation traits in Guanling cattle may involve partly independent but interconnected biological processes. However, the current conclusions are primarily based on association analysis, gene annotation, and functional enrichment analysis, and the biological functions of these genes still require further validation in independent populations and functional studies. Overall, this study provides useful candidate loci and gene resources for future in-depth studies on the molecular basis of body conformation traits in Guanling cattle, and lays a preliminary foundation for marker-assisted selection, genomic evaluation, and genetic improvement of this local breed.

Declarations

Institutional Review Board Statemen

All animal procedures in this study were approved by the Animal Welfare and Ethics Review Committee of Guizhou Provincial Institute of Animal Husbandry and Veterinary Medicine (Approval No. AWE-GZSXMSY-2025-29).

Consent for publication:

Not applicable.

Conflicts of Interest:

The authors declare that they have no competing interests.

Author Contributions

Conceptualization, X.W., L.X. and B.Y.; investigation, D.Z., R.Y. and J.W.; data curation, R.Y., J.L. and K.Z.; formal analysis, X.W., L.X. and Y.L.; funding acquisition, X.W. and L.X.; methodology, X.W., L.X. and B.Y.; project administration, X.W.; resources, L.X.; software, Y.Z., H.Y. and S.Y.; supervision, L.X. and B.Y.; validation, W.Z., J.W. and X.W.; writing—original draft, X.W. and L.X.; writing—review and editing, L.X. and B.Y. All authors have read and agreed to the published version of the manuscript.

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Author Contribution

Author Contributions: Conceptualization, X.W., L.X. and B.Y.; investigation, D.Z., R.Y. and J.W.; data curation, R.Y., J.L. and K.Z.; formal analysis, X.W., L.X. and Y.L.; funding acquisition, X.W. and L.X.; methodology, X.W., L.X. and B.Y.; project administration, X.W.; resources, L.X.; software, Y.Z., H.Y. and S.Y.; supervision, L.X. and B.Y.; validation, W.Z., J.W. and X.W.; writing—original draft, X.W. and L.X.; writing—review and editing, L.X. and B.Y. All authors have read and agreed to the published version of the manuscript.

Availability of data and materials:

The datasets generated and/or analysed during the current study are publicly available without restriction. The body size measurement data of Guanling cattle in this study can be accessed at: https://zenodo.org/uploads/20210721. The raw sequencing data generated in this study have been deposited in the NCBI Sequence Read Archive (SRA) under BioProject accession PRJNA1479215. The dataset is publicly accessible via: https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1479215. and can be downloaded through the SRA Run Selector: https://www.ncbi.nlm.nih.gov/Traces/study/?

acc=PRJNA1479215. All raw FASTQ files can be retrieved using the NCBI SRA Toolkit. The data were accessed on 18 Jun 2026.

