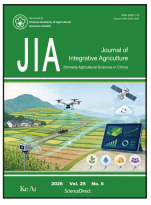
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REVIEW

Recent advances in genomic studies for domestication and genetic improvement of traits in goats

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Highlights

- A thorough review of goat domestication, integrating evidence from nuclear genomes, mitochondrial DNA, and Y chromosomes.
- An overview of genomic and transcriptomic researches focused on identifying critical production and functional traits in goats.
- Key insights into current challenges and suggest future strategies to enhance goat breeding programs.

Abstract

Goats (*Capra hircus*) provide a rich source of products, such as meat, milk, and wool, and are important domestic animals in many parts of the world. Goats were one of the first domesticated livestock species during the late Neolithic period, approximately 11,000 years ago, in the Fertile Crescent. In the past decades, genomic studies of goats have provided insight into their domestication and genetic basis of economically important traits. This review outlines the latest advancements that have been made in reference to domestication and genetic improvement of production traits such as meat and carcass quality, reproduction, milk, cashmere, and functional traits such as environmental adaptation and disease-resistance. Genomic research is entering a new era with the availability of graphical pan-genomics and telomere-to-telomere (T2T) gap-free genome assembly, which will extend our understanding of domestication and molecular mechanistic dissection of economic traits in goats. We provide new perspectives and future directions for genomics and suggest how the ever-increasing multi-omics dataset will facilitate future studies and molecular breeding in goat.

Keywords: goat, genomics, genes, domestication, genetic improvement

1. Introduction

Goats (*Capra hircus*) descended from a mosaic of wild bezoar populations (*Capra aegagrus*) approximately 11,000 years before the present and were domesticated in the Fertile Crescent. They are widely distributed across six continents and then adapt to different environmental and climatic regions like mountainous, high alpine, steppe and semi-desert zones (Ramachandran and Sejian 2022). Nowadays, the domestic goats stand at approximately 1.2 billion heads, and are used for meat, milk and fibre production that has a great influence on the socio-economic life of the population, especially in rural and less affluent regions (Amills *et al*. 2017). The allocation of wild and domestic goat breeds worldwide depicted in Fig. 1.

Traditionally, goat breeding was conducted mainly on phenotypic traits based on quantitative evaluation of live

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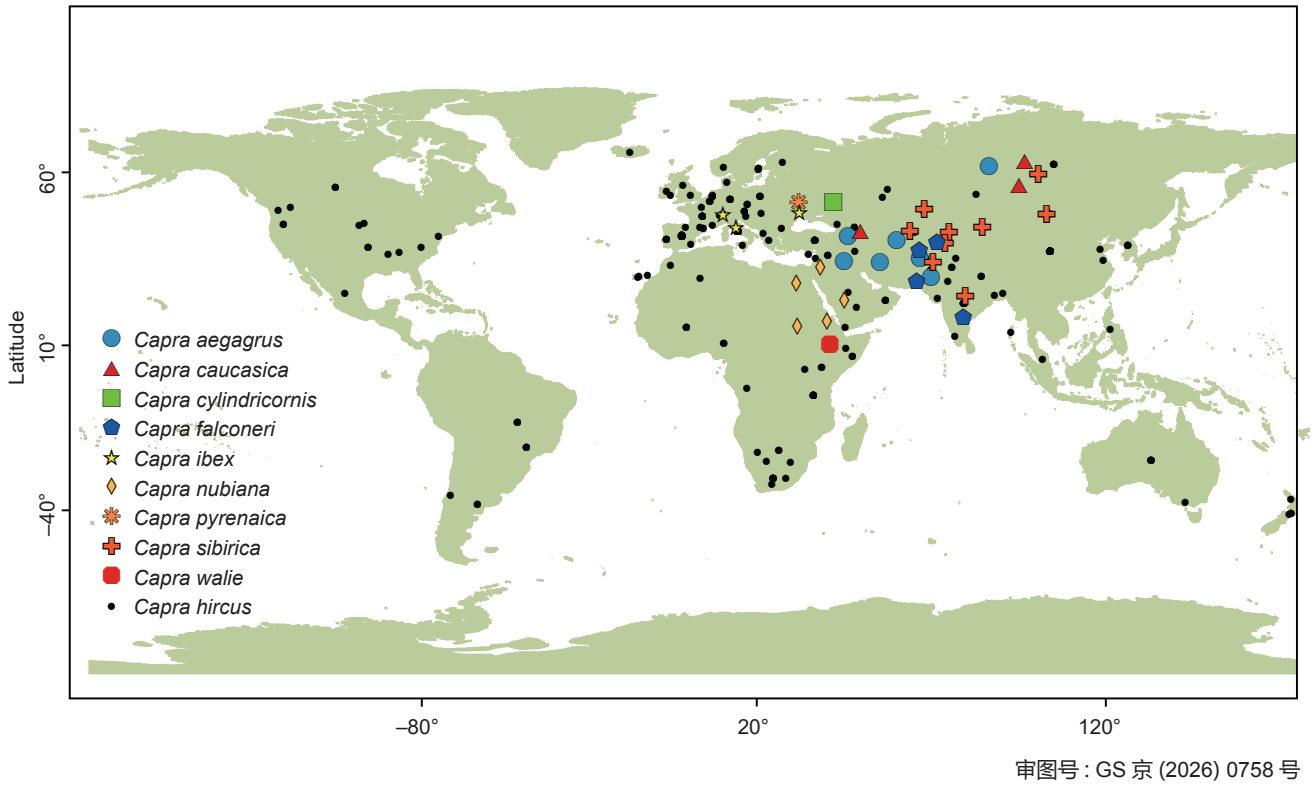


Fig. 1 The distribution of wild and domestic goats globally.

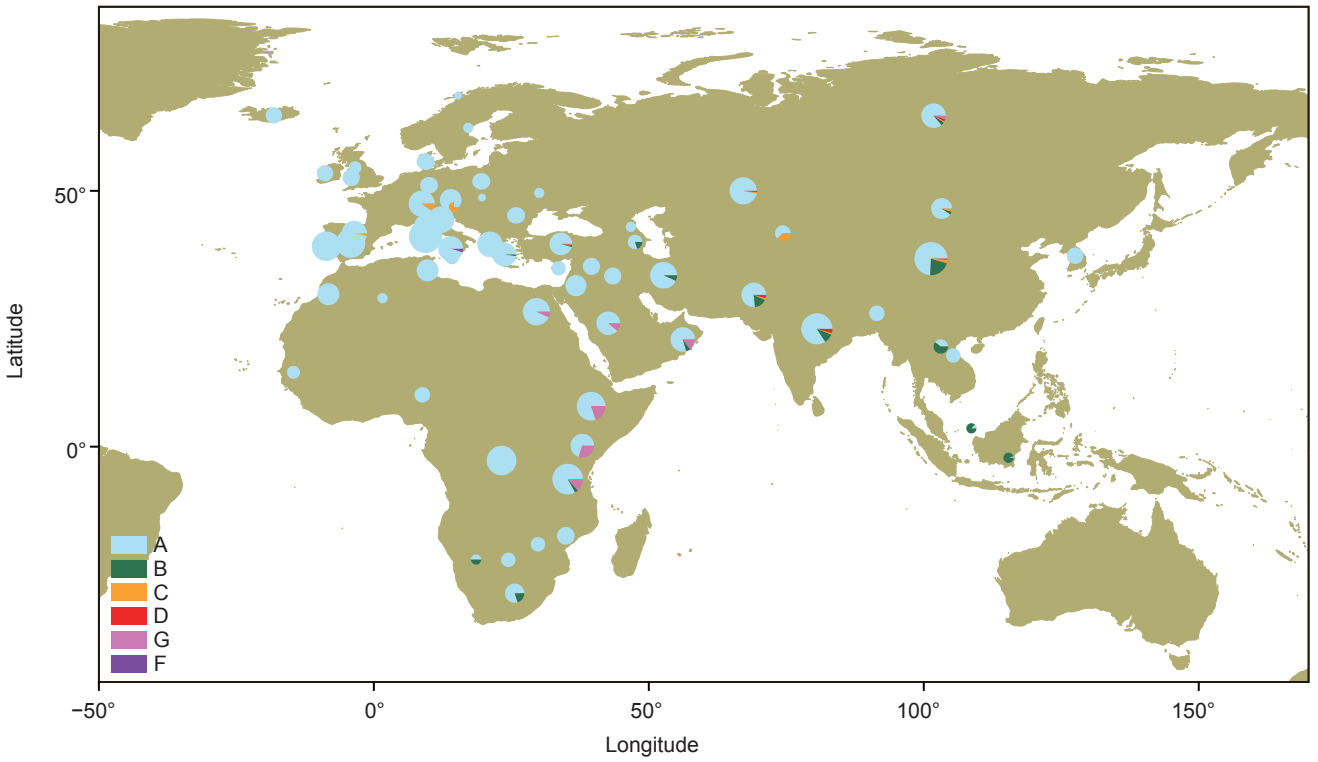
weight, carcass yield, etc. In recent years, advances in DNA technology and genome sequencing have revolutionized our understanding of goat genetics and resources, facilitated innovative discoveries of important production traits (Liu X *et al*. 2024). There has been an augmenting interest in the genomic characterization of goats, driven by numerous studies targeting candidate genes that govern economically important traits.

This review endeavors to summarize the recent advancements in goat genomic research, elucidating the intricate interplay between genetic loci and phenotypic traits. By critically examining these findings, this overview aims to furnish a comprehensive understanding of goat genetics, while also providing insight into the domestication and the improvement of economically important traits.

2. Goat domestication

The genetic basis of domestication in domestic animals is a key issue in the management of genetic resources. In order to understand the origins of goat domestication, numerous studies have concentrated on mitochondrial DNA (mtDNA), which is passed down through the mother and evolves quickly. The geographical distribution of mtDNA haplogroups encompassing A, B, C, D, F, G in goats worldwide is shown in Fig. 2 and Appendix A (Luikart *et al*. 2001; Joshi *et al*. 2003; Sultana *et al*. 2003; Naderi *et al*. 2007). The high diversity of mtDNA in European goats suggested that domestication may have occurred in Europe far from the Middle East (Fernández *et al*. 2006). Based on maternal mtDNA haplogroups, however, Naderi *et al*. (2008) established that the center of domestication of the modern domestic goat may have been in the Northern and Central Zagros. Additionally, findings from nearly all mitochondrial protein-coding genes indicated that a preferential selection of domestic goats from their wild ancestors within an Asian-specific haplogroup during the initial stages of domestication, followed by their arrival in South and Southeast Asia through China–Mongolia, probably led to significant genetic bottlenecks (Nomura *et al*. 2013). Of note, 90% of modern goats belong to haplogroup A, indicating that they perhaps evolved from a single maternal individual of *C. aegagrus* (Colli *et al*. 2015). In addition, goats from Ganj Dareh and Tepe Abdul Hosein were regarded as the oldest representatives of the livestock genome by integrating archaeozoological and genetic studies (Daly *et al*. 2021).

