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The Study on the Growth Pattern of Ovine Horn

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ABSTRACT

The study on the growth pattern of sheep horn is helpful to understand the development mechanism of horn, and lay foundation for the study on the molecular mechanism of horn. This study preliminarily explored the growth pattern of sheep horns by comparing the horns length and size in the small-tailed Han Sheep and Dorper×small-tailed Han sheep with different age. Sheep horn growth pattern can be divided into three phases: accelerated growth phase, decelerated growth phase, and stable growth phase. Generally speaking, different species and gender of sheep have different rates of horn growth. Average growth rate of the male small-tailed Han sheep horns was 4.93 cm/month during the accelerated growth phase, decelerating to an average rate of 2.90 cm/month and remaining at about 2.98 cm/month; average growth rate of male Dorper×small-tailed Han sheep horns in the accelerated growth period was 2.51 cm/month, and the subsequent deceleration growth to an average speed of 0.87 cm/month; average growth rate of female small-tailed Han sheep horns was 1.36 cm/month during the accelerated growth period, decelerating to an average rate of 0.27 cm/month and maintaining a growth rate of about 0.10 cm/month; average growth rate of female Dorper×small-tailed Han sheep horns was 0.96 cm/month during the accelerated growth period, and subsequently decelerated to an average rate of 1.17 cm/month. For Small-tailed Han Sheep, compared with males, female sheep have a slower overall growth rate of the horns and are relatively later in growth phase. For Dorper×small-tailed Han sheep, the growth phases of male and female are generally the same with small-tailed Han sheep. The horn growth rate of male Small-tailed Han sheep was significantly faster than that of male Dorper×small-tailed Han sheep. The basal perimeter has a similar growth pattern of distance between base and top. This study preliminarily revealed the growth pattern of sheep horn, and found that sheep horn is segmented development, which provides evidence for stage selection when explore the key genes of horn growth, and also provides a basis for future hornless breeding.

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Authors' Contribution
ZP and MC conceived and designed the study. JT, HW and FL were responsible for sample collection. XZ, JS, HL, and XH conducted bioinformatic analysis. XZ, ZP and JS wrote the initial draft of the manuscript. ZP, MC, XZ and SL revised the manuscript. All coauthors contributed to the final manuscript.

Key words
Growth pattern, Small tailed Han sheep, Horn growth, Dorper× small-tailed Han sheep

INTRODUCTION

With the continuous development of the economy and society, people's living standards are getting higher and higher, leading to significant changes in consumption behavior. People are increasingly concerned with dietary health and improving their daily eating habits. At present, lamb is becoming increasingly popular among consumers, and it's delicious taste and rich nutritional value are generally recognized. As the market demand for lamb increases each year, market prices are also rising. Therefore, producing more and higher quality lamb is now a social demand.

Successive environmental and behavioral changes have led to the development of various appendages in ruminant animals. Cranialf appendages, such as bovids' bony horns, are among the acquired structures during their evolution. Sheep, as a member of the bovid family (Johnston *et al*., 2013; Robinson *et al*., 2006), exhibit similar adaptations, yet the genetic mechanisms underlying horn formation and evolution remain inconclusive (Chen *et al*., 2019). Archaeological discoveries have revealed the existence of sheep horns since the Bronze Age, dating back 1500-2500 years ago, indicating an ancient origin of this trait (Cai *et al*., 2011). However, the lack of adequate sample sizes and incomplete studies hinder the exploration

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of the evolutionary processes based solely on appearance. Recent research has identified the multiple phenotypes of sheep horns, which include polled, two-horned, and multi-horned phenotypes. Sheep with more than two horns, up to nine, but typically four, are referred to as four-horned sheep (Dýrmundsson, 2005). Multi-horned sheep are considered an ideal model for studying the genetic regulation of sheep horns. Zhao *et al*. (2010) constructed a phylogenetic tree that included four domestic and wild sheep species, finding that multi-horned sheep were more closely related to domestic sheep than to wild sheep. He *et al*. (2016) analyzed the SNP loci of the four-horned trait in three Chinese sheep breeds, concluding that the four-horned phenotype exhibited greater dominance in inheritance than the two-horned phenotype. This phenotype was regulated by multiple loci; some dictated the presence or absence of horns, while others determined the number of horns (Alderson. 1992). In a study by Guo *et al*. (2021), they sequenced the whole genome of 120 fine-fleeced sheep and identified genes related to horn formation, namely *FRYL*, *FDX*, *RIC3*, *GDNF-AS1*, and *GRM4*. They discovered that *FRYL*, which affects wool quality, is a potential candidate gene regulating the relationship between wool traits and horn type (García-Gámez *et al*,. 2011; Zhang *et al*., 2013), implying that there may be a potential physiological correlation between wool traits and horn type (Guo *et al*. 2021). Sim and Coltman (2019) identified two motifs in the domestic sheep genome associated with horn length that were localized to *GFRA2* and *FIGNL2*. Montgomery *et al*. (1996) localized domesticated sheep to chromosome 10 in 1996, while a decade later, Beraldi *et al*. (2006) located the polled phenotype of wild sheep (Soay sheep) to this same chromosome. Johnston *et al*. (2011) conducted a GWAS and identified the insulin-like/relaxin family peptide receptor 2 (RXFP2) genotype present in this region, which directly affects horn length (Dominik *et al*., 2012; Wiedemar and Drögemüller, 2015). Furthermore, Pan *et al*. (2018) conducted an association study on a semi-wild sheep flock (steppe Tibetan sheep) and found that the *RXFP2* gene affected the size and shape of horns. Recently, the *RXFP2* gene has been shown to regulate both the size and shape of sheep horns, as the deformed horn phenotypes of Soay and wild bighorn sheep were localized to this gene (He *et al*., 2021; Johnston *et al*., 2011). Despite its importance, few studies have investigated the growth pattern of sheep horns. A study conducted on horn growth in the Qilian mountains demonstrated that the use of horn formation time to determine the absolute age of sheep is a simple, fast, and accurate method, and that the growth process and shape changes of sheep horns follow regular patterns (Mi *et al*., 2012; Wang *et al*., 2012).