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Figures

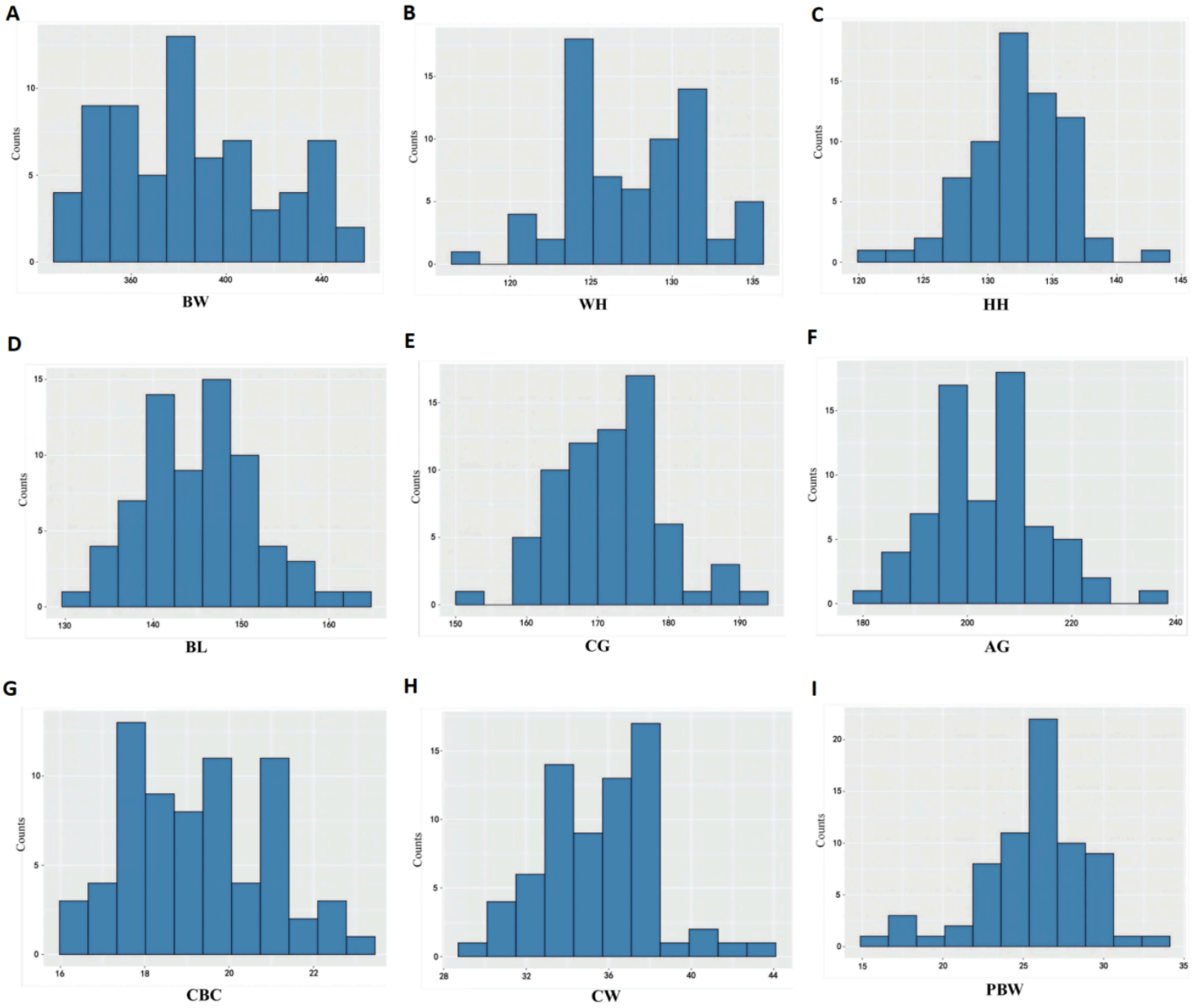


Figure 1

Histogram of phenotypic value frequency distribution of 9 growth traits. (A) BW, body weight. (B) WH, withers height. (C) HH, hip height. (D) BL, body length. (E) CG, chest girth. (F) AG, abdominal girth. (G) CBC, cannon bone circumference. (H) CW, chest width. (I) PBW, pin bone width.