Y-chromosome variations, alternative genetic markers for domestication, provide enlightening data on paternity history in domesticated species. The first study for goat Y-chromosome variation using the amelogenin Y-linked (*AMELY*) and zinc finger protein Y-linked (*ZFY*) genes, suggested introgression of mtDNA between ancestral taxa (Pidancier *et al*. 2006). In Turkish breeds, the different distribution of haplotypes between breeds indicated that Y-chromosome variants are more dependent on breed than autosomal or mtDNA (Cinar Kul *et al*. 2015). In European goat breeds, low Y-chromosome diversity has been detected by analyzing Y-linked genes such as the sex-determining region Y (*SRY*), DEAD-box helicase 3 Y-linked (*DDX3Y*), *ZFY*, and *AMELY*. This low diversity may be attributed to the fact that modern goats were domesticated in Eastern Anatolia (Vidal *et al*. 2017). Recently, the feasibility of utilizing Y-chromosomal variants to trace the evolutionary history of



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Fig. 2 The geographical distribution of mtDNA haplogroups in goats worldwide.

domestic goat populations across diverse geographic regions has been demonstrated through whole genome sequencing (WGS) (Consortium *et al*. 2022).

The Y-chromosome is often more complex than mtDNA due to its lower genetic variability, recombination rates, and the presence of palindromic sequences (Xiao *et al*. 2021). While mtDNA studies have established reference genomes for many species, Y-chromosome reference sequences for goats are less developed. The insufficient representation of diverse goat populations hinders a comprehensive understanding of the range of Y-chromosome variations and their impact on domestication. However, the newly developed Y-chromosomal reference sequence, T2T-CHIY1.0, represents a significant advancement in this field, boasting a comprehensive length of 20.96 Mb and superior quality metrics compared to existing assemblies, such as Saanen_v16 (9.6 Mb) and ARS1-based scaffolded contigs (11.5 Mb), thereby providing a more complete genomic framework that can enhance research on male-specific traits, evolutionary studies, and the genetic mechanisms underlying production traits (Wu *et al*. 2024). Nevertheless, to address these challenges, a comprehensive approach should be employed that includes increasing collaboration, utilizing advanced sequencing technologies, and prioritizing diverse sampling strategies to ensure a more representative understanding of Y-chromosome variation in goats.

Genomic selection during domestication is a target for further selection of goats for desirable traits. The use of genomic re-sequencing aids in uncovering variations associated with domestication. Zheng *et al*. (2020) discovered a targeted genetic region with a prominent selection signal containing the mucin 6 (*MUC6*) gene, potentially pathogens in domestic and ancient goats. Importantly, a recent study revealed structural variants in domestication-associated genomic regions of bezoars and domesticated goats, with 63 overlapping genes (e.g., *MUC6*, ATP binding cassette subfamily C member 4 (*ABCC4*), myeloid associated differentiation marker (*MYADM*)), highlighting key genetic differences between the two populations (Wu *et al*. 2024). Meanwhile, a pan-genome of goats, constructed through a map-to-pan assembly involving 813 individuals, uncovered several immune and inflammation-related genes, including C-type lectin domain family 2 member D (*CLEC2D*), family with sequence similarity 26 member F (*FAM26F*), GTPase of immunity associated protein 6 (*GIMAP6*), and C-type lectin domain family 1 member A (*CLECL1*). These findings are significant for understanding goat improvements and domestication (Liu J *et al*. 2024). In addition, a graph-based goat pangenome discovered the galectin-9 gene and additional copies of the ruminant-specific galectin-9-like genes (*LGALS9L*) as part of a novel immune-related domestication locus that underscores the genetic adaptations that have occurred in goats during domestication (Bian *et al*. 2024).

The agouti signaling protein 1 (*ASIP1*) gene, involved in the formation of the coat color phenotype, had shown evidence of strong selection during goat domestication (Dong *et al*. 2015; Signer-Hasler *et al*. 2022). Signer-Hasler *et al*. (2022) conducted a comprehensive comparison of WGS from both domestic and wild bezoar goats, during which

they identified the thyrotropin receptor (*TSHR*) and the stanniocalcin 1 (*STC1*) genes. The *TSHR* gene is implicated in the regulation of reproductive seasonality, and the *STC1* gene plays a critical role in the homeostatic maintenance of calcium and phosphorus levels within the organism (Signer-Hasler *et al*. 2022). Moreover, Zhang B *et al*. (2018) identified several genes, such as fragile X mental retardation, adrenoceptor alpha 2A *(ADRA2A)*, tumor necrosis factor superfamily member 13 (*TNFSF13*), stromal interaction molecule 1 (*STIM1*), signal transducer and activator of transcription 6 (*STAT6*), nuclear receptor subfamily 6 group A member 1 (*NR6A*) associated with domestication, which were linked to immunity, behavior and trait-related quality. As such, a more detailed exploration of the goat genome is imperative to fully appreciate and harness the genetic potential and adaptability of this crucial livestock species.

3. Genetic analysis of production and functional traits in goats

Advances in selection techniques and modern biotechnological approaches have improved the efficiency and accuracy of goat breeding programs. In contemporary genetic research, scientists are investigating goat populations for various purposes, including analyzing their genetic structure, identifying quantitative trait loci that govern complex traits, and implementing genomic selection strategies using genetic markers to uncover patterns of both recent and historical selection pressures, which ultimately aids in enhancing breeding programs and improving goat productivity.

The International Goat Genome Consortium has engineered an advanced high-processing platform that facilitates genome-wide association studies (GWAS), the estimation of genomic breeding values, and the integration of these insights into selective breeding protocols for goat populations (Tosser-Klopp *et al*. 2016). Over the past decade, establishment of molecular-assisted selection (MAS) and promotion of functional genomics have greatly accelerated the goat breeding. For instance, there has been significant progress in the application of genomic selection within Alpine and Saanen dairy goat populations (Massender *et al*. 2022). Remarkable leaps have also been made in goat meat breeding programs, particularly regarding selective breeding for enhanced meat production, with a focus on breeds like the Boer goats (Yang *et al*. 2021). Furthermore, advancements in reproductive traits have been observed through targeted selection strategies aimed at increasing litter sizes and ovulation rates (Notter 2012). The resistance against caprine parasites have also been enhanced through comprehensive selection programs (Wang *et al*. 2024). Besides, there is an increasing focus on breeding goats like Tibetan goats that can tolerate specific environmental challenges, including drought, high-altitude, and temperature alterations (Wang *et al*. 2016). In addition, the advanced reproductive technologies, including artificial insemination and embryo transfer allowed the faster spread of desirable traits through herds (Souza-Fabjan *et al*. 2023). Collectively, these developments underscore the potential of genomics and innovative breeding approaches to optimize goat husbandry and contribute to sustainable agricultural practices.

3.1. Identification of genes associated with production and functional traits

Advancement in DNA re-sequencing has greatly enhanced the ability to identify genes and genetic variants associated with productive traits such as meat, milk, cashmere, reproductive and functional traits such as environmental adaptation and disease-resistance in goats, thereby enhancing our understanding of goat genetics and accelerating goat breeding. The GoatSNP50 BeadChip (Illumina, Inc., USA) has greatly elevated the capability to identify single nucleotide polymorphisms (SNPs) experiencing selection pressure in goats (Berihulay *et al*. 2019; Mahmoudi *et al*. 2022). In this regard, the SNPs are now widely favored as GWAS, assessing levels of inbreeding, high-resolution genetic mapping, etc.

Moreover, RNA sequencing has successfully helped to identify critical genes responsible for various traits, especially for the quality and quantity of cashmere, meat and carcass traits in goats. Omics technologies, encompassing transcriptomics, proteomics, metabolomics and epigenomics, are now emerging to help expand goat genome annotation (Wang *et al*. 2023). Concurrently, analysis of the epigenetic markers across genome extended our understanding of phenotypic variation (Wang S *et al*. 2020). In addition, single cell sequencing technology combining with a number of bulk omics such as genomic variation, DNA methylation and chromatin accessibility is of interest to monitor alterations in cell populations and gene expression at different developmental stages (Ge *et al*. 2021). Genes and loci associated with production traits in goats are given in Table 1 and Fig. 3.

Table 1 Genes and loci associated with production traits in goats

Traits	Breed and sample sizes	Genes, polymorphisms, pathways	Approaches	Sources
Meat traits	Guizhou Black (*n*=30)	*CHUK*, *GAB2*, *PLAAT3*, *EP300*, etc.	Selection signatures	Chang *et al.* (2024)
	Liaoning rams (*n*=5), Ziwuling rams (*n*=5)	*FABP3*, *PEBP1*, *SPARC*, *COL3A1*, *SOCS2*, *BTG2*, *PRKAG3*, *CCDC80*, etc.	RNA-seq	Shen *et al.* (2021)
	Barbari (*n*=4), Changthangi (*n*=4)	*FABP3*, *FASN*, *SCD*, *THRSP*, *DGAT2*, etc.		Kumar *et al.* (2021)
	Crossbred Chongming white (*n*=24)	*FABP3*, *TNNI1*, *MYBPC2*, *MYL2*, *MHY7*, *TNNT1*, *TPM3*, *PPP1R27*, *AKAP13*, etc.		Lin *et al.* (2024)
	Huanghuai breed (*n*=16)	*MDM2*, *MFNG*, *ZNF385C*, *SFRP5*, *ROCK2*, *AMK2A*, *PPP3CC*, *PPP3CA*, *PPP3R1*, etc.		Wang *et al.* (2015)

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Table 1 (Continued from preceding page)

