

## Review

# Molecular Genetics of Fibre Quality Traits in Indian Sheep and Goat Breeds: A Review

Sakshi Kaith<sup>1\*</sup>, Shubham Loat<sup>2</sup>, Kanaka K.K.<sup>1</sup>, Amit Kumar<sup>1</sup> and Soumen Naskar<sup>1</sup>

<sup>1</sup>ICAR–Indian Institute of Agricultural Biotechnology, Garkhatanga - 834003, Ranchi, Jharkhand, India

<sup>2</sup>ICAR–National Research Centre on Yak, Dirang - 790101, Arunachal Pradesh, India

## ABSTRACT

India maintains one of the largest and most diverse populations of sheep and goats in the world, distributed across four agro-climatic eco-zones ranging from the arid regions of Rajasthan to the cold high-altitude deserts of Ladakh. These indigenous genetic resources produce fibres of considerable economic importance which supports the livelihoods of millions of pastoralists and agro-pastoralist households. The fibre types span from the coarse carpet wool of the Chokla and Magra breeds of Rajasthan to the ultrafine pashmina of the Changthangi goat of Ladakh. Over the past two decades, molecular genetic research on animal fibre has moved from breed-level phenotypic characterization toward gene- and pathway-level analysis of the traits that determine fibre fineness, length, and lustre. This review compiles the current understanding of the structural genes- keratins (KRT) and keratin-associated proteins (KRTAP), and regulatory genes (*FGF5*, *WNT10B*, *LEF1*, *BMP2*, and related follicle-cycling factors) that govern fibre quality in sheep and goats, with particular emphasis on the Indian breeds Chokla, Magra, Harnali, Chegu and the extensively studied Changthangi pashmina goat. The review critically compares findings across breeds and studies. It highlights gaps in the molecular characterization of Indian fibre-producing breeds relative to the Changthangi goat. It also discusses future prospects for marker-assisted selection, genomic and multi-omic approaches, and conservation of indigenous fibre-yielding genetic resources.

**Keywords:** Changthangi, Chokla, *FGF5*, Keratin-associated proteins, *KRTAP*, Magra, Pashmina, WNT/LEF1 signaling, Wool fineness

\*Corresponding author: kaithsakshi@gmail.com

Received: July 15, 2026

Accepted: August 10, 2026

## INTRODUCTION

Wool and pashmina/cashmere are keratinous fibres produced mostly by the secondary hair follicles of sheep and goat. Their commercial value is determined mainly by four measurable quality traits: most important is fibre diameter (fineness), staple length, crimpiness, and shine or lustre in the fibre, together with medullation and color. India possesses a diverse range of livestock, comprising 46 registered sheep breeds and 43 registered goat breeds, which are distributed across four distinct eco-zones (ICAR-NBAGR, 2025). Conventionally, this diversity has been characterized at the phenotypic level and, more recently, through microsatellite markers. This phenotypic spectrum stretches from the exceptionally white, resilient carpet wools produced by northwestern arid sheep breeds (such as the Chokla and Magra) to the ultra-fine luxury undercoat harvested from the Ladakhi Changthangi pashmina goat.

Fibre producing livestock are not merely a genetic resource; they are a direct mainstay for the pastoral communities that raise them. In the Changthang region of Ladakh, pashmina is reported to generate roughly

55% of household income for Changpa pastoralist families, who herd an estimated 150,000-160,000 Changthangi goats to produce around 35,000-40,000 kg of raw pashmina annually (Namgail *et al.*, 2010). Both Ladakhi and Kashmiri pashmina, along with the recently recognized Basohli pashmina of Jammu, hold Geographical Indication (GI) status emphasizing their important socio-economic and cultural value. However, despite its fineness and aesthetic value, India's overall pashmina production remains a small fraction – approximately 1% of global production, with China and Mongolia remain the dominant producers (Shakyawar *et al.*, 2013). Similarly, carpet-wool sheep breeds such as the Chokla and Magra play a vital role in sustaining pastoral livelihoods across the arid regions of Rajasthan by supplying raw material to India's carpet handloom, and rug-weaving industries (Shakyawar *et al.*, 2013). Thus, molecular characterization of the genes governing fibre quality traits is fundamental to understanding fibre biology and translating molecular knowledge into genetic improvement, sustainable production, and the conservation of indigenous livestock genetic resources (Yadav *et al.*, 2011). In contrast to the comprehensive

gene-level characterization carried out in Merino sheep and in Chinese and Mongolian cashmere goats, the molecular basis of fibre quality in most Indian breeds remains comparatively underexplored.

Fibre quality is basically determined by two broad classes of genes: i) Structural genes and ii) Regulatory genes. The structural genes are physically incorporated into the fibre. These consist of the hair and wool keratins (*KRT* genes), which constitute the intermediate filaments of the cortex and cuticle, as well as the keratin-associated proteins (KRTAPs), which cross-link these filaments into a cohesive matrix. The second class comprises of regulatory genes that are responsible for controlling hair follicle morphogenesis, cycling, and the transition between primary and secondary follicle fates. This includes fibroblast growth factor 5 (FGF5), a master inhibitor of follicle elongation (Li *et al.*, 2017b), components of signaling pathways such as WNT/ $\beta$ -catenin pathway along with its downstream effector lymphoid enhancer-binding factor 1 (LEF1); and bone morphogenetic proteins (BMPs). Both regulatory classes have been directly implicated in sheep and goat hair follicle biology through transcriptomic network analysis and targeted expression studies (He *et al.*, 2022; Wu *et al.*, 2019; Su *et al.*, 2009).

Variation in structural genes has similarly been associated with measurable differences in fibre diameter, wool length, and greasy fleece weight across sheep and goat breeds. FGF5 variants, for example, have been linked to wool length, greasy wool weight, and mean fibre diameter in fine-wool sheep, and WNT2 has been shown to promote sheep hair follicle growth and development (Li *et al.*, 2022). In Changthangi goats specifically, the transcription factors HOXC13 and FOXN1, together with the follicular receptors such as GPRC5D, were among the regulator genes showing transcript abundance in Pashmina-producing skin (Ahlawat *et al.*, 2020). Additionally, in cashmere goat fetal skin, the BMP/TGF- $\beta$  antagonists *SMAD6* and *SMAD7* were identified among the differentially expressed genes active during hair follicle development and cycling (Geng *et al.*, 2013). Skin transcriptome analysis of Changthangi goats has further indicated that positive regulation of WNT signaling and negative regulation of Oncostatin M signaling are likely contributors to hair follicle development and hair shaft differentiation (Ahlawat *et al.*, 2020).