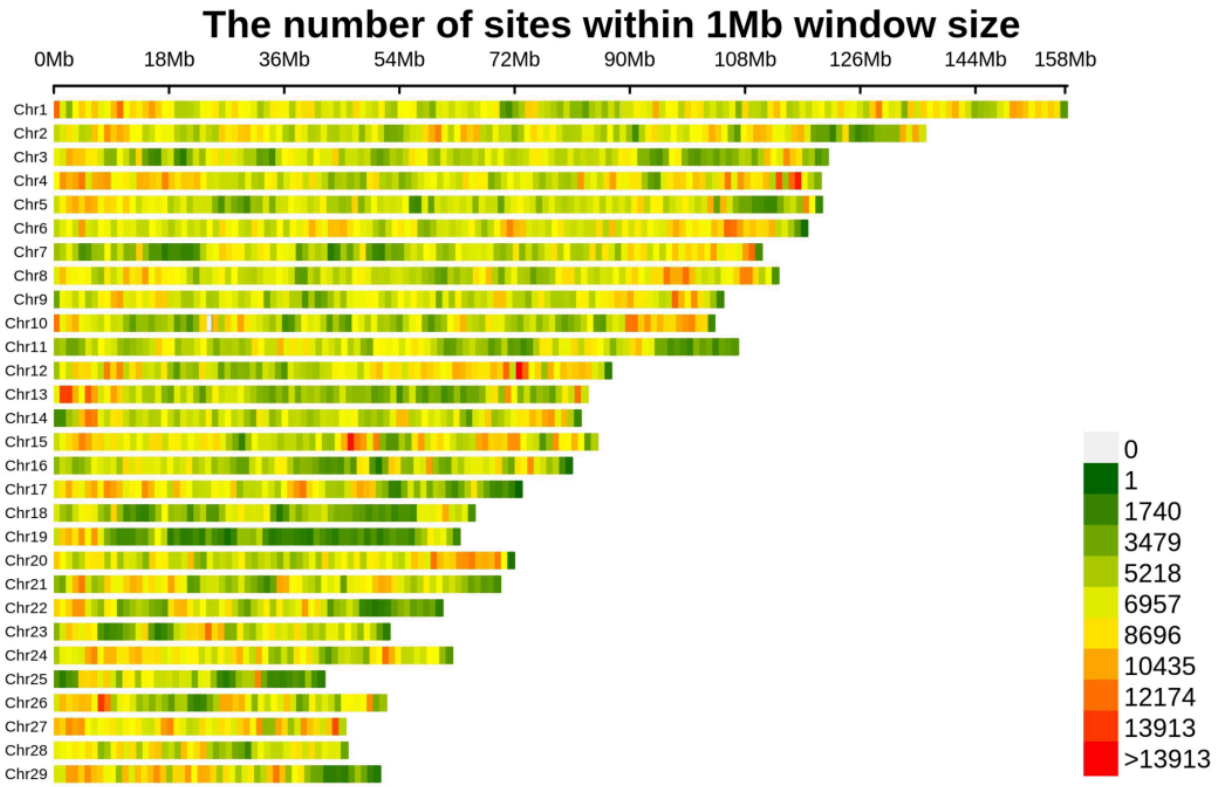


Figure 2

The physical location of SNPs in the chromosome.