Traits	Breed and sample sizes	Genes, polymorphisms, pathways	Approaches	Sources
Reproductive traits	Markhoz goats (*n*=136)	*GABRA5*, *AKAP13*, *SV2B*, *PPP1R1C*, *SSFA2*, *TRNAS-GCU*	Selection signatures	Mahmoudi *et al.* (2022)
	Domestic goat (*n*=281), wild goat (*n*=84), modern sheep (*n*=532)	*BMPR1B*, *BMPR2*		Yang *et al.* (2024)
	Yunshang black goat (*n*=40)	*OSBPL8*; *PPP2R5C, CDC25A, ESR1, RPS26, SERPINBs*; *DIO3, BTG1, CRYM*	Selection signatures, GWAS, ROH	Tao *et al.* (2020)
	Yunshang black (*n*=10)	*BMPR1B*, *FGFR1*, *IGF1*, *CREB1*	RNA-seq	Liang *et al.* (2021)
	Yunshang black goat (*n*=10)	*NUP107*, *ANXA11*, *COX2*, *AKP13*, *ITF140*, etc.	Proteome and transcriptome	Sun *et al.* (2022)
	Beetal, Barbari, Sirohi and Sojat (*n*=285)	g.2540C>T in *KISS1*	PCR–RFLP	Jeet *et al.* (2022)
	Xinong Saanen (*n*=257), Guanzhong (*n*=231), Boer goat (*n*=192)	SNPs in *KISS1*		An *et al.* (2013a)
	SBWC (*n*=1,511)	Q320P and V397I SNPs in *GDF9*		Wang *et al.* (2019)
	Inner Mongolia cashmere (*n*=761)	p.Val397Ile in *GDF9*		Zhao *et al.* (2016)
	Xinong Saanen (*n*=241), Guanzhong (*n*=197), Boer (*n*=203)	*GNRH1* (g.3548A>G, g.3699G>A); *GDF9* (g.4093G>A, p.Val397Ile)		An *et al.* (2013b)
	Xinong Saanen (*n*=306), Guanzhong dairy (*n*=231)	g.13090G>T and g.13664C>A in *KITLG*	PIRA-PCR	An *et al.* (2015b)
	Xinong Saanen (*n*=290), Guanzhong (*n*=193), Boer (*n*=198)	g.769T>C, g.817G>T, g.9760G>C in *KITLG*	PCR-SSCP	An *et al.* (2012)
	Guanzhong (*n*=321), Boer (*n*=191)	g.151435C>T and g.173057T>C in *PRLR*	PCR-RFLP	An *et al.* (2015a)
	Guanzhong (*n*=321), Boer (*n*=191)	c.1457G>A and c.1645G>A in *PRLR*		Hou *et al.* (2015)
	SBWC (*n*=600)	16-bp deletion in *AKAP13*	PCR, gel electrophoresis	Zhang *et al.* (2023)
	SBWC (*n*=1,104)	5-, 10-, and 24-bp InDels in *SPEF2*		Chen *et al.* (2019)
	SBWC (*n*=2,057)	17- and 20-bp InDel in *SNX29*		Wang Q *et al.* (2022)
	SBWC (*n*=1,479)	InDels in *CFAP43, CFAP69, QRICH*		Wang Z *et al.* (2020)
	SBWC (*n*=1,390)	18- and 7-bp InDels in *SMAD1*		Wijayanti *et al.* (2022)
	SBWC (*n*=1,816)	12-bp InDel in *GDF9*		Wang *et al.* (2017)
	SBWC (*n*=1,101)	SNPs and InDel in *DNAH1*		Wang Z *et al.* (2022)
	SBWC (*n*=1,101)	7- and 13-bp InDels in *AKAP12*		Kang *et al.* (2021)
	SBWC (*n*=1,616)	13-bp InDel in *KMT2A*		Tang *et al.* (2021)
	SBWC (*n*=1,131)	14-bp InDel in *CMTM2*		Kang *et al.* (2019b)
	SBWC (*n*=2,162)	15-,16-, and 31-bp InDels in *DSCAML1*		Wang K *et al.* (2020)
	SBWC (*n*=918)	13-, and 12-bp InDels in *IGF2BP2*		Xin *et al.* (2021)
	SBWC (*n*=2,844)	7-, 15-, and 18-bp InDels *MARCH1*		Kang *et al.* (2019a)
	SBWC (*n*=1,534)	11-bp insertion in *DNMT3B*		Hui *et al.* (2020)
	SBWC (*n*=532)	c.71A>G in *PRNT*	PCR, seq	Bi *et al.* (2021b)
	SBWC (*n*=312)	CNV1 (2,000 bp), CNV2 (2,400 bp), CNV3 (2,000 bp), CNV4 (2,000 bp), and CNV5 (1,600 bp) in *BMPRIB*	qPCR	Bi *et al.* (2021a)
	SBWC (*n*=1,402)	CNV1 (1,600 bp), CNV2 (2,000 bp), CNV3 (1,600 bp), CNV4 (200 bp), CNV5 (2,400 bp) in *SNX29*		Wang Q *et al.* (2022)
	SBWC (*n*=1,101)	CNV1 (1,999 bp), CNV2 (1,599 bp), CNV3 (1,500 bp) in *DNAH1*		Wang Z *et al.* (2022)
Milk traits	Cashmere (*n*=48), Alpine (*n*=403), Canadian (Alpine, Boer, LaMancha, Nubian, Saanen, Toggenburg (*n*=976), Boer, Cashmere and Rangeland (*n*=175)	*CDH12* and *FAM13A*	Selection signatures	Brito *et al.* (2017)
	Pakistani goat (*n*=26), domestic goats (*n*=184)	*IGFBP3*, *LPL*, *LEPR*, *TSHR*, *ACACA*		Zhang *et al.* (2024)
	Pakistani goat (*n*=192)	*ABCG2*, *SPP1*, *CSN1S2*, *CSN2*, *CSN3*, *PRL*		Kumar *et al.* (2018)
	Alpine (*n*=833), Saanen (*n*=874)	*CSN1S1*, *CSN2*, *CSN1S2*, *CSN3*, *DGAT1*, *ZNF16*	GWAS	Massender *et al.* (2023)
	Saanen (*n*=1,436), crossbred (*n*=1,669), unknown (*n*=789)	*RNASEK*, *ASGR2*, *DLG4*, *ELP5*, *MYH10*, *PTPN5*, *LDHC*, *OR8B4*, *ZDHH1*		Scholtens *et al.* (2020)
	French dairy goat (*n*=2,209)	*DGAT1*		Martin *et al.* (2017)
	French Alpine (*n*=44), French Saanen (*n*=37)	*CRYBA2*, *CDK5R2*, *FEV*		Talouarn *et al.* (2020)

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Table 1 (Continued from preceding page)

Traits	Breed and sample sizes	Genes, polymorphisms, pathways	Approaches	Sources
Milk traits	Saanen, Toggenburg, Alpine (*n*=2,381)	*ALOX12*, *SLC1A1*, *LALBA*, *POU1F1*, *DGAT1*, *MTHFR*, *STAT5A*, *PRLR*	GWAS	Mucha *et al.* (2018)
	Bezoar (*n*=9), Appenzell goat, Grisons Striped goat, Peacock goat, St. Gallen Booted goat, Valais Blackneck goat (*n*=119), Capra Grigia, Chamois Colored, Nera Verzasca, Saanen, Toggenburg (*n*=90)	*STC1*		Signer-Hasler *et al.* (2022)
	Murciano-Granadina (*n*=1,197)	*CSN3* and *CSN1S2*	Selection scan and RNA-seq	Guan *et al.* (2021)
	Monticellana (*n*=125), Capestrina (*n*=27), Ciociara Grigia (*n*=36)	XmnI in *CSN1S1*	AS-PCR	Cosenza *et al.* (2023)
	Alpine (*n*=60), Saanen (*n*=105), Toggenburg (*n*=74)	*CSN1S1*	PCR-RFLP	Vázquez-Flores *et al.* (2012)
	Sarda (*n*=825)	SNPs in *CSN1S1*, *CSN2*, *CSN1S2*, *CSN3*	KASP method	Dettori *et al.* (2023)
	Sarda (*n*=814)	Alleles in *CSN1S1*, *CSN2*, *CSN1S2*, *CSN3*	AS-PCR, PCR-SSCP, PCR-RFLP	Vacca *et al.* (2014)
Cashmere traits	Northern China cashmere and Indian populations (*n*=46)	*FGFs* and *KRTs*; *ABCC4*	Selection signatures	Wu *et al.* (2024)
	Cashmere goats (*n*=336) and other goats (*n*=226)	*EDAR2*		Bian *et al.* (2024)
	Inner Mongolia cashmere (*n*=70)	*FGF5*, *SGK3*, *IGFBP7*, *OXTR*, *ROCK1*		Li *et al.* (2017)
	Inner Mongolia cashmere (*n*=192)	*FGF12*, *SEMA3D*, *EVPL*, *SOX5*	GWAS	Wang *et al.* (2021)
	Inner Mongolia cashmere (*n*=3)	*KAP3-1*, *KRTAP 8-1*, *KRTAP 24-1*	RNA-seq	Yang *et al.* (2020)
	Tibetan cashmere (*n*=50)	*GC*, *VTN*, *AEBP1*, *GPR142*		Zhao *et al.* (2022)
	Aerbasi cashmere (*n*=3)	*IL17RB*, *ZNF347*		Su *et al.* (2018)
	SBWC (*n*=6)	*HOXC13*, *SOX9*, *SOX21*, *JUNB*, *LHX2*, *VDR*, *GATA3*		Wang S *et al.* (2020)
	SBWC (*n*=6)	*KRT* and *KRTAPs*; *GPRC5D*, *PAD3*, *HOXC13*, *PRR9*, etc.		Gao *et al.* (2016)
	SBWC (*n*=10)	*Wnt*, *TGF-β* and Notch signaling pathways		Geng *et al.* (2013)
	Jiangnan cashmere (*n*=8)	*SOX18*, *SOX4*, *WNT5A*, *IGFBP4*, *KAP8*, *KRT36*, *FA2H*	RNA-seq	Wu *et al.* (2022)
	Jiangnan (*n*=32), Tibetan (*n*=32)	*HES1*, *WNT1*, *WNT5A*, *PRLR*, *ITGB7*, *JAK2*, *FGF21*, etc.	RNA-seq, WGS	Wu *et al.* (2023)
	Liaoning cashmere (*n*=6)	*KRT26*, *KRT32*, *KRT82*, *EGR3*, *FZD6*	MeRIP-seq, RNA-seq	Wang Y *et al.* (2020)
	SBWC (*n*=3)	*SOX18*, *KRT14*, *KRT17*, *KRT79*, *HOXC13*, *BMP4*, *LHX2*, etc.	Single-cell seq	Ge *et al.* (2021)
	Liaoning cashmere (*n*=12)	*PLA2G12A*, *KRT79*, *prostaglandin B2*	Multi-omics	Xu *et al.* (2023)

3.2. Meat and carcass traits

Goat meat is highly nutritious and one of the leanest meat available, with lower fat content and higher protein levels compared to common meat. Consequently, both the quality of goat meat and their growth performance are crucial economic factors that greatly impact the viability and profitability of the goat meat industry. The interplay between genetic selection, feeding practices, and environmental factors affects variations in meat and carcass traits. Understanding both the biological and economic implications is essential for improving productivity and sustainability.

Several genes related to meat quality traits in goats have been identified through selection signals, including GRB2 associated binding protein 2 (*GAB2*), component of inhibitor of nuclear factor kappa B kinase complex (*CHUK*), phospholipase A and acyltransferase 3 (*PLAAT3*), E1A binding protein p300 (*EP300*), etc. (Chang *et al*. 2024). Among these, the *GAB2* has been associated with metabolic phenotypes in human (Williams *et al*. 2020).