This review compiles the existing molecular literature on these two gene classes, and places it in the context of what is specifically known about Indian fibre-producing breeds, more specifically the Rajasthani carpet-wool sheep Chokla and Magra, the synthetic fine-wool Harnali, the Himalayan Chegu goat and the Ladakhi pashmina goat Changthangi. It also covers the broader

comparative literature from Chinese, New Zealand, and Tibetan flocks and herds, which has provided the most of the functional evidence to date.

### Structural components of the fibre: Keratins and Keratin-Associated Proteins

Fibre quality is fundamentally determined by the structural proteins that form the fibre shaft. Among these keratins (KRTs) and keratin-associated proteins (KRTAPs) constitute the principal structural components responsible for the mechanical strength, elasticity, fineness and other physical properties of wool, pashmina, and cashmere fibres.

#### Keratin (*KRT*) genes

Hair and wool keratins are intermediate filament proteins divided into acidic type I and basic type II gene families, located on ovine chromosomes 11 and 3 respectively. A total of seventeen *KRT* genes have been described in the wool follicle. Their expression is spatially and temporally ordered along the length of the growing follicle. Transcription of trichohyalin and *KRT27* precedes that of *KRT85*, *KRT35*, and *KRT31*, which in turn precede *KRT38* and the *KRTAP6-1* gene. This sequence traces a pattern of expression zones that moves progressively further from the germinal matrix as the follicle matures (Yu *et al.*, 2009; Zhou *et al.*, 2024). Genotypic variation at *KRT31* has been linked to fibre diameter. Variation at *KRT36* affects both wool fineness score and fibre diameter. Variation at *KRT38* is linked to crimp number, and variation at *KRT85* to crimp score, body size, and fibre diameter. Combined three-locus genotypes across *KRT36*, *KRT38*, and *KRT85* show a greater cumulative effect than any single locus (Sulayman *et al.*, 2018). In Gansu Alpine fine-wool sheep, three *KRT84* haplotypes generated from exonic SNPs were associated with fibre curvature, staple length and strength, mean fibre diameter, its coefficient of variation, and comfort factor (Yu *et al.*, 2024).

Characterization of structural genes in caprine genomes has historically lagged behind ovine benchmarks. Initial candidate-gene studies were largely restricted to the goat orthologues of *KRT31* and *KRT33A*, identified using sheep sequences as a scaffold (Zhou *et al.*, 2024). However, recent skin transcriptome (RNA-Seq) profiling of the high-altitude Changthangi pashmina goat has successfully identified and characterized a far wider array of actively transcribed caprine keratins. Comparative expression models against short-haired, meat-type breeds reveal significant transcriptional upregulation of *KRT25*, *KRT27*, and *KRT35* in pashmina-producing skin tissue during the active follicle growth phase (Ahlawat *et al.*, 2020). Another transcriptomic study of Changthangi skin biopsies across the telogen-

to-anagen transition identified 150 genes significantly upregulated during the active fibre growth phase, further characterizing the genes and signaling pathways underlying seasonal follicle cycling in this breed (Bhat *et al.*, 2021b). Expression profiling in goat coat hair has confirmed that *KRT33A*, is localized to cortex of cashmere fibre and shows seasonal, breed dependent expression differences, consistent with a structural role in fibre formation (Seki *et al.*, 2011).

#### *Keratin-associated protein (KRTAP) genes*

Keratin-associated proteins (KRTAPs) form an extensively diverse, and multigene superfamily. Their structural role is to establish an amorphous, highly cross-linked protein matrix that embeds the rigid keratin intermediate filaments. The KRTAP family is comprised of around one hundred members identified across mammals. These are grouped into high-sulphur (HS), ultra-high-sulphur (UHS), and high-glycine-tyrosine (HGT) classes based on amino acid composition (Bai *et al.*, 2019). Unlike the keratins, KRTAP genes are typically small, intron-less, and arranged in tight chromosomal clusters. This has made systematic cataloguing difficult and means that the KRTAP repertoire, particularly in small ruminants, remains incompletely characterized (Zhou *et al.*, 2021).

Numerous candidate-gene association studies utilizing targeted genotyping platforms (such as PCR-SSCP) have successfully mapped specific *KRTAP* variants directly to wool traits in sheep. *KRTAP28-1*, a high-sulphur KRTAP occupying the chromosomal position where the human orthologue *KRTAP25-1* would be expected but is absent in sheep, showed six sequence variants across 383 Southdown × Merino-cross lambs, with two genotypes associated with reduced mean fibre diameter (Bai *et al.*, 2019). *KRTAP26-1* variants in the same cross were linked to higher average fibre diameter, fibre curvature, and prickly factor for one variant. Another variant was linked to higher wool yield and staple length, along with reduced fibre diameter and its standard deviation, indicating that the second variant generally signifies better wool quality (Li *et al.*, 2017a). Similarly, *KRTAP20-1*, a high-glycine-tyrosine KRTAP carrying a 12-base-pair indel and several SNPs, has been associated with variation in mean fibre diameter and wool yield (Gong *et al.*, 2019).

In goats, *KRTAP* characterization has focused heavily on cashmere fibre diameter. A caprine homologue of *KRTAP28-1* was identified on goat chromosome 1 by sequence similarity to the ovine gene, with five variants detected among 385 Longdong cashmere goats (Wang *et al.*, 2020). A *KRTAP6* family homologue, *KRTAP6-5*, was likewise identified in goats for the first time by cross-species comparison with the five known ovine

*KRTAP6* genes, several of which had previously been linked to wool fibre diameter, and twelve sequence variants were detected in 300 Longdong cashmere goats (Li *et al.*, 2021). Comparative proteomic study across sheep and goat hair types has further identified *KRTAP15-1*, alongside *KRT85*, *KRTAP3-1*, and *KRTAP9-2*, as differentially expressed genes relevant to Fibre diameter determination in goats (Zhang *et al.*, 2022). The newly identified high-glycine-tyrosine gene *KRTAP22-2* was found to be associated with cashmere fibre diameter in goats (Chen *et al.*, 2023).

Genome-wide association analyses complement this candidate-gene study. A 50K SNP GWAS in 765 Chinese Merino sheep identified 28 genome-wide significant markers for fibre diameter, its coefficient of variation, fineness dispersion, and crimp, with roughly 43 percent of significant markers localized within or near genes including *YWHAZ*, *KRTCAP3*, *TSPEAR*, and *TCF9* rather than within the classical structural *KRT* or *KRTAP* clusters themselves. This distribution indicates that fibre fineness is a highly complex, polygenic trait shaped by regulatory and signaling loci operating outside core structural gene families as well as within them (Wang *et al.*, 2014). Modern fine-mapping strategies have identified specific regulatory switches in this polygenic framework. They show that a key missense mutation in *KRT74* changes the structure of cells in the inner root sheath's Huxley layer, leading to fibre refinement. This works together with upstream *EDAR* regulatory variants to control the overall density and fineness of fleece (Liang *et al.*, 2023).