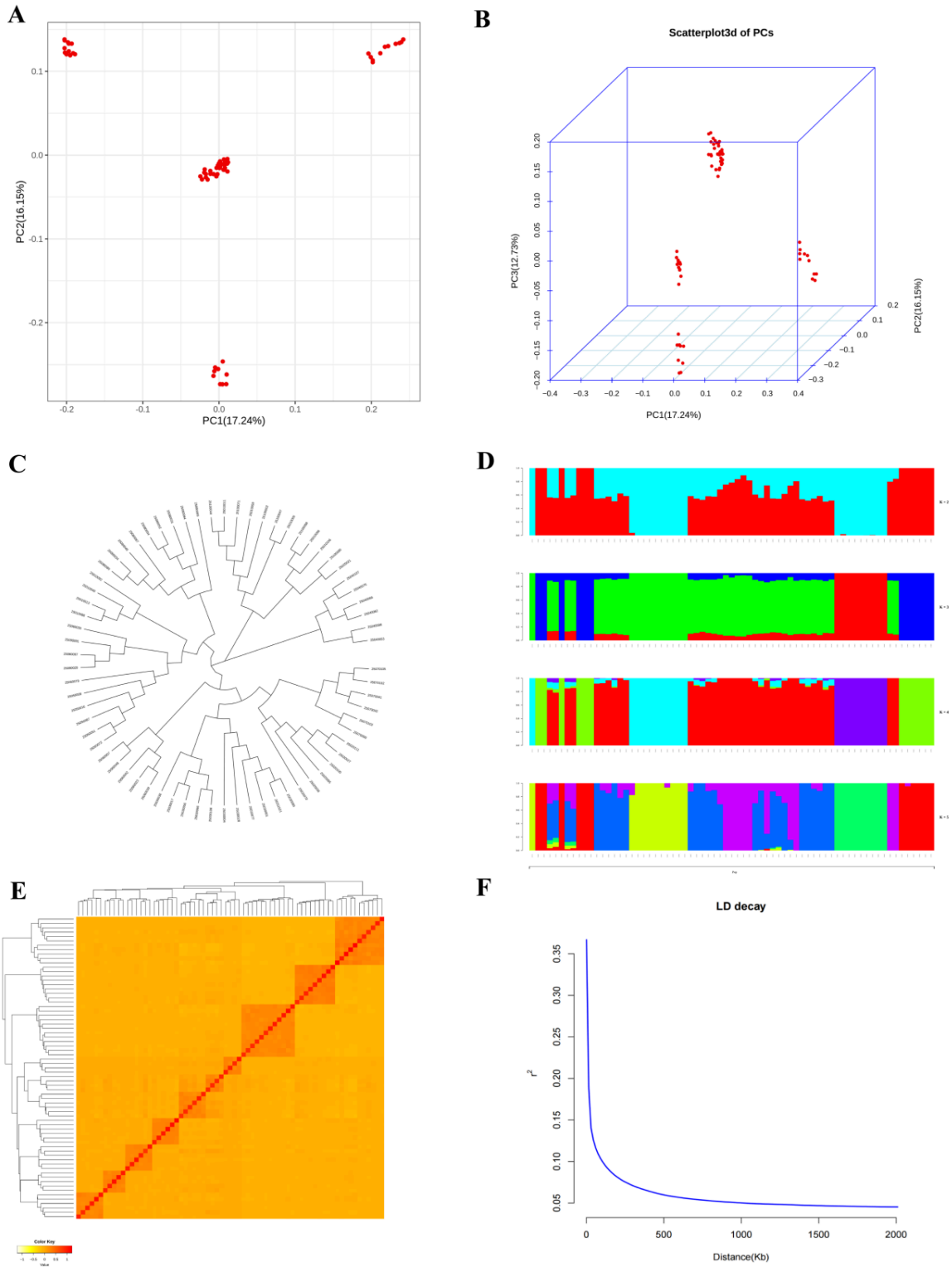


Figure 3

Principal Component Analysis and Phylogenetic Analysis. (A, B) PCA Analysis Visualization. (C) Phylogenetic Tree Analysis Results. (D) Population Structure Diagram. (E) Phylogenetic Visualization Results. (F) LD Decay Diagram.