Furthermore, the transcriptomic analysis of *longissimus dorsi* muscle tissues in goats have identified several DEGs associated with meat production characteristics, including but not limited to fatty acid-binding protein 3 (*FABP3*), myosin light chain 2 (*MYL2*), troponin T1 (*TNNT1*), troponin I1 (*TNNI1*), etc. (Kumar *et al*. 2021; Shen *et al*. 2021; Lin *et al*. 2024). Notably, members of the *TnT* family play a critical role in muscle contraction and calcium regulation, while *FABP3* participates actively in the modulation of lipid metabolism (Lin *et al*. 2024). Additionally, RNA sequencing methodologies identified phosphoprotein phosphatases-related genes, including phosphatase 3 catalytic subunit gamma (*PPP3CC*), protein phosphatase 3 catalytic subunit alpha (*PPP3CA*), and protein phosphatase 3 regulatory subunit 1 (*PPP3R1*), which involved in calcineurin signaling pathway (Wang *et al*. 2015).

Together, these findings highlight the intricate genetic

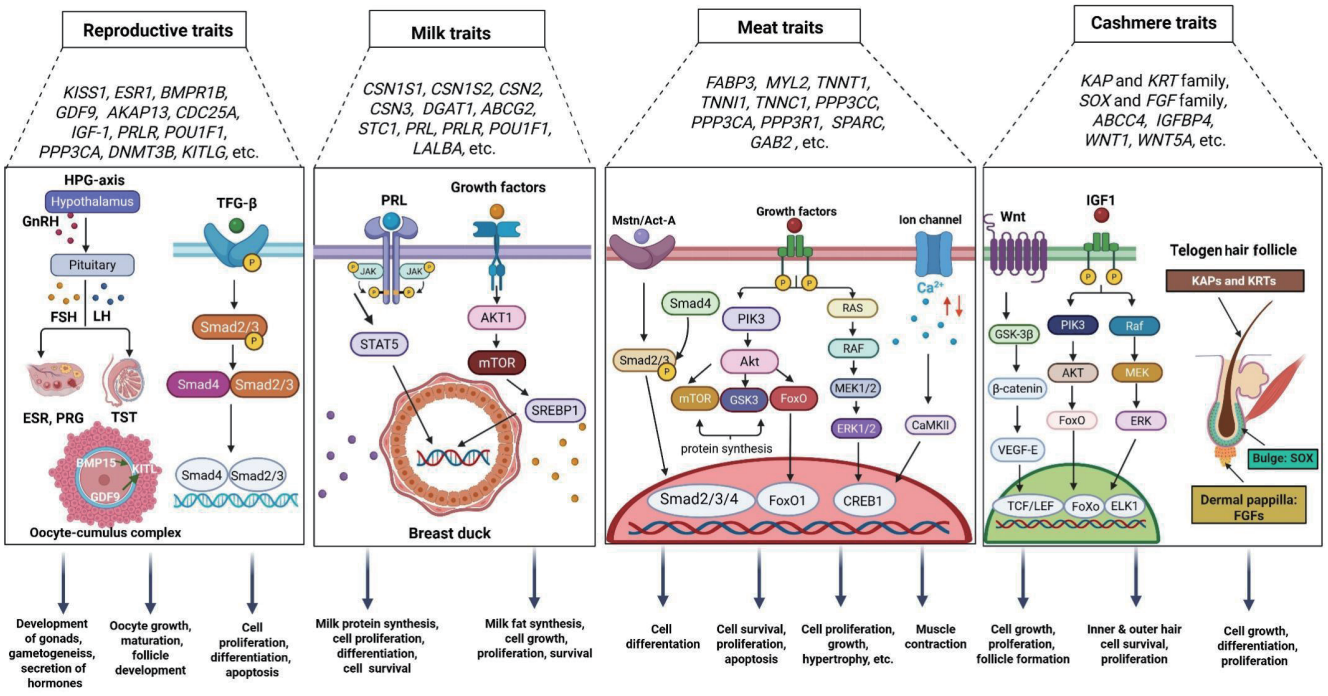


Fig. 3 Genes and their mechanisms of action in economically important traits in goats. Genes involved in the HPG axis play a crucial role in regulating reproductive functions, including the development of gametes, hormonal release, and sexual differentiation, while TGF-β signaling is involved in folliculogenesis, influences the growth and maturation of ovarian follicles as well as regulate the function of Sertoli cells, which support and nourish developing sperm cells in the testes. In mammary gland epithelial cells, the PRL and Akt/mTor pathways orchestrate the growth, differentiation, and metabolic adaptations of mammary cells, playing a vital role in lactation and overall mammary gland function. In muscle cells, genes are primarily regulated through several key pathways such as PI3K/Akt, mTOR, TGF-β, MAPK signaling pathways and calcineurin pathway that influence muscle development, function, and adaptation to various stimuli. The interplay of Wnt, IGF-1 pathways, *KAP* and *KRT* gene families, *SOX* and *FGF* genes reflects a highly coordinated network that drives cashmere growth and maintenance.

regulatory mechanisms underpinning muscle development and meat production in goats, providing potential targets for improving meat quality and production efficiency.

3.3. Reproductive traits

Prolificacy traits have a distinguishable and multifaceted impact on the economy of goat production industry, influencing not only the productivity metrics of individual herds but also the broader market dynamics and profitability for producers. Differences in litter size among goat breeds can be attributed to genetic variations in key genes, making it essential to summarize these genetic factors for targeted breeding and improvement strategies. Consequently, understanding the genetic architecture associated with reproductive traits is paramount not only for advancing the goat genetics but also for ensuring sustainable practices within the goat production industry.

Genes identified by genomic studies Several studies utilizing selective sweeps have highlighted key genes associated with reproductive traits in Chinese goat breeds, underscoring the complexity of genetic influences on reproduction. Notable among these genes are phosphatase 1 regulatory inhibitor subunit 1C (*PPP1R1C*), SMAD family member 9 (*SMAD9*), kit proto-oncogene, receptor tyrosine kinase (*KIT*), bone morphogenetic protein receptor type 1B (*BMPR1B*), bone morphogenetic protein receptor type 2 (*BMPR2*) (Mahmoudi *et al*. 2022; Yang *et al*. 2024). The *PPP3CA* gene encodes an isoform of the calcineurin subunit, with research demonstrating that its catalytic subunit plays a crucial role in oocyte maturation (Daei-Farshbaf *et al*. 2021). As a vital growth factor responsible for pigmentation and female fertility, kit ligand (*KITLG*) is expressed in the ovaries, suggesting that both *KIT* and *KITLG* may play significant roles in reproduction (Hutt *et al*. 2006). More recently, a comprehensive whole-genome landscape study observed that deletions in the *BMPR1B* gene, which play a role in regulating litter size, have undergone convergent selection in goat and sheep (Yang *et al*. 2024). Moreover, the integration of signature selection, GWAS and runs of homozygosity (ROH) has led to the identification of several genes linked to litter size in goats, including A-kinase anchoring protein 13 (*AKAP13*), estrogen receptor (*ESR1*), protein phosphatase 2 regulatory subunit B'gamma (*PPP2R5C*), cell division cycle 25A (*CDC25A*), etc. (Mahmoudi *et al*. 2022). Notably, *AKAP13* interacts with the estrogen and progesterone receptors to modulate their activity (Zhang *et al*. 2023). CDC25A, a phosphatase that facilitates the G2 and mitosis phases in mouse oocytes (Li *et al*. 2008), along with *PPP2R5C*, which is involved in DNA methylation in ovarian cancer and associated with the PI3K/AKT signaling cascade (Gong *et al*. 2020).

Transcriptomic studies The hypothalamic transcriptome analysis in goats has uncovered crucial genes related to

reproductive functions, including *BMPR1B*, fibroblast growth factor receptor 1 (*FGFR1*), insulin-like growth factor 1 (*IGF1*), cAMP response element-binding protein 1 (*CREB1*), along with key signaling pathways such as prolactin, janus kinase-signal transducer and activator of transcription (Jak-STAT), and gonadotropin-releasing hormone (GnRH) signaling (Liang *et al*. 2021). This suggests that *BMPR1B* may also play a significant role in goat reproduction and could be considered a major gene influencing litter size. Notably, SMAD family serves as a vital intracellular mediator in the transforming growth factor-beta (TGF-β) signaling pathway. This pathway is essential for numerous reproductive processes, including embryonic development and placental formation, and can significantly influence reproductive traits in goats (Wijayanti *et al*. 2022).

Genetic variations impacting litter size in goats Numerous genetic variants (SNPs, insertions/deletions (InDels), and copy number variations (CNVs)) have been identified in key reproductive genes associated with litter size in goats, highlighting the complex genetic architecture underlying litter size in goats.

SNPs have been studied, particularly those in the growth differentiation factor 9 (*GDF9*) gene, with two specific non-synonymous mutations, including Q320P (g.3905A>C) and V397I (g.4135G>A), showing significant associations with litter size across various Chinese goat breeds (An *et al*. 2013b; Zhao *et al*. 2016; Wang *et al*. 2019). Importantly, *GDF9* and bone morphogenetic protein 15 (*BMP15*) have a synergistic effect on the proliferation of granulosa cells, emphasizing their collaborative role in reproductive processes (Juengel *et al*. 2004). Other polymorphisms were found in prolactin receptor (*PRLR*) (An *et al*. 2015a; Hou *et al*. 2015); *KITLG* (An *et al*. 2012; An *et al*. 2015b) to be associated with goat litter size. Numerous studies in goat MAS have detected SNPs in the *KISS1* gene, such as g.2540C>T, g.2124T>A, and g.2270C>T, which have been linked to variations in litter size (An *et al*. 2013a; Jeet *et al*. 2022).

In terms of InDels, the 11 bp variant in the DNA methyltransferase 3 beta (*DNMT3B*) gene, which is important for *de novo* methylation and essential for oocyte methylation, has been significantly linked to litter size in goats. Furthermore, the expression of this gene was found to be higher in mothers who had multiple lambs (Hui *et al*. 2020). Additional InDel polymorphisms within candidate genes are summarized in Table 1.

CNVs have also gained attention, particularly in the *BMPR1B* gene, where intronic CNVs have been shown to have a major effect on litter size within goat populations (Bi *et al*. 2021a). Besides, CNVs in sorting nexin 29 (*SNX29*) (Wang Q *et al*. 2022) and dynein axonemal heavy chain 1 (*DNAH1*) (Wang Z *et al*. 2022) were reported to be associated with litter size in goats.