#### **Growth factor and signaling pathways regulating fibre growth**

The structural synthesis of fibre intermediate filaments and matrix proteins is tightly governed by complex, epithelial-mesenchymal crosstalk within the hair follicle. Rather than functioning in isolation, these signaling pathways operate as an integrated molecular circuit that dictates the transition between active fibre production (anagen), follicle regression (catagen), and quiescence (telogen).

##### *The Wnt/beta-catenin cascade*

The Wnt/beta-catenin signaling pathway serves as the definitive biochemical switch required to initiate hair follicle morphogenesis and maintain the proliferative, active growth phase known as anagen. Upon ligand activation by upstream elements such as WNT10A and WNT10B, cytoplasmic beta-catenin is protected from degradation and translocates into the nuclei of dermal papilla cells (DPCs). Within the nucleus, beta-catenin interacts with downstream effectors such as T-cell factor (TCF) and lymphoid enhancer-binding factor 1 (LEF1)

transcription factors to drive cell cycle progression and activate developmental target genes. In sheep hair follicles, *WNT10B*, *CTNNB1* ( $\beta$ -catenin), and *LEF1* have been identified as marker genes of this pathway during the telogen-to-anagen transition (Zhang *et al.*, 2024; Li *et al.*, 2011). Endogenous inhibitors such as Dickkopf-4 (*DKK4*) restrict this pathway spatially to establish uniform, ordered spacing between developing follicles (Sick *et al.*, 2006; Sudderick and Glover, 2024). This nuclear integration directly induces the proliferation of fibre matrix cells by upregulating proliferation-related genes like *MYC* and *CCND1* (Cyclin D1), driving the downstream expression of core structural proteins that lay down the physical framework of wool and cashmere fibres (Wang *et al.*, 2022).

#### *Fibroblast growth factor (FGF5)*

*FGF5* is one of the crucial negative regulators (inhibitor) of the mammalian hair cycle (Carrion *et al.*, 2024; Higgins *et al.*, 2014). It is primarily expressed in the outer root sheath of the hair follicle during the late anagen phase, acting as a signaling molecule that triggers the transition from active growth (anagen) to the regression phase (catagen) (Carrion *et al.*, 2024). When a loss-of-function mutation or gene disruption occurs in *FGF5* gene, the hair follicles experience an abnormally prolonged anagen phase, which directly induces “long-hair” (or angora) phenotype across multiple mammalian species, including humans (Higgins *et al.*, 2014), rabbits (Xu *et al.*, 2020), and fine-wool sheep (Zhao *et al.*, 2021). In sheep, CRISPR/Cas9-mediated knockout of *FGF5* produced offspring with significantly increased wool staple length, directly confirming the gene’s inhibitory role in an economically important production trait (Li *et al.*, 2017b). In parallel with gene-editing studies, population genetics studies of fine-wool sheep have mapped natural allelic variation within the *FGF5* locus. The identification of five SNPs within fine-wool sheep *FGF5* gene revealed significant association with wool length, greasy wool weight, and growth performance. Because several of these SNPs reside in strong linkage disequilibrium, their combined genotypes are significantly associated with both mean fibre diameter and overall body weight (Zhao *et al.*, 2021). Bioinformatic analysis of the ovine *FGF5* coding sequence has further shown that the gene is evolutionarily conserved with its goat orthologue and carries several positively selected residues in its signal peptide region, consistent with a role in fibre-related adaptation (Zhang *et al.*, 2019).

In cashmere and pashmina goats, *FGF5* and its alternatively spliced, truncated isoform *FGF5S* act antagonistically to modulate hair development: full-length *FGF5* triggers the anagen-to-catagen transition

in dermal papilla cells, whereas *FGF5S* counteracts this signal to maintain active growth (He *et al.*, 2016). Correspondingly, CRISPR/Cas9-mediated disruption of *FGF5* in cashmere goats eliminates this inhibitory pathway, significantly increasing both cashmere fibre length and seasonal fleece yield (Wang *et al.*, 2016). In Tibetan cashmere goats, the mRNA expression profiles of *FGF5*, *IGF-1*, and *KAP1.4*, were examined for their relationship with down growth across different ages and high-altitude regional populations, reinforcing these genes as critical regulatory markers in specialized cashmere-producing livestock (Song *et al.*, 2023). Notably for Indian breeding programs, a localized SNP survey of *KAP1.4* across native Indian goat breeds including the Changthangi, Bakerwal, and Kargil, revealed no statistically significant association between the identified genotypes and guard-hair or down-fibre length and diameter (Shah *et al.*, 2013). This highlights that genetic markers validated in one breed or country cannot automatically be assumed to exert identical phenotypic effects within native Indian livestock.

Most notably for Changthangi-specific work, a genome-wide selection signature and network analysis of pashmina-producing Changthangi goats identified *FGF5* as one of three central hub genes, alongside *SMAD7* and *COL1A2*. These hubs are part of gene interaction networks that are highly enriched for the Wnt, BMP/TGF- $\beta$ , Hedgehog, Rap1, PI3K-Akt, and ECM-receptor interaction pathways, which collectively regulate hair follicle morphogenesis and fibre structure (Parsad *et al.*, 2025).

#### *Bone morphogenetic proteins (BMPs): Spatial patterning and differentiation*

While the Wnt cascade promotes follicle cell proliferation, Bone Morphogenetic Proteins act as antagonists that restrain this activation and enforce follicle quiescence. In Merino sheep skin, *BMP7* was identified as a key gene within the same hair follicle morphogenesis network that includes *WNT10A*, alongside developmental regulators *SOX10* and *GLI2* (He *et al.*, 2022). The balance between BMP and WNT signaling, rather than either pathway in isolation, determines the timing of the telogen-to-anagen transition: elevated *BMP6* delays this transition, while *Wnt10b* promotes it (Wu *et al.*, 2019). In cashmere goats specifically, *BMP2* expression is tightly tied to the follicle cycle stage, being highest in early anagen and undetectable by late anagen in both primary and secondary follicles (Su *et al.*, 2009).