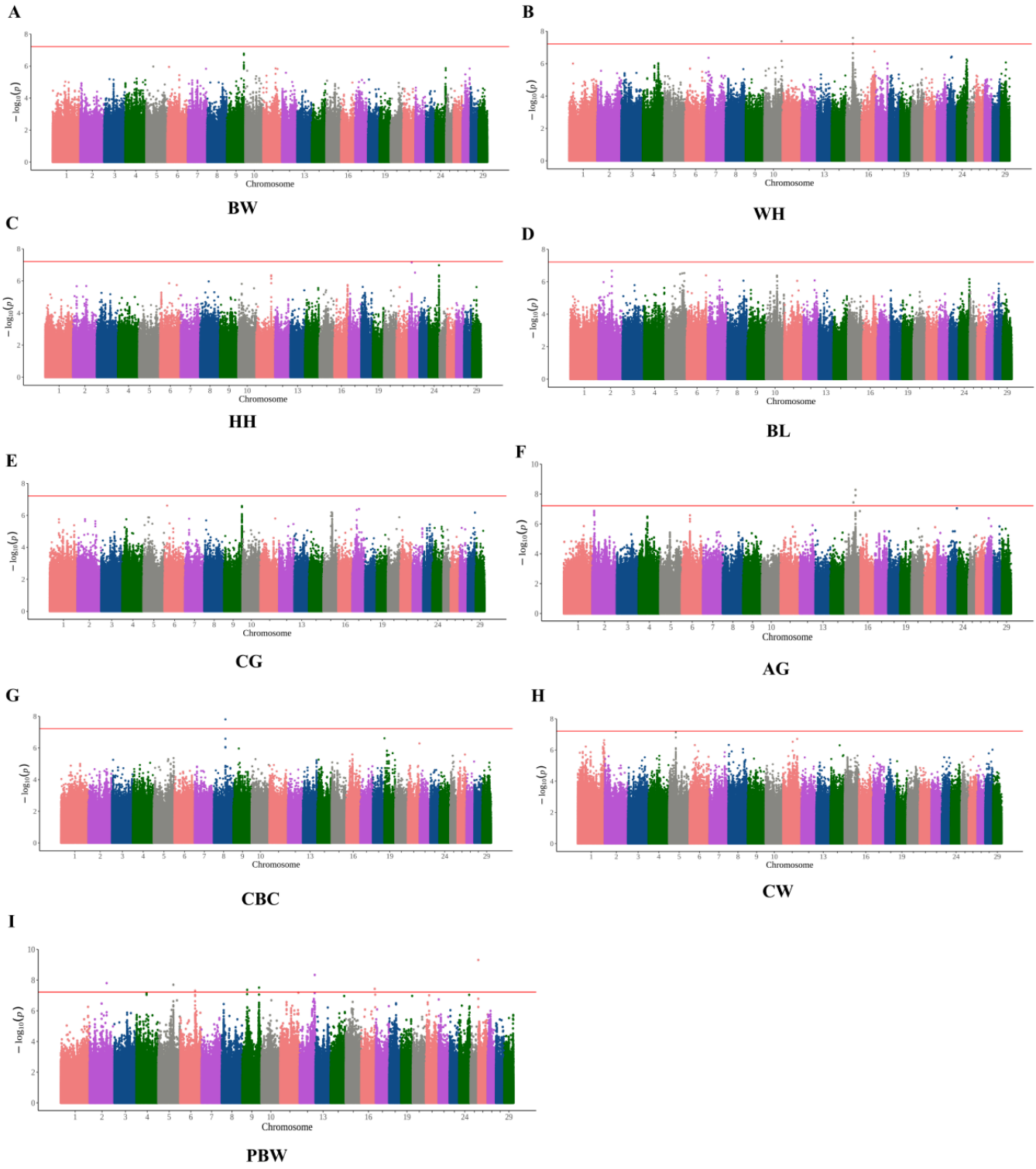


Figure 4

Manhattan plot of association results from genome-wide association analysis. (A) BW, body weight. (B) WH, withers height. (C) HH, hip height. (D) BL, body length. (E) CG, chest girth. (F) AG, abdominal girth. (G) CBC, cannon bone circumference. (H) CW, chest width. (I) PBW, pin bone width. Y axis shows −log10 (p-value) of the association result for each SNP. The horizontal dashed line is the threshold for the Bonferroni level of significance ($p < 3.54 \times 10-6$).