These findings underscore the complex genetic underpinnings of reproductive traits in goats, highlighting key genes that may be targeted for improving breeding strategies.

3.4. Milk traits

Goat milk is gaining recognition as a valuable raw material for products with significant biological and therapeutic benefits, particularly in infant nutrition. This growing recognition can be attributed to its unique compositional profile and its potential health advantages over conventional dairy products. The primary determinants of goat dairy output encompass various interrelated factors, such as total milk yield, protein and fat content. Thus, the known genes associated with dairy traits function mainly by regulating milk protein and fat synthesis.

Casein (CSN) family and diacylglycerol o-acyltransferase 1 (*DGAT1*) genes A broad range of genes encoding the major proteins of milk are known to be associated with its nutritional value and the formation of milk productivity. There is evidence that casein family genes (e.g., casein alpha S1 (*CSN1S1*), casein alpha S2 (*CSN1S2*), casein beta (*CSN2*), casein kappa (*CSN3*)) are the most extensively studied genes associated with dairy traits in goats, especially in southern and western European countries (Vázquez-Flores *et al*. 2012; Vacca *et al*. 2014; Guan *et al*. 2021; Cosenza *et al*. 2023; Dettori *et al*. 2023). Notably, these well-known genes have been identified through GWAS in Canadian Alpine and Saanen populations (Massender *et al*. 2023), as well as *via* selective sweeps in Pakistani goats (Kumar *et al*. 2018). Goat *CSN1S1* has been shown to affect β-casein protein production in mammary cells through activation of STAT5a to bind the *CSN2* promoter (Song *et al*. 2020). Furthermore, beneficial allelic variants (A, B1, B1, B2, B3, B4, etc.) of *CSN1S1* have been validated in goats (Vacca *et al*. 2014; Dettori *et al*. 2023). Confirmation of allelic variants of genes linked to traits contributes to economic value by enabling targeted breeding and selection processes. This knowledge has enabled the MAS of goat with a higher milk production and improvement of dairy goat breeding.

Another GWAS in French dairy goats based on the milk production traits revealed two missense mutations (R251L and R396W) out of 29 polymorphisms in the *DGAT1* gene. Further association studies showed that both substances lead to a significant reduction in milk fatness (Martin *et al*. 2017). *DGAT1* is involved in the final step of triglyceride synthesis by catalyzing the conversion of diacylglycerol (DAG) and acyl-CoA into triglycerides that is crucial for lipid synthesis and affects the fat content of milk (Martin *et al*. 2017).

Other candidate genes related to milk traits More recently, the p.Lys139Arg variant in *STC1* involved in milk yield trait was identified in Swiss goats *via* GWAS. The *STC1* gene encodes glycoprotein hormone that perform role in lipid metabolism (Signer-Hasler *et al*. 2022). Additionally, multiple GWAS studies have identified genes, such as *PRL*, *PRLR*, *POU1F1*, lactalbumin alpha (*LALBA*), signal transducer and activator of transcription 5A (*STAT5A*), etc. that could be involved in mammary development and milk production (Mucha *et al*. 2018; Talouarn *et al*. 2020). Essential functions of the hypothalamic-pituitary-adrenal axis, including regulation of stress and metabolism, indicate that genes of this axis, such as *PRL*, *PRLR*, *POU1F1* and etc., influence various milk quality traits as well as milk yield. It is well-established that prolactin plays a crucial role in mammary gland development and the onset of milk production, primarily through the Jak/STAT signaling pathway (Bernard *et al*. 2015).

Together, the genes associated with the casein family, *DGAT1*, *PRLR*, and other genes related to the Jak/STAT

pathway show significant promise for improving dairy goat breeding.

3.5. Cashmere traits

The harsh climate conditions and temperature fluctuations have influenced the evolution of a distinctive undercoat composed of high-quality fiber or wool in goats adapted to severe conditions. Presently, a diverse array of cashmere goat breeds can be found across vast territories, including but not limited to China, Mongolia, India, Russian Federation, Uzbekistan, Kyrgyzstan, Kazakhstan, Afghanistan, Iran, Iraq, and Turkey. Recent advancements in genomic research have yielded promising insights into the identification of candidate genes that appear to be significantly associated with both the quantity and quality of cashmere production. These genetic markers may play a crucial role in providing a potentially early prognostic assessment tool for evaluating the genetic potential of cashmere goats.

Fibroblast growth factor (*FGF*) family genes FGF family is a group of highly conserved proteins that play critical roles in various biological processes, including development, cell differentiation, and tissue regeneration. Among the family members, *FGF5*, *FGF9*, and *FGF12* have garnered attention for their impact on cashmere traits in cashmere goats, especially through the application of genomic selection approaches (Li *et al*. 2017; Wang *et al*. 2021; Wu *et al*. 2024). Notably, *FGF5* functions as a negative regulator of the hair growth cycle and is primarily expressed in the outer root sheath (Higgins *et al*. 2014). In contrast, *FGF12* promotes hair formation and stimulates cellular proliferation (Woo *et al*. 2022).

Keratin (KRT) and keratin-associated protein (*KRTAPs*) family genes Keratins are a group of fibrous structural proteins that play a crucial role in forming hair, wool, and various other types of fibers. Previous RNA-sequencing evidence found a plethora of *KRT* and *KRTAP* genes, such as *KRTAP3-1*, *KRTAP8-1*, *KRTAP 24-1*, *KAP8-1*, etc., across various cashmere goat populations (Gao *et al*. 2016; Yang *et al*. 2020). Additionally, recent studies examining m^6A methylation patterns in goat skin tissues have illuminated the critical roles of keratin genes, including *KRT26*, *KRT32*, and *KRT82*, in regulating cashmere fiber growth (Wang Y *et al*. 2020). Of interest, the distinct repositories and expression profiles of *KAP* genes have been correlated with specific hair characteristics across mammalian species (Khan *et al*. 2014).

SRY-box transcription factor (*SOX*) family It is crucial to address the significant role of *SOX* genes in cashmere production. The members of *SOX* gene family, specifically *SOX4*, *SOX5*, *SOX9*, *SOX18* encode transcription factors related to the Sry-related high-mobility group box, serving as markers for hair follicle development (Wang S *et al*. 2020). A comprehensive study combining methylome and transcriptome analyses revealed that several key transcription factors, including SOX9, SOX21 along with others, are involved in the differentiation of hair follicles (Wang S *et al*. 2020). For instance, *SOX9* has been identified as a pivotal factor in guiding embryonic epidermal stem cells toward becoming hair follicle stem cells (Yang *et al*. 2023), while *SOX18* is involved in formation of the dermal papilla *via* Wnt-signaling (Villani *et al*. 2017). In addition, gene expression analysis of the skin tissues from cashmere goats indicated that *SOX4* and *SOX18* could influence the fineness of cashmere (Wu *et al*. 2022). This highlights the intricate involvement of *SOX* genes in hair follicle development and cashmere production.

Other genes associated with cashmere traits A multi-omics analysis was conducted to identify key regulators of cashmere fineness, highlighting genes, such as WNT family member 1 (*WNT1*), WNT family member 5A (*WNT5A*), prolactin receptor (*PRLR*), integrin subunit beta 7 (*ITGB7*), insulin like growth factor binding protein 4 (*IGFBP4*), etc., which may play a potential role in cashmere development (Wu *et al*. 2022, 2023). Further research has indicated that Wnt, Notch, TGF-β signaling pathways and the associated genes are fundamental in regulating cashmere characteristic (Geng *et al*. 2013). Specifically, the Wnt/β-catenin pathway operates by binding to the T-cell factor (TCF) and lymphoid enhancer factor (LEF) subunits, subsequently activating genes responsible for cell proliferation (Choi 2020). Given that IGF1 signaling plays a vital role in hair growth and is associated with conditions such as alopecia (Trüeb 2018), it is likely that related genes are important for cashmere characteristics as well.

Collectively, these findings suggest that the *KRT* and *KRTAP* family genes, along with members of the *FGF* and *SOX* families, play a critical role in enhancing both the yield and quality of cashmere.

3.6. Environmental adaptation traits

Stressful habitats are known to be is one of the driving forces behind the evolution of organisms. Goats are well adapted to high thermal harsh climatic conditions and able to survive on limited pastures suggests that the genomes of goat breeds contain clear traces of selection, formed during centuries of adaptation to these conditions. The investigation of adaptive mechanisms is of practical importance of goat breeders. Both humans and animals exhibit varying degrees of acclimatization to environmental conditions, influenced by genetic diversity among populations. This phenomenon is particularly important when considering factors such as hypoxic conditions, frigid climates, and elevated levels of ultraviolet (UV) radiation, all of which create challenging habitats for most species (Bertolini *et al*. 2018). Studying goat genomes give sense into the evolutionary forces that have formed the structure and function of genes associated with adaptation (see Table 2 and Fig. 4).

Adaptation to high-altitude (1) Genomic studies and candidate genes. In high-altitude environments where oxygen levels are drastically reduced, the physiological responses of goats may differ markedly based on their genetic predispositions. Some breeds may possess enhanced respiratory efficiency or a greater capacity for generating red blood cells, thereby enabling them to thrive in these low-oxygen conditions. Thus, Tibetan goats are considered to be ideal models for studying the genetic mechanism of hypoxia related complications and high-altitude adaptation.