#### *Downstream master transcription factors: HOXC13 and FOXN1*

The biochemical signals generated by upstream follicular pathways eventually converge onto master

transcription factors that physically coordinate structural gene activity. The homeobox gene *HOXC13* serves as a critical transcription factor driving the direct activation of hair keratins, engaging in functional interactions with structural targets like *KRT84* and *KRT38* (Wang *et al.*, 2018). Forkhead box transcription factors such as *FOXP1* function as terminal effectors during follicle development. In mice, *FOXP1* has been noticed to be a direct downstream regulatory target of *HOXC13*, with two genes coordinating the terminal differentiation of follicle and nail keratinocytes (Potter *et al.*, 2011). In pashmina-producing Changthangi goats, *LEF1* expression is significantly elevated alongside *HOXC13*, *FOXP1*, *GPRC5D*, and other regulator genes, running parallel to the upregulation of structural proteins *KRT84* and *KRT38*. This pattern suggests that *LEF1* contributes specifically to the development and

high productivity of secondary hair follicles by working in close concert with *HOXC13* (Ahlawat *et al.*, 2020).

### Molecular genetics of premium Indian carpet and fine-wool breeds

India's sheep population is distributed across breed groups adapted to different agro-climatic zones. Nowadays, research into their fibre genetics has transitioned from classic phenotypic and quantitative models to molecular gene mapping. Genetic evaluation of indigenous wool focuses heavily on polymorphisms and expression patterns within the keratin intermediate filaments (KRT) and keratin-associated proteins (KRTAPs). The elite Chokla and Magra breeds serve as the primary structural and transcriptional models for these investigations.



**Fig.1:** Representative Indian fibre-producing sheep and goat breeds discussed in this review. (A) Chokla, a carpet-wool sheep breed of Rajasthan. (B) Magra, a lustrous carpet-wool sheep breed of the Bikaner region, Rajasthan. (C) Changthangi, the pashmina-producing goat breed of Ladakh. Photographs in (A) and (B) are reproduced from Yadav & Singh (2016). Photograph in (C) sourced from Wikimedia.

#### Chokla

The Chokla also known locally as Shekhawati, Chhappar, and Raata Munda, is native to the Sikar, Churu, Jhunjhunu, Nagaur, Bikaner, and Jaipur districts of Rajasthan. It is identified in the foundational FAO breed monograph for India as a key carpet-wool breed of the nation. This documentation places it alongside the Nali, Marwari, Magra, Jaisalmeri, and Pugal breeds, which are part of the northwestern arid “Bikaneri” breed complex (Acharya, 1982). At the molecular level, a study examined the type I intermediate filament wool keratin gene (*KRT1.2*) in native Indian sheep breeds, including those from the Chokla and related groups. It found genetic variations at this gene location, providing an early basis for understanding keratin genes in Indian sheep (Arora *et al.*, 2008).

#### Magra

The Magra breed, centred on Bikaner district, is valued for its naturally lustrous, ultra-white, high-quality carpet wool. Real-time PCR analysis of Magra wool follicles found that the Type I hair cortex keratin *K33A* (previously *KRT1.2*) was significantly

upregulated ( $P \leq 0.05$ ) in lustrous Magra wool follicles compared to less-lustrous wool, while other keratin and keratin-associated protein genes examined were downregulated. Sequencing of the *K33A* open reading frame in Magra has mapped 17 missense mutations, 12 of which are novel single nucleotide polymorphisms (SNPs) unique to the breed. Nucleotide sequence analysis of the high glycine-tyrosine matrix family indicated that *KAP6*, *KAP7*, and *KAP8* genes in this population identified 4, 30, and 7 single nucleotide polymorphisms respectively, providing a documented, breed-specific molecular basis for the characteristic lustre of Magra wool (Kumar *et al.*, 2019).

#### Other Indian fine- and carpet-wool breeds

Related carpet-wool breeds of the northwestern “Bikaneri” complex, including the Nali, Jaisalmeri, Pugal, and Marwari, share overlapping production environments and coarse-to-medium fleece profiles with the Chokla and Magra lines (Acharya, 1982). At the finer end of the indigenous production spectrum, the Gaddi breed of the western Himalayan region remains historically significant due to its foundational

role in the development of the composite Kashmir Merino. Harnali, a synthetic fine-wool crossbred line developed by inter-se mating of Corriedale and Russian Merino with Nali sheep, has been comprehensively characterized for structural fleece metrics. Systematic genetic evaluations of wool quality parameters in Harnali, based on pedigree records of over 1000 animals, reported heritability estimates of  $0.32 \pm 0.07$  for greasy fleece weight,  $0.17 \pm 0.05$  for staple length,  $0.27 \pm 0.06$  for mean fibre diameter, and  $0.29 \pm 0.06$  for medullation percentage, using the paternal half-sib correlation method (Dahiya *et al.*, 2026). Across these regional breed groups, the broader literature follows a consistent pattern where traditional phenotypic and quantitative-genetic parameters run ahead of direct structural gene validation. This gap presents an opportunity to apply high-throughput transcriptomics and targeted candidate sequencing to investigate *KRTAP*, *KRT*, and downstream signaling pathways (*FGF5*, *WNT*) at a depth now standard in international fine-wool research.

#### *Molecular genetics of the Changthangi (Pashmina) goat*

The Changthangi (Pashmina/Chegu) goat is managed by Changpa nomadic pastoralists in the high-altitude, hypoxic zone of Ladakh. It produces pashmina which is internationally known as cashmere with an average fibre diameter of 11 to 13  $\mu\text{m}$ , representing one of the finest natural animal fibres known (Bhat *et al.*, 2021a). Due to its extreme cold adaptation and high economic value, it is the most comprehensively characterized fibre-producing breed in India.

#### *Skin transcriptome architecture and follicle regulation*

A comparative skin transcriptome analysis between the fibre-producing Changthangi and meat-type Barbari goats identified 525 significantly upregulated and 54 significantly downregulated genes in Changthangi skin. Functional enrichment maps these differentials directly to cornified envelope formation, keratinization, and hair follicle developmental pathways. Within this architecture, structural keratins *KRT84* and *KRT38* exhibit high transcript abundance, alongside significant upregulation of the *LEF1*, *HOXC13*, *FOXN1*, *GPRC5D*, *PADI3*, and *ELF5*, indicating a key regulatory role in secondary hair follicle development (Ahlawat *et al.*, 2020). Comparative transcriptomics revealed how specific signaling pathways differentiate high-altitude caprine pashmina from ovine wool (Ahlawat *et al.*, 2024). This baseline was extended by contrasting high-altitude Changthangi with low-altitude Muzzafarnagri sheep, which identified higher expression of *KRTAP6*, *KRTAP7*, *KRTAP13*, and *KRTAP2* in the fine-wool-producing Changthangi, alongside up-regulation of

melanogenesis genes (*TYR*, *TYRP1*, *DCT*, *SLC45A2*, *PMEL*, *MLANA*, *OCA2*) consistent with a role for melanin in both coat colour and UV protection at high altitude (Vasu *et al.*, 2024).