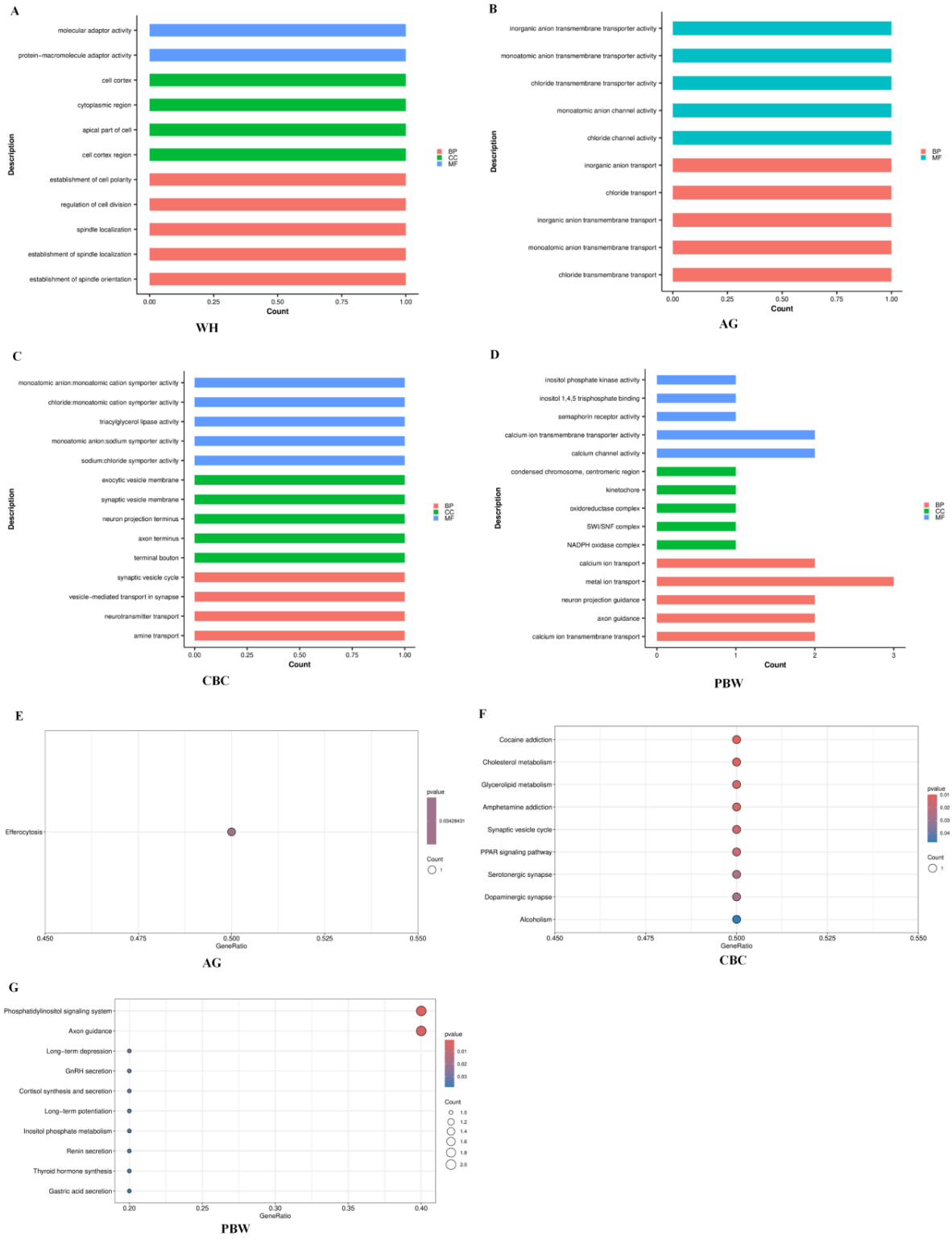


Figure 5

Bar chart of GO enrichment analysis and bubble chart of KEGG enrichment. (A) WH (withers height) GO enrichment analysis histogram, (B) AG (abdominal girth) GO enrichment analysis histogram, (C) CBC (cannon bone circumference) GO enrichment analysis histogram, (D) PBW (pin bone width) GO enrichment analysis histogram, (E) AG (abdominal girth) KEGG enrichment bubble map. (F) CBC

(cannon bone circumference) enrichment bubble map. (G) PBW (pin bone width) KEGG enrichment bubble map.

Supplementary Files

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- SupplementaryMaterialsImages.zip