Table 2 Candidate selective genomic regions related to the environmental adaptative traits in goats

Traits	Breeds	Genes, GO terms	Approaches	Source
High-altitude tolerance	Bange (*n*=60), Ritu (*n*=68), Chaidamu (*n*=45), Nanjiang (*n*=58), Inner Mongolian (*n*=39), Liaoning (*n*=60)	*EPAS1*	Selection signatures (exome sequencing)	Song *et al.* (2016)
	Tibetan (*n*=17), Xinjiang (*n*=17), Taihang (*n*=16), Huanghuai (*n*=16)	*EGFR*, *LEPR*, *LDB1*, *FGF*	Selection signals	Jin *et al.* (2020)
	Tibetan goats (*n*=145) and other goats (*n*=584)	*PAPSS2*		Bian *et al.* (2024)
	Bezoar (*n*=9), Appenzell goat, Grisons Striped goat, Peacock goat, St. Gallen Booted goat, Valais Blackneck goat (*n*=119), Capra Grigia, Chamois Colored, Nera Verzasca, Saanen, Toggenburg (*n*=90)	*HMOX2*	ROH	Signer-Hasler *et al.* (2022)
	Tibetan goat (*n*=6) Low altitude goat (*n*=6)	*SLC26A9*, *GPX3*, *ARRDC4*, *COX1*	Transcriptome and microbiome	Pan *et al.* (2024)
Thermotolerance	Pakistani goat (*n*=26), domestic goats (*n*=184)	*KITLG*, *HSPB9*, *HSP70*, *HSPA12B*	Selection signatures	Zhang *et al.* (2024)
	Guizhou black goat (*n*=30)	*HBEGF*, *SOSTDC1*, *ARNT*, *COL4A1/2*, *EP300*		Chang *et al.* (2024)
	Domestic goats (*n*=130)	*DLG1*, *ENOX1*, *GPC5*, *DNAJC16*, *FTO*, *GFI1*, *SLC2A2*		Peng *et al.* (2024)
Coat color	Male bezoar and domestic goats	*ASIP1*, *Adamts20*, *MITF*, *SLC7A11*, *GNAQ*	*De novo*	Dong *et al.* (2015)
	Northern China cashmere, Indian populations (*n*=46)	*ASIP*, *KITLG*, *TYRP1*, *SLC24A4*	Selection signatures	Wu *et al.* (2024)
	Diverse breeds (*n*=244)	*KIT* and *ASIP*		Henkel *et al.* (2019)
	144 goat breeds (*n*=4,563)	*ADAMTS20*, *MC1R*, *ASIP*, *SOX18* and *TIMP3*		Bertolini *et al.* (2018)
	Alpine, Angora, Corse, Fossés, Poitevine, Provençale, Pyrénées, Saanen (*n*=223)	*ADAMTS20* and *ASIP*		Oget *et al.* (2019)
	Murciano-Granadina (*n*=1,183)	*GLI3*, *MC1R*, *MITF*		Guan *et al.* (2021)
	Pakistani goat (*n*=192)	*KIT*		Kumar *et al.* (2018)
	Chongming white (*n*=10), Boer (*n*=10), Haimen (*n*=10), Xuhuai (*n*=10), Matou (*n*=10), Da'er (*n*=10), Nanjiang yellow (*n*=10), Macheng black (*n*=10), Yichang white (*n*=10), Qin (*n*=10)	*KITLG*, *ASIP*, *AHCY*, *RALY*, *MC1R*		Gao *et al.* (2020)
	Saanen (*n*= 936)	*ASIP*		Martin *et al.* (2016)
	Jintang black (*n*=65)	*ASIP*		Guo *et al.* (2022)
	Boer goats (*n*=236)	*EDNRA*		Menzi *et al.* (2016)
	Bezoar (*n*=9), Appenzell goat, Grisons Striped goat, Peacock goat, St. Gallen Booted goat, Valais Blackneck goat (*n*=119), Capra Grigia, Chamois Colored, Nera Verzasca, Saanen, Toggenburg (*n*=90)	*ASIP*	ROH	Signer-Hasler *et al.* (2022)
Disease tolerance	*C. hircus*, *C. aegagrus*, *C. falconeri*, *C. sibirica*, *C. ibex*, *C. caucasica*, hybrids of *C. nubiana*×C. *hircus* (*n*=106)	*MUC6* gene	Selection signatures	Zheng *et al.* (2020)
	Bezoars and domesticated goat populations	*MUC6*, *GIMAP8*, *CNTNAP2*, *KCND3*, *NBEAL1*		Wu *et al.* (2024)
	Bezoar and native goat populations	*CLEC2D*, *FAM26F*, *GIMAP6*, *CLECL*		Liu J *et al.* (2024)
	Bohuai goats (*n*=30), Huai goats (*n*=5), Europe (*n*=15), Africa (*n*=16), Middle East (*n*=15), China (*n*=73)	*CD274*, *DHPS*, *PDCD1LG2*		Yao *et al.* (2023)
	Guizhou black goat (*n*=30)	*CD28*, *CD274*, *IL1A*, *TLR2*, *SLC25A31*		Chang *et al.* (2024)
	Male bezoar and domestic goats	*ABCC4*, *PRAME*, *CD163L1*, *KIR3DL1*, *CFH*, *TRIM5*	*De novo*	Dong *et al.* (2015)
	Boer goats (*n*=4)	Resistance to *H. contortus*: *NFKBIA* and *NFKBID*	scRNA-Seq	Wang *et al.* (2024)
	Yichang white (*n*=122)	Resistance to *H. contortus*: *IL10BP*, *IL6R*, *IL1R1*, *IL1R2*, etc.	RNA-seq	Bhuiyan *et al.* (2017)

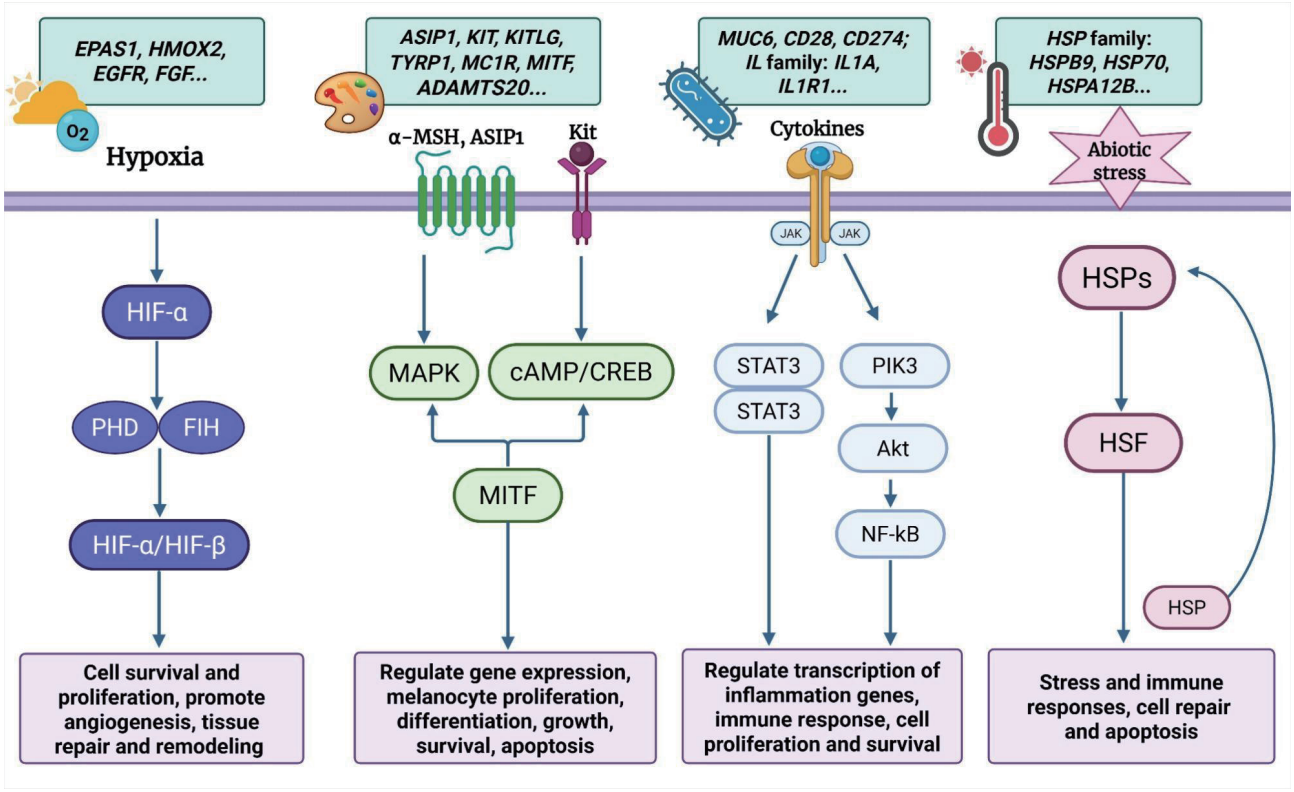


Fig. 4 General scheme of action of some important genes involved in environmental adaptation in goats. Upon hypoxia conditions, prolyl hydroxylases (PHDs) and factor-inhibiting HIF (FIH) hydroxylate enzymes are inhibited, allowing HIF-α to accumulate, dimerize with HIF-β, and translocate to the nucleus, driving the expression of genes involved in angiogenesis, metabolism, and survival, thereby enabling cells to adapt to low oxygen environments; ASIP/MC1R and KIT/KITLG can regulate the melanin synthesis *via* microphthalmia-associated transcription factor (MITF), which in turn drives the expression of target genes; interleukins (ILs) binds to their receptor IL-R and triggers the JAK/STAT pathway, leading to transcriptional regulation of target gene; under increased temperature, the misfolded heat-shock proteins (HSPs) accumulated, and heat shock transcription factor (HSF) regulates downstream genes, which increase HSPs in cytosol.

The study by Song *et al*. (2016) compared goat populations living at high and low altitudes in China to understand how natural selection might have shaped their genomes. For instance, the endothelial PAS domain protein 1 (*EPAS1*) gene was identified *via* screening the selection signatures at the exome regions, which has been documented to be linked to high-altitude adaptation in other species, including human, cashmere goats, horses, chickens, sheep, etc. (Song *et al*. 2016). Previous studies on high-altitude adaptation suggested that human and livestock flock had acclimatized to hypoxic environments in convergent ways (Witt and Huerta-Sánchez 2019). In addition, the *EPAS1* gene is known to encode a transcription factor involved in the initiation of oxygen-regulated genes that are induced when oxygen levels are reduced (Påhlman and Mohlin 2018). Alternative research has expanded the understanding of altitude adaptation in various goat populations, highlighting additional candidate gene such as heme oxygenase 2 (*HMOX2*) (Signer-Hasler *et al*. 2022). These genes are involved in the hypoxia-inducible factor (HIF) pathway, which plays an essential role in the physiological responses of organisms under hypoxic conditions. A recent study by Bian *et al*. (2024) identified novel SV in the 3′-phosphoadenosine 5′-phosphosulfate synthase 2 (*PAPSS2*) gene that may have been introduced to Tibetan goats through graph-based genotyping. This finding suggests the need for further experimental research. The HIF pathway orchestrates a complex network of adaptive mechanisms that enable organisms to thrive in oxygen-poor environments, thus underscoring the evolutionary significance of these genetic traits in facilitating survival and performance in high-altitude ecosystems.

(2) Comparative transcriptome studies. More recently, Pan *et al*. (2024) identified that the genes such as arrestin domain containing 4 (*ARRDC4*), solute carrier family 26 member 9 (*SLC26A9*), cytochrome C oxidase I (*COX1*), glutathione peroxidase 3 (*GPX3*) might be involved in how tissues adapt to varying oxygen levels. This finding suggests the need for further investigation into how these genes contribute to the ability of Tibetan goats to thrive in high-altitude conditions. The complexity of genetic interactions and environmental factors in high-altitude adaptations necessitates further research that integrates multi-omics, environmental, and phenotypic data.