#### *Pathway crosstalk and comparative genomics*

Subsequent integrative pathway and network analyses have identified *FGF5*, *SMAD7*, and *COL1A2* as major hub genes within the WNT, BMP/TGF- $\beta$ , Hedgehog, Rap1, PI3K-Akt, and extracellular-matrix-receptor signaling networks governing follicle morphogenesis and fibre cycling (Parsad *et al.*, 2025). Furthermore, comparative genomic profiles contrasting the Changthangi with Chinese Jiangnan cashmere goats have identified key regional divergences within *KRT*, *KRTAP*, and *BMP* family gene clusters (Gong *et al.*, 2025). At the structural level, a high-coverage *de novo* whole-genome assembly and annotation for the Changthangi provide a stable reference genome for ongoing locus-specific mapping and genome-wide association studies (Bhat *et al.*, 2021a).

#### *Other caprine fibre breeds*

The Chegu (premium fine-wool model) is a fibre-producing goat breed native to the high-altitude tracts of the Western Himalayas. A microsatellite-based genetic diversity study comparing Chegu with Black Bengal goat, using heterologous microsatellite markers, reported high genetic variability in Chegu, with polymorphism information content values around 0.80, indicating that Chegu retains substantial genetic diversity useful for conservation and selection purposes (Vijh *et al.*, 2010).

#### **Summary of key genes, traits, and breeds**

Table 1 consolidates the structural and regulatory genes reviewed in section 2, 3, and 5, alongside the fibre traits, breeds and species in which each has been studied. This summary highlights two patterns discussed throughout this review: first, the concentration of variant-level, genotype-resolved findings in international sheep studies (particularly from Chinese and New Zealand groups) and in the Changthangi goat; and second, the corresponding scarcity of comparable data for Indian sheep breeds beyond Magra and Chokla.

#### **Research gaps and future directions**

A primary limitation within the surveyed molecular small ruminant literature is the deficit in systematic *KRTAP* and *KRT* structural genotyping within elite Indian carpet-wool sheep (such as Chokla and Magra) compared to international lines, alongside an asymmetrical concentration of regulatory gene pathways (*FGF5*, *WNT10B*, *LEF1*, *BMP2*) in the Changthangi goat over ovine models. Addressing these

**Table 1:** Candidate genes associated with fibre quality traits

| Gene                            | Category                           | Fibre trait(s) associated                                    | Breed(s)/ Species studied                   | Key finding / reference                                                                                                                                        |
|---------------------------------|------------------------------------|--------------------------------------------------------------|---------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>KRTAP28-1</i>                | Structural (KRTAP)                 | Mean fibre diameter                                          | Sheep (Southdown × Merino)                  | Two genotypes linked to reduced MFD (Bai <i>et al.</i> , 2019)                                                                                                 |
| <i>KRTAP26-1</i>                | Structural (KRTAP)                 | Fibre diameter, curvature, wool yield, staple length         | Sheep (Southdown × Merino)                  | Variant-specific effects; one variant marks higher wool quality (Li <i>et al.</i> , 2017a)                                                                     |
| <i>KRTAP20-1</i>                | Structural (KRTAP)                 | Mean fibre diameter, wool yield                              | Sheep                                       | 12-bp indel + SNPs associated with variation (Gong <i>et al.</i> , 2019)                                                                                       |
| <i>KRTAP28-1 (caprine)</i>      | Structural (KRTAP)                 | Cashmere fibre diameter                                      | Longdong cashmere goat                      | Five variants identified on goat chromosome 1 (Wang <i>et al.</i> , 2020)                                                                                      |
| <i>KRTAP6-5</i>                 | Structural (KRTAP)                 | Cashmere fibre diameter                                      | Longdong cashmere goat                      | First goat KRTAP6-family homologue; 12 variants (Li <i>et al.</i> , 2021)                                                                                      |
| <i>KRTAP22-2</i>                | Structural (KRTAP)                 | Cashmere fibre diameter                                      | Goat                                        | Newly identified HGT gene associated with fineness (Chen <i>et al.</i> , 2023)                                                                                 |
| <i>KRT1.2 / K33A</i>            | Structural (KRT)                   | Fibre lustre, keratin expression                             | Magra sheep                                 | Upregulated in lustrous wool; 17 missense SNPs (Kumar <i>et al.</i> , 2019)                                                                                    |
| <i>KRT1.2</i>                   | Structural (KRT)                   | General polymorphism                                         | Native Indian sheep breeds incl. Chokla     | Early molecular characterization (Arora <i>et al.</i> , 2008)                                                                                                  |
| <i>KRT84</i>                    | Structural (KRT)                   | Fibre curvature, staple length/strength, MFD, comfort factor | Gansu Alpine fine-wool sheep                | Three haplotypes with multi-trait associations (Yu <i>et al.</i> , 2024)                                                                                       |
| <i>KRT74</i>                    | Structural (KRT)                   | Fibre fineness, fleece density                               | Chinese fine-wool sheep                     | Missense mutation alters Huxley layer architecture (Liang <i>et al.</i> , 2023)                                                                                |
| <i>KRT25/27/35</i>              | Structural (KRT)                   | Fibre production (upregulated)                               | Changthangi goat                            | Elevated transcript abundance vs. Barbari (Ahlawat <i>et al.</i> , 2020)                                                                                       |
| <i>KRTAP6/7/13/2</i>            | Structural (KRTAP)                 | Fine wool production                                         | Changthangi vs. Muzzafarnagri sheep         | Higher expression in Changthangi (Vasu <i>et al.</i> , 2024)                                                                                                   |
| <i>FGF5</i>                     | Regulatory (growth factor)         | Wool/hair staple length, growth performance                  | Sheep (multiple breeds), rabbit, human      | Master negative regulator of anagen; CRISPR knockout increases staple length (Li <i>et al.</i> , 2017b; Higgins <i>et al.</i> , 2014; Xu <i>et al.</i> , 2020) |
| <i>FGF5 (5 SNPs)</i>            | Regulatory (growth factor)         | Wool length, greasy wool weight, MFD, body weight            | Fine-wool sheep                             | Combined genotypes associated with multiple traits (Zhao <i>et al.</i> , 2021)                                                                                 |
| <i>FGF5 / FGF5S</i>             | Regulatory (growth factor)         | Cashmere fibre length, fleece yield                          | Cashmere/pashmina goat                      | Antagonistic isoforms regulate anagen-catagen transition (He <i>et al.</i> , 2016; Wang <i>et al.</i> , 2016)                                                  |
| <i>FGF5, SMAD7, COL1A2</i>      | Regulatory (hub genes)             | Follicle morphogenesis, fibre structure                      | Changthangi goat                            | Central hub genes in WNT/BMP/Hedgehog network (Vasu <i>et al.</i> , 2022-23; Parsad <i>et al.</i> , 2025)                                                      |
| <i>WNT10A/10B, CTNNB1, LEF1</i> | Regulatory (WNT pathway)           | Follicle induction, telogen-anagen transition                | Sheep, Changthangi goat                     | Marker genes of canonical WNT signalling (He <i>et al.</i> , 2022; Zhang <i>et al.</i> , 2024; Ahlawat <i>et al.</i> , 2020)                                   |
| <i>BMP2, BMP6, BMP7</i>         | Regulatory (BMP pathway)           | Follicle cycling (quiescence/reactivation)                   | Sheep, cashmere goat                        | BMP-WNT balance sets telogen-anagen timing (Wu <i>et al.</i> , 2019; Su <i>et al.</i> , 2009; He <i>et al.</i> , 2022)                                         |
| <i>HOXC13, FOXN1</i>            | Regulatory (transcription factors) | Terminal keratinocyte differentiation                        | Cashmere goat, mouse, Changthangi goat      | HOXC13 upregulates KRT84/KRT38; FOXN1 is a HOXC13 target (Wang <i>et al.</i> , 2018; Potter <i>et al.</i> , 2011; Ahlawat <i>et al.</i> , 2020)                |
| <i>KAP1.4</i>                   | Structural (KRTAP)                 | Guard-hair/down-fibre length and diameter                    | Changthangi, Bakerwal, Kargil goats (India) | No significant genotype-trait association found (Shah <i>et al.</i> , 2013)                                                                                    |
| <i>IGF-1, FGF5, KAP1.4</i>      | Regulatory + structural            | Down growth                                                  | Tibetan cashmere goat                       | Age- and region-dependent expression profiles (Song <i>et al.</i> , 2023)                                                                                      |

developmental bottlenecks requires moving beyond single-candidate approaches to embrace high-coverage whole-genome resequencing across diverse indigenous Indian flocks, which will enable the comprehensive discovery of novel structural and regulatory variants and unearth population-specific signatures of selection associated with extreme environmental adaptation and elite fibre profiles. Furthermore, integrating genomics with transcriptomics, proteomics, and metabolomics will be essential to map the dynamic regulatory cascades governing hair follicle morphogenesis, cyclic transitions, and keratin synthesis. Introducing artificial intelligence and machine learning frameworks on these high-dimensional datasets will provide unprecedented potential to model complex, polygenic traits like fibre diameter, crimp, and fleece weight, establishing a directly comparable molecular atlas that translates theoretical genomics into actionable marker-assisted selection (MAS) and genomic conservation prioritization.

### CONCLUSION

Fibre quality in sheep and goats is governed by a two-tier genetic architecture comprising structural *KRT* and *KRTAP* genes physically incorporated into the Fibre cortex, and upstream regulatory networks, principally *FGF5*, *WNT/LEF1*, and *BMP* signaling pathways, that control follicle induction, cycling, and the primary-to-secondary follicle ratio from which fibre diameter ultimately derives. This architecture has been mapped in deep molecular detail within Chinese, New Zealand, and Tibetan flocks and herds, and, within India, inside the Changthangi pashmina goat, where transcriptomic profiles converge on *FGF5*, *LEF1*, and *KRT84/KRT38* as key markers of pashmina-associated follicle biology. Extending this depth of molecular characterization to India's carpet-wool and fine-wool sheep breeds, utilizing the structural and regulatory gene targets reviewed here, represents a tractable, high-value strategy to advance Indian small ruminant genomics and accelerate marker-assisted selection programs.

### REFERENCES

- Acharya RM. 1982. Sheep and goat breeds of India (FAO Animal Production and Health Paper No. 30). Food and Agriculture Organization of the United Nations.
- Ahluwat S, Arora R, Sharma R, Sharma U, Kaur M, Kumar A, Singh KV, Singh MK, and Vijn RK. 2020. Skin transcriptome profiling of Changthangi goats highlights the relevance of genes involved in Pashmina production. *Scientific Reports*, 10: 6050. <https://doi.org/10.1038/s41598-020-63023-6>
- Ahluwat S, Vasu M, Mir MA, Singh MK, Arora R, Sharma R, Chhabra P, and Sharma U. 2024. Molecular insights into Pashmina Fiber production: Comparative skin transcriptomic analysis of Changthangi goats and sheep. *Mammalian Genome*, 35(2): 160–169. <https://doi.org/10.1007/s00335-024-10040-9>
- Arora R, Bhatia S, Sehrawat A, Pandey AK, Sharma R, Mishra BP, Jain A, and Prakash B. 2008. Genetic polymorphism of type 1 intermediate filament wool keratin gene in native Indian sheep breeds. *Biochemical Genetics*, 46: 549–556. <https://doi.org/10.1007/s10528-008-9169-3>
- Bai L, Wang J, Zhou H, Gong H, Tao J, and Hickford JGH. 2019. Identification of ovine *KRTAP28-1* and its association with wool fibre diameter. *Animals*, 9(4): 142. <https://doi.org/10.3390/ani9040142>
- Bhat B, Yaseen M, Singh A, Ahmad SM, and Ganai NA. 2021b. Identification of potential key genes and pathways associated with the Pashmina Fiber initiation using RNA-Seq and integrated bioinformatics analysis. *Scientific Reports*, 11(1): 1766. <https://doi.org/10.1038/s41598-021-81471-6>
- Bhat B, Ganai NA, Singh A, Mir R, Ahmad SM, Zargar SM, and Malik F. 2021a. Changthangi Pashmina goat genome: Sequencing, assembly, and annotation. *Frontiers in Genetics*, 12: 695178. <https://doi.org/10.3389/fgene.2021.695178>
- Carrion EA, Moses MM, and Behringer RR. 2024. *FGF5*. *Differentiation*, 139: 100736. <https://doi.org/10.1016/j.diff.2023.10.004>
- Chen Z, Cao J, Zhao F, He Z, Sun H, Wang J, Liu X, and Li S. 2023. Identification of the Keratin-Associated Protein 22-2 Gene in the *Capra hircus* and Association of Its Variation with Cashmere Traits. *Animals*, 13(17): 2806. <https://doi.org/10.3390/ani13172806>
- Dahiya S, Sehgal T, Ratwan P, Dalal DS, Patil C, Sharma R, and Bangar Y. 2026. Genetic evaluation of wool quality parameters in Harnali sheep. *Indian Journal of Animal Sciences*, 96(2). <https://doi.org/10.56093/ijans.v96i2.157289>
- Geng R, Yuan C, and Chen Y. 2013. Exploring differentially expressed genes by RNA-Seq in cashmere goat (*Capra hircus*) skin during hair follicle development and cycling. *PLoS ONE*, 8(4): e62704. <https://doi.org/10.1371/journal.pone.0062704>
- Gong G, Bi S, Liang X, Ao Y, and Xu F, Sulaiman Y. 2025. Molecular mechanisms underlying cashmere quality differences between Jiangnan cashmere goats and Changthangi pashmina goats. *Frontiers in Veterinary Science*, 12: 1571803. <https://doi.org/10.3389/fvets.2025.1571803>
- Gong H, Zhou H, Bai L, Li W, Li S, Wang J, Luo Y, and Hickford JGH. 2019. Associations between variation in the ovine high glycine-tyrosine keratin-associated protein gene