Thermotolerance Temperature-associated genes can be used to model genotype-environment relationship and forecast response to climate changes as well as maintain the biodiversity of breeds facing extinction. Within this context, heat tolerance emerges as a crucial phenotypic trait, especially in goats, which have evolved various adaptive mechanisms to withstand elevated thermal stress (Abioja *et al*. 2023). Through the identification and characterization

of key temperature-associated genes, we can enhance breeding programs, ensuring that these animals retain their adaptability in changing environments, thereby contributing to the sustainability of agricultural systems.

Heat shock proteins are a highly conserved family of molecular chaperones that play crucial roles in cellular stress response, protein folding, and the regulation of immune processes across various organisms. A recent study suggested candidate genes such as heat shock protein family B member 9 (*HSPB9*), heat shock protein family A member 12B (*HSPA12B*), heat-shock protein 70 (*HSP70*) for acclimatization to tropical or hot climates in Pakistani goats (Zhang *et al*. 2024). For instance, the differential mRNA expression of *HSP70* in individuals susceptible to heat stress exhibited a greater fold expression compared to goats that are tolerant to heat stress (Kaushik *et al*. 2022). Mammalian HSPs are involved in autoimmune processes and immune regulation. Different types of cellular stress lead not only to an increase in the intracellular content of HSPs, but also in some cases induce translocation of these proteins to the plasma membrane and release into the extracellular space (Gu *et al*. 2023). Further research and genetic engineering solutions that preserve goat productivity at extreme temperatures are essential for future advancements in the goat breed.

Coat color Coat color in mammals serves several vital functions beyond mere aesthetics. For instance, it plays a crucial role in predator avoidance, mate preference, UV protection (Hoekstra 2006). This multifaceted importance of coat color highlights its evolutionary significance in the survival and reproductive strategies of mammals.

(1) The *ASIP* and *KIT* genes. In comparing the genomes of domestic goats, numerous studies have identified the well-established genes, such as *ASIP* and *KIT* (Dong *et al*. 2015; Henkel *et al*. 2019; Oget *et al*. 2019; Gao *et al*. 2020; Signer-Hasler *et al*. 2022; Wu *et al*. 2024). The *ASIP* gene, encoding an agouti-signaling protein, affects the production and distribution of the black pigment eumelanin and allows eumelanin to accumulate only on certain parts of the body (hair) (Kumari *et al*. 2023). Guo *et al*. (2022) showed that 13,420-bp duplication upstream of the *ASIP* gene linked to the non-classic Swiss marking pigmentation in Jinanag Black goat. Notably, ASIP inhibits MC1R signaling, resulting in the arrest of melanogenesis (Zhang *et al*. 2017).

The KITLG and its receptor are the major control system for melanocytes and is involved in hair, skin, and eye pigmentation (Sevilla and Grichnik 2024). The migration and differentiation of melanoblast are regulated by a number of signaling pathways (e.g., KIT/KITLG, protein kinase C-dependent pathway) and transcription factors (e.g., Sox family, microphthalmia associated transcription factor (MITF), etc.) (D'Mello *et al*. 2016).

(2) Other genes related to coat color. Studies focusing on pigmentation trait identified the melanocortin 1 receptor (*MC1R*) as a candidate for coat color in goats (Gao *et al*. 2020; Guan *et al*. 2021). The MC1R is the G protein-coupled receptor that controls skin pigmentation, and act *via* α-MSH/MC1R/m-MITF axis to synthesize melanosomes (Yardman-Frank and Fisher 2021).

In a recent study conducted by Wu *et al*. (2024), tyrosinase-related protein 1 (*TYRP1*) was identified in goats through the analysis of selection signatures. Research has shown that the cAMP signaling pathway plays a significant role in regulating the expression of both TYRP1 and TYRP2 proteins, primarily through the action of the transcription factor MITF (D'Mello *et al*. 2016).

Additionally, genomic studies in goats identified the ADAM metallopeptidase with thrombospondin type 1 motif 20 (*ADAMTS20*) gene (Bertolini *et al*. 2018; Oget *et al*. 2019). *Adamts20* is found in dermal mesenchymal cells and is involved in promoting cell survival and enhancing Kit signaling as melanoblasts migrate into the skin (Silver *et al*. 2008).

Collectively, the genetic pathways and candidate genes implicated in coat pigmentation in domestic goats, such as *ASIP*, *KIT*, *TYRP*, and *MC1R*, offer valuable insights into the regulation of coloration and its underlying molecular mechanisms. Future research should explore the functional roles of these genes in diverse goat breeds and their potential applications in breeding programs aimed at enhancing desirable pigmentation traits.

Disease-resistance The immune system provides a general defense against disease based on the combined action of innate and adaptive elements of the immune system. Disease can cause significant economic damage to the goat industry, as it leads to a reduction in milk productivity, slow live weight gain, deterioration of wool quality (Kappes *et al*. 2023). Many helminthic pathogens are also dangerous for humans, and therefore have an acute social impact. Therefore, genes associated with host susceptibility to disease and pathogen resistance genes are important for achieving sustainable disease resistance.

Interleukins and interleukin 1 receptors (IL1R) perform an important roles in the development of immunity in goats. Several interleukins, including *IL1A*, *IL1R1*, *IL1R2* have been identified in goats (Bhuiyan *et al*. 2017; Chang *et al*. 2024). ILs are pro-inflammatory cytokines that stimulate local and systemic immune response and activate NF-κB, p38, c-Jun N-terminal kinase (JNK), extracellular-signal-regulated kinase (ERK), and mitogen-activated protein kinase (MAPK) signaling cascades (Al-Qahtani *et al*. 2024).

Robust selection signals associated with the *MUC6* gene have been identified, which is a pivotal component of the mucin family, across a plethora of wild and domestic goat specimens, reflecting evolutionary pressures that may have shaped mucosal immunity in these populations (Zheng *et al*. 2020; Wu *et al*. 2024). In more contemporary research, a comprehensive genomic analysis revealed the involvement of the T-cell-specific surface glycoprotein (*CD28*) and programmed cell death 1 ligand 1 or *CD274* molecule (*CD274*) genes within the immune-related signaling pathways, thereby further enriching our understanding of the genomic landscape underpinning immune function in goats (Yao *et al*. 2023; Chang *et al*. 2024). Notably, the *CD28* gene was highlighted for its critical role in orchestrating the immune response by modulating T cell activation and proliferation, which underscores its potential importance in the adaptive immune system (Ciesielska-Figlon and Lisowska 2024).

Improving disease tolerance in goats through genetic selection is a viable strategy that requires a multifaceted approach involving genetics, environmental management, and sustainable practices. Further research and technological advancements will be essential to realize the full potential of genetic improvements in disease resilience.

4. Challenges and future perspectives

Goat breeding plays a critical role in meeting the population's demand for traditional raw materials and food products, including meat, milk, and cashmere. This review demonstrates the advances that have resulted from implementing classic genetic methods and new technological approaches to understand the genetic basis underlying economically useful traits in goats. Significant advancements have been achieved in the understanding of goat genomics through the application of contemporary technological methodologies; nevertheless, numerous obstacles still persist. Fig. 5 presents a schematic representation of contemporary technologies aimed at enhancing goat breeding.

4.1. Inadequate genetic resources and genomic data

The fundamental importance of genetic resources cannot be overstated when it comes to enhancing breeding efforts. The efficacy of both breeding programs and conservation initiatives is predominantly contingent upon the diversity and accessibility of genetic variations found within existing repositories. Although the population re-sequencing data are rapidly increasing, analysis of existing datasets remains insufficient in goats. While there exist several chromosomal-level genome assemblies for goats, their quantity remains insufficient when compared to those available for other livestock species (Dong *et al*. 2015; Bickhart *et al*. 2017; Li *et al*. 2021; Wu *et al*. 2024). At present, goat germplasms are emerging as an invaluable foundational resource for the genomic advancement. Unprecedented demand for improved reference goat genomes and broad variation repositories requires the development of specialized databases to speed up scientific breakthroughs. Nonetheless, the majority of the existing accessions that have been gathered, along with a limited number of wild goats or their proximate relatives, have yet to be incorporated into the overarching framework. Because wild species contain genetic diversity that is likely missing in their domesticated relatives, it is crucial to study the genomes of wild species before they become extinct, as global biodiversity is rapidly declining. This is particularly relevant for goat breeds, where research advancements have predominantly focused on Chinese breeds. In contrast, other

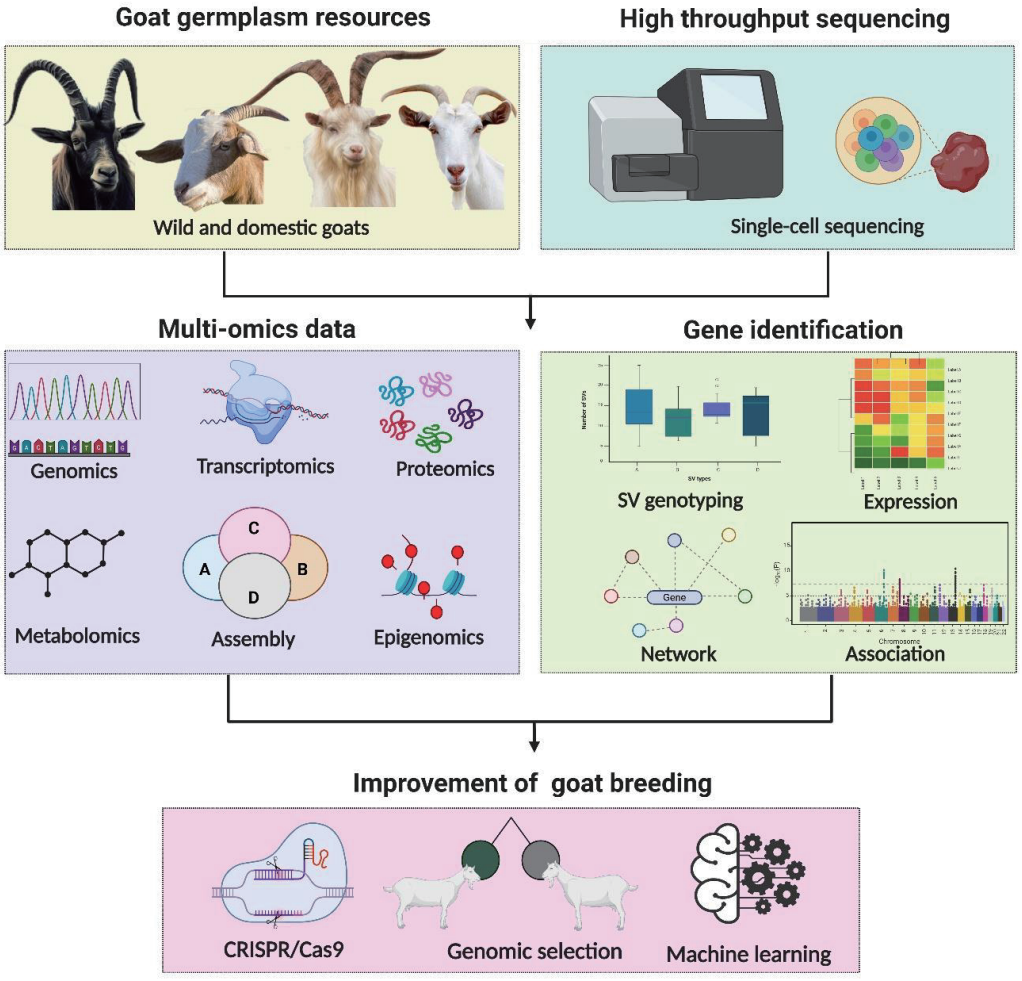


Fig. 5 Utilization of modern technologies for improving goat breeding.

regions are witnessing the decline of certain goat breeds, pushing them closer to extinction (Deniskova *et al*. 2021). Besides, indigenous breeds are overlooked or not properly characterized, making conservation efforts challenging. To address this urgent issue, collaborative international genomics initiatives can play a pivotal role in expanding goat genomic research and conserving valuable genetic resources.

Balancing data sharing and utilization with the protection of intellectual property (IP) rights is a critical challenge in the development of comprehensive genomic databases. To balance data sharing and IP, researchers can use licenses and establish formal agreements to specify how the data can be shared and used, allowing researches to retain certain rights while permitting others to utilize the data under specified conditions. Besides, utilizing tools like data anonymization and controlled access can help maintain privacy and ownership while fostering collaboration. Additionally, promoting open data initiatives but include restrictions on commercial use or derivative works that could infringe on existing patents or copyrights. Collaborating on projects that emphasize joint ownership or co-creation of knowledge, can potentially lead to shared benefits and further enhance both research progress and IP protection.

4.2. Enhancing the accuracy of genomic selection

Genomic selection is considered very promising for improving genetic traits that are influenced by many genes, each having a minor impact, by leveraging genomic data along with observed phenotypic information. Consequently, utilizing a larger dataset enables more accurate assessments of genetic influences. Furthermore, advancements in phenotyping techniques, particularly through high-throughput technologies, facilitate more precise measurement of the desired traits.

Genomic prediction typically involves calculating breeding values using a range of statistical techniques. Sophisticated statistical techniques, including machine learning and deep learning, can effectively capture complex genetic architectures and non-linear associations between markers, which are essential for traits with low heritability. For instance, the recent study demonstrates that machine learning models significantly enhance the accuracy and reliability of genomic predictions for udder traits in Saanen dairy goats, surpassing traditional methods (Yao *et al*. 2025). Besides, including environmental covariates in genomic models addresses genotype-environment interactions, which significantly affect trait expression.

Eventually, integrating genomic data with omics technologies offers insights into the biological mechanisms behind complex traits, enhancing prediction accuracy. For instance, validation of transcriptome, proteome, and metabolome data revealed that the kidding traits in goats are influenced by pathways related to fatty acid, unsaturated fatty acid, and steroid hormone biosynthesis (Dai *et al*. 2024). Nevertheless, further researches are necessary to explore the genomic selection of traits in goat that exhibit low heritability.

In summary, a complex approach combining extensive data collection, advanced modeling, environmental considerations, and use of multi-omics approaches can significantly enhance genomic selection in goat breeding.

4.3. Towards goat pan-genomics

Owing to progress in sequencing technologies, employing cutting-edge sequencing approaches and advanced assembly algorithms, it is possible to create comprehensive reference goat genomes in which previously obscure sequences critical to understanding genome structure and function can be discovered. Most genomic studies have been conducted using small variants (SNPs), while large variants are not be available, so there is a need for graph-based pan-genome design. Long reads enable the detection of structural sequence variants that are often elusive when relying solely on short-read technology. The advancement of goat genome assemblies through the use of long read sequencing technologies, such as Oxford Nanopore Technology (ONT) and Pacific Biosciences (PacBio), presents significant opportunities for expanding our understanding of goat genetics and biology (Li *et al*. 2021; Wu *et al*. 2024). These technologies facilitate the generation of high-quality haplotype-resolved and T2T gapless genome assemblies, which represent the forefront of genomic research. For instance, the recent T2T-goat1.0 assembly of goat boosted variant calling rates and uncovered previously unreported novel selective signatures (Wu *et al*. 2024). By producing more *de novo* goat genomes, researchers can gain deeper insights into biological diversity and evolutionary pathways in goats. Detailed assemblies not only enhance our comprehension of genetic variation but also facilitate investigations into how these variations influence the important production traits. Consequently, the provision of publicly accessible T2T assemblies, complemented by comprehensive genome annotations *via* open-access databases, is poised to expedite research endeavors and breeding initiatives.

The advancement of genetic analysis techniques utilizing complete genome studies has significantly broadened the avenues for pinpointing genomic regions responsible for regulating the physiological and biochemical mechanisms underlying phenotypic variations in livestock. The genome sequence from a single specimen of a goat does not encompass the entire genetic diversity present within goats. This highlights the concept of pangenomes, which acknowledges the genetic variability within a species. Different individuals within a species may carry unique alleles, gene variants, and structural variations that contribute to the overall genetic diversity. Currently, the work on population-specific sequences or the goat pangenome is gradually being done, which may allow more structural variations to be identified and help improve selection (Li R *et al*. 2019; Bian *et al*. 2024; Liu J *et al*. 2024). Additionally, integrating pangenomes with *de novo* assembly or haplotype-resolved assembly is more effective at identifying variants. Nevertheless, following the successful sequencing of the goat genome, additional research is imperative to delve deeper into the pan-genomic landscape of goats across various breeds. This approach facilitates a more comprehensive

understanding of the genetic landscape, paving the way for improved goat breeding strategies and conservation efforts.

4.4. Single-cell multi-omics

The burgeoning number of transcriptomic analyses elucidating the intricate interplay between genotype and phenotypic traits is pivotal for discovering gene functionality and advancing prospective strategies in goat breeding. The research in goat genomes has now entered the multi-omics world that help to deeper understanding of biological processes and molecular mechanisms underlying certain traits (Sun *et al*. 2022; Yang *et al*. 2023; Zhang *et al*. 2023). The advent of single-cell RNA sequencing (scRNA-seq) is profoundly transforming our understanding of transcriptomic landscapes, enabling us to glean intricate molecular profiles at the resolution of individual cells, rather than merely at the tissue level. The jointly profiling by scRNA-seq and single-nucleus assay for transposase-accessible chromatin sequencing (snATAC-seq) enables researchers to correlate chromatin accessibility with gene expression at the single-cell level across distinct cell types (Lee *et al*. 2023). In contrast to relying on single-cell transcriptomics alone, integrative multi-omics analysis of single cells offers deeper insights into the transcriptional regulation of cellular states, interactions, and behaviors. The emergence of single-cell multi-omics platforms, such as the 10x Genomics Visium, Single Cell Multiome ATAC+Gene Expression, etc., which simultaneously profiles the genome, epigenome, transcriptome, proteome, and metabolome from individual cells, has made it increasingly feasible to carry out comprehensive assessments at the single-cell level (Baysoy *et al*. 2023). These innovative and highly advanced single-cell analytical methodologies have emerged, offering researchers unprecedented capabilities to investigate the intricacies of goat development and physiology with remarkable resolution and extensive scope.

However, effectively integrating multi-omics data to understand complex traits requires addressing significant technical and analytical challenges. Multi-omics data comes in various forms (e.g., sequences, expression levels, protein interactions, metabolic profiles) and the massive volume of generated data can be overwhelming, requiring significant storage and computational resources. Therefore, utilizing high-performance computing resources can handle the large-scale data processing and analysis required for multi-omics integration. Also, multi-omics datasets often have high dimensionality, making it challenging to identify meaningful patterns and relationships. Developing algorithms that can effectively integrate and analyze multi-omics data is non-trivial, requiring sophisticated statistical and machine learning techniques. By employing machine learning and deep learning to combine different forms of data, researchers can identify additional genetic features that influence complex traits. These approaches deepen our understanding of the biological mechanisms involved, going beyond what is usually revealed through traditional methods.

4.5. Genome editing

Genome editing technology has the remarkable ability to rapidly alter specific genes that affect desired traits. Although zinc finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs) were initial innovators in gene editing, their complexity and constraints limited their practicality, whereas clustered regularly interspaced short palindromic repeats/CRISPR-associated protein (CRISPR-Cas9) has become a more user-friendly and adaptable tool, significantly enhancing critical traits in livestock (Kalds *et al*. 2019). So far, CRISPR-Cas9 was widely applied in goat functional studies (Zhang J *et al*. 2018; Li X *et al*. 2019; Hu *et al*. 2021; Tian *et al*. 2022). For instance, it was shown that the system enhances the quantity of secondary hair follicles (SHF) and cashmere length in goats, and germline transmission studies indicate that the genomic modifications can be passed on to the offspring (Wang *et al*. 2016). Both the phenotypic and genotypic analyses following the disruption of the myostatin (*MSTN*) gene *via* CRISPR/Cas9 in goats showed that the resulting mutations can be passed down to future generation, which has significant implications for goat breeding (Wang *et al*. 2018). The promised advances in genome editing technology may lead to increasing commercialization of genetically modified goats. Nevertheless, alongside the prospective advantages, there are many ethical dilemmas and safety concerns that warrant careful contemplation. Decisions made today about genome editing could have long-term consequences for future generations, both in terms of ethical legacy and social impact. Given the impacts of genetic modifications on animal welfare are not fully understood, this may raise concerns about possible unintended consequences. From the social aspect, the introduction of genetically modified goats might disrupt traditional breeding practices, affecting cultural heritage and livelihoods. Besides, there may be issues about whether products from genetically modified goats should be labeled, and how transparent the process should be to consumers. In light of these considerations, it is imperative that we approach genome editing with caution, prioritizing ethical deliberation and societal input to ensure that any advancements serve to enhance both animal welfare and cultural integrity for generations to come.

4.6. Use of artificial intelligence

A critical issue in breeding is the methodology for extracting enhanced and more accurate information about desired traits from the vast array of existing databases. Meanwhile, artificial intelligence has become a pioneering technology and a shortcut to modern computer processes, providing great potential for application in breeding. Breeders can improve the accuracy and efficiency of predicting phenotypes from genotypes and identify molecular markers associated with specific traits using machine learning models (Hayes *et al*. 2023). The implementation of precision agriculture can be achieved through the thoroughly quantification of *caprine* traits *via* advanced imaging methodologies, followed by the systematic evaluation of the dependable data extracted through sophisticated machine learning algorithms. Thus, the integration of biological data and AI can accelerate modern goat breeding.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

Ethical statements

Not applicable.

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