- KRTAP20-1* and wool traits. *Journal of Animal Science*, 97(2): 587–595. <https://doi.org/10.1093/jas/sky465>
- He J, Zhao B, Huang X, Fu X, Liu G, Tian Y, Wu C, Mao J, Liu J, Gun S, and Tian K. 2022. Gene network analysis reveals candidate genes related with the hair follicle development in sheep. *BMC Genomics*, 23: 428. <https://doi.org/10.1186/s12864-022-08552-2>
- He X, Chao Y, Zhou G, and Chen Y. 2016. Fibroblast growth factor 5-short (*FGF5s*) inhibits the activity of *FGF5* in primary and secondary hair follicle dermal papilla cells of cashmere goats. *Gene*, 575(2): 393–398. <https://doi.org/10.1016/j.gene.2015.09.034>
- Higgins CA, Petukhova L, Harel S, Ho YY, Drill E, Shapiro L, Wajid M, and Christiano AM. 2014. *FGF5* is a crucial regulator of hair length in humans. *PNAS*, 111(29): 10648–10653. <https://doi.org/10.1073/pnas.1402862111>
- ICAR-National Bureau of Animal Genetic Resources. 2025. Breed registration cell. Retrieved July 15, 2026, from <https://nbagr.res.in/brc>
- Kumar R, Meena AS, Chopra A, and Kumar A. 2019. Keratin gene expression differences in wool follicles and sequence diversity of high glycine-tyrosine keratin-associated proteins (KAPs) in Magra sheep of India. *Journal of Natural Fibers*, 16(8): 1257–1263. <https://doi.org/10.1080/15440478.2018.1558157>
- Li S, Zhou H, Gong H, Zhao F, Hu J, Luo Y, and Hickford JGH. 2017a. Identification of the Ovine Keratin-Associated Protein 26-1 Gene and Its Association with Variation in Wool Traits. *Genes*, 8(9): 225. <https://doi.org/10.3390/genes8090225>
- Li S, Xi Q, Zhao F, Wang J, He Z, Hu J, Liu X, and Luo Y. 2021. A highly polymorphic caprine keratin-associated protein gene identified and its effect on cashmere traits. *Journal of Animal Science*, 99(9): skab233. <https://doi.org/10.1093/jas/skab233>
- Li S, Wang X, and Su R. 2022. Editorial: Sheep and goat gene exploration. *Frontiers in Genetics*, 13: 802709. <https://doi.org/10.3389/fgene.2022.802709>
- Li W-R, Liu C-X, Zhang X-M, et al. 2017b. CRISPR/Cas9-mediated loss of *FGF5* function increases wool staple length in sheep. *The FEBS Journal*, 284(17): 2764–2773. <https://doi.org/10.1111/febs.14144>
- Li YH, Zhang K, Ye JX, Lian XH, and Yang T. 2011. Wnt10b promotes growth of hair follicles via a canonical Wnt signalling pathway. *Clinical and Experimental Dermatology*, 36(5): 534–540. <https://doi.org/10.1111/j.1365-2230.2011.04019.x>
- Liang B, Bai T, Zhao Y, et al. 2023. Two mutations at *KRT74* and *EDAR* synergistically drive the fine-wool production in Chinese sheep. *Journal of Advanced Research*. <https://doi.org/10.1016/j.jare.2023.04.012>
- Namgail T, van Wieren SE, and Prins HHT. 2010. Pashmina production and socio-economic changes in the Indian Changthang: Implications for natural resource management. *Natural Resources Forum*, 34(3): 222–230. <https://doi.org/10.1111/j.1477-8947.2010.01303.x>
- Parsad R, Ahlawat S, Vasu M, Chhabra P, Sharma U, and Arora R. 2025. Genome-wide selective sweep analysis in high-altitude Changthangi goats reveals candidate genes for pashmina Fiber production. *Mammalian Genome*. <https://doi.org/10.1007/s00335-025-10155-7>
- Potter CS, Pruett ND, Kern MJ, et al. 2011. The nude mutant gene *Foxn1* is a *HOXC13* regulatory target during hair follicle and nail differentiation. *Journal of Investigative Dermatology*, 131(4): 828–837. <https://doi.org/10.1038/jid.2010.391>
- Seki Y, Yokohama M, Wada K, et al. 2011. Expression analysis of the type I keratin protein keratin 33A in goat coat hair. *Animal Science Journal*, 82(6): 773–781. <https://doi.org/10.1111/j.1740-0929.2011.00912.x>
- Shah RM, Ganai TA, Sheikh FD, Shanaz S, Shabir M, and Khan HM. 2013. Characterization and polymorphism of keratin associated protein 1.4 gene in goats. *Gene*, 518(2): 431–442. <https://doi.org/10.1016/j.gene.2012.12.021>
- Shakyawar DB, Raja ASM, Kumar A, Pareek PK, and Wani SA. 2013. Pashmina fibre: Production, characteristics and utilization. *Indian Journal of Fibre & Textile Research*, 38(2): 207–214.
- Sick S, Reinker S, Timmer J, and Schlake T. 2006. *WNT* and *DKK* determine hair follicle spacing through a reaction-diffusion mechanism. *Science*, 314(5804): 1447–1450. <https://doi.org/10.1126/science.1130088>
- Song T, Tan Y, Cuomu R, Liu Y, Ba G, Suo L, Wu Y, Cao X, and Zeng X. 2023. Polymorphisms and mRNA Expression Levels of *IGF-1*, *FGF5*, and *KAP 1.4* in Tibetan Cashmere Goats. *Genes*, 14(3): 711. <https://doi.org/10.3390/genes14030711>
- Su R, Zhang W-G, Sharma R, Chang Z-L, Yin J, and Li J-Q. 2009. Characterization of *BMP2* gene expression in embryonic and adult Inner Mongolia Cashmere goat (*Capra hircus*) hair follicles. *Canadian Journal of Animal Science*, 89(4): 457–462. <https://doi.org/10.4141/CJAS08130>
- Sudderick ZR, and Glover JD. 2024. Periodic pattern formation during embryonic development. *Biochemical Society Transactions*, 52(1): 75–88. <https://doi.org/10.1042/BST20230197>
- Sulayman A, Tursun M, Sulaiman Y, et al. 2018. Association analysis of polymorphisms in six keratin genes with wool traits in sheep. *Asian-Australasian Journal of Animal Sciences*, 31(6): 775–783. <https://doi.org/10.5713/ajas.17.0349>

- Vasu M, Ahlawat S, Chhabra P, Sharma U, Sharma R, Arora R, Mir MA, and Singh MK. 2022-23. Identification of potential miRNA-mRNA regulatory networks contributing to Changthangi sheep hair follicle development. *Journal of Livestock Biodiversity*, 12(1). <https://epubs.icar.org.in/index.php/JLB/article/view/157990>
- Vasu M, Ahlawat S, Chhabra P, Sharma U, Arora R, Sharma R, Mir MA, and Singh MK. 2024. Genetic insights into Fiber quality, coat color and adaptation in Changthangi and Muzzafarnagri sheep: A comparative skin transcriptome analysis. *Gene*, 891: 147826. <https://doi.org/10.1016/j.gene.2023.147826>
- Vijh RK, Tantia MS, Behl R, Mishra B. 2010. Genetic architecture of Black Bengal and Chegu goats. *Indian Journal of Animal Sciences*, 80(11): 1134–1137.
- Wang J, Zhou H, Hickford JGH, Zhao M, Gong H, Hao Z, Shen J, Hu J, Liu X, Li S, and Luo Y. 2020. Identification of Caprine *KRTAP28-1* and Its Effect on Cashmere Fiber Diameter. *Genes*, 11(2): 121. <https://doi.org/10.3390/genes11020121>
- Wang S, Luo Z, Zhang Y, Yuan D, Ge W, and Wang X. 2018. The inconsistent regulation of *HOXC13* on different keratins and the regulation mechanism on *HOXC13* in cashmere goat (*Capra hircus*). *BMC Genomics*, 19(1): 630. <https://doi.org/10.1186/s12864-018-5011-4>
- Wang X, Cai B, Zhou J, et al. 2016. Disruption of *FGF5* in Cashmere Goats Using CRISPR/Cas9 Results in More Secondary Hair Follicles and Longer Fibers. *PLoS ONE*, 11(10): e0164640. <https://doi.org/10.1371/journal.pone.0164640>
- Wang X, Liu Y, He J, Wang J, Chen X, and Yang R. 2022. Regulation of signaling pathways in hair follicle stem cells. *Burns & Trauma*, 10: tkac022. <https://doi.org/10.1093/burnst/tkac022>
- Wang Z, Zhang H, Yang H, Wang S, Rong E, Pei W, Li H, and Wang N. 2014. Genome-wide association study for wool production traits in a Chinese Merino sheep population. *PLoS ONE*, 9(9): e107101. <https://doi.org/10.1371/journal.pone.0107101>
- Wu P, Zhang Y, Xing Y, Xu W, Guo H, Deng F, Ma X, and Li Y. 2019. The balance of Bmp6 and Wnt10b regulates the telogen-anagen transition of hair follicles. *Cell Communication and Signaling*, 17(1): 16. <https://doi.org/10.1186/s12964-019-0330-x>
- Xu Y, Liu H, Pan H, Wang X, Zhang Y, Yao B, Li N, Lai L, and Li Z. 2020. CRISPR/Cas9-mediated disruption of Fibroblast Growth Factor 5 in rabbits results in a systemic long hair phenotype by prolonging anagen. *Genes*, 11(3): 297. <https://doi.org/10.3390/genes11030297>
- Yadav HS, Gupta R, and Arora R. 2011. Genetic variation at ASIP and KAP1.1 gene loci in indigenous sheep. *Journal of Livestock Biodiversity*, 3(1). <https://epubs.icar.org.in/index.php/JLB/article/view/157761>
- Yadav AK, and Singh J. 2016. Registered indigenous sheep breeds of India: An overview. *Indian Farmer*, 3(2): 86–103.
- Yu X, Li S, Zhou H, Zhao F, Hu J, Wang J, Liu X, Li M, Zhao Z, Hao Z, Shi B, and Hickford JGH. 2024. Spatiotemporal expression and haplotypes identification of *KRT84* gene and their association with wool traits in Gansu Alpine Fine-Wool sheep. *Genes*, 15(2): 248. <https://doi.org/10.3390/genes15020248>
- Yu Z, Gordon SW, Nixon AJ, Bawden CS, Rogers MA, Wildermoth JE, Maqbool NJ, and Pearson AJ. 2009. Expression patterns of keratin intermediate filament and keratin associated protein genes in wool follicles. *Differentiation*, 77(3): 307–316. <https://doi.org/10.1016/j.diff.2008.10.009>
- Zhang C, Qin Q, Liu Z, Xu X, Lan M, Xie Y, Wang Z, Li J, and Liu Z. 2022. Identification of the key proteins associated with different hair types in sheep and goats. *Frontiers in Genetics*, 13: 993192. <https://doi.org/10.3389/fgene.2022.993192>
- Zhang N, Wang Y, Wang J, Zhang L, Sun H, Yuan X, Wang S, Wang C, and Li X. 2024. Transcriptomic analysis of regulatory mechanisms in the telogen-anagen transition of ovine hair follicles. *BMC Genomics*, 25: 1166. <https://doi.org/10.1186/s12864-024-11059-7>
- Zhang R, Wu H, and Lian Z. 2019. Bioinformatics analysis of evolutionary characteristics and biochemical structure of *FGF5* Gene in sheep. *Gene*, 702: 123–132. <https://doi.org/10.1016/j.gene.2019.03.040>
- Zhao H, Hu R, Li F, and Yue X. 2021. Five SNPs Within the i Gene Significantly Affect Both Wool Traits and Growth Performance in Fine-Wool Sheep (*Ovis aries*). *Frontiers in Genetics*, 12: 732097. <https://doi.org/10.3389/fgene.2021.732097>
- Zhou H, Gong H, Wang J, Luo Y, Li S, Tao J, and Hickford JGH. 2021. The complexity of the ovine and caprine keratin-associated protein genes. *International Journal of Molecular Sciences*, 22(23): 12838. <https://doi.org/10.3390/ijms222312838>
- Zhou H, Bai L, Li S, Li W, Wang J, Tao J, and Hickford JGH. 2024. Genetics of wool and cashmere fibre: Progress, challenges, and future research. *Animals*, 14(22): 3228. <https://doi.org/10.3390/ani14223228>