Horns serve as the primary defensive weapons of sheep and also play a crucial role in sexual selection. However, in the production process, horns are prone to causing injuries to both livestock and humans, thereby negatively affecting wool quality, sheep health, and production efficiency (Brenneman *et al*., 1996). Chinese Hu sheep, on the other hand, are typically polled and exhibit high production performance. They are easy to domesticate to suit human needs, and the polled trait also eliminates the risk of damaging livestock products. Chinese Hu sheep, therefore, provide an excellent example of the polled trait in production.

Although artificial dehorning has been widely used in animal husbandry, it is both contrary to animal welfare and wasteful of human resources, and it was expected that molecular breeding would improve the rate of sheep polled with the aim of achieving a more manageable flock (Wiedemar and Drögemüller, 2015). However, the molecular mechanism of sheep horn development is still unclear, and the study of the growth pattern of sheep horns can help to understand the developmental process and growth mechanism of this organ, and provide a theoretical basis for the later study of the molecular mechanism of sheep horn formation, which will provide a reference basis for future sheep breeding.

MATERIALS AND METHODS

Selection of experimental individuals

This study selected a total of 127 small-tailed Han sheep and Dorper×small-tailed Han sheep from the breeding farm of Shunyuan Farm, Lanling County, Shandong Province. The sample included 89 small-tailed Han sheep of varying ages: 18 were 1 month old, 17 were 2 months old, 10 were 3 months old, 7 were 4 months old, 13 were 6 months old, 14 were 12 months old, and 10 were 36 months old. The remaining 38 Dorper×small-tailed Han sheep were selected at different ages, including 5 that were 2 months old, 15 that were 3 months old, 8 that were 4 months old, 7 that were 6 months old, and 3 that were 12 months old. Details of the distribution of female and male samples are presented in Table I.

Collection of sheep horn data

Distance between base and top: The arc distance between the base point of the longitudinal rib on the back of the corner base and the corner end.

Basal perimeter: The perimeter around the corner base passing through the base of the longitudinal rib on the back of the corner (Zhong, 2007).

The measurement method entailed direct caliper measurements of the straight-line distance, while the arc distance was measured using a uniform thin line.

Table I. Experimental samples selection.

Breed	Sex	Age/(Month)	Sample size	Sum
Small-tailed Han sheep	Male	1	10	
		2	7	
		3	5	
		6	6	
		12	7	35
	Female	1	8	
		2	10	
		3	5	
		4	7	
		6	7	
		12	7	
		36	10	54
Dorper × small-tailed Han sheep	Male	2	3	
		3	10	
		4	5	
		6	4	
		12	3	25
	Female	2	2	
		3	5	
		4	3	
		6	3	13

The completed thin line was then straightened and measured with calipers. As both sides of the horns of a given small-tailed Han sheep and Dorper×small-tailed Han sheep had nearly identical measured values, only unilateral horn data were measured for statistical analysis.

The mean ($\bar{x}$) and standard deviation (SD) of each dataset for sheep of varying ages were calculated from the measured values. The average growth rate of horns was determined using the mean distance between the horn base and top for two adjacent months of age. The average growth rate of horns was computed as follows: (mean distance between the horn base and top for older months – mean distance between the horn base and top for younger months)/(older months – younger months), where units are in cm/month. The growth curve was utilized to examine the horn's growth process in sheep.

RESULTS

Growth of the horns in male small-tailed Han sheep

Table II depicts the differences in horn distance between base and top and horn basal perimeter of male small-tailed Han sheep in which the adult horn distance between base and top averaged 39.86±9.686 cm, with a corresponding horn basal perimeter of 23.29±4.821 cm. The average horn end distance and the average horn growth rate were divided into three periods: Accelerated growth (1 month-3 months of age), decelerated growth (3 months-6 months of age) and stable growth (6 months-12 months of age). The scatter diagram in Figure 1A shows that the average growth rate of the horns of male small-tailed Han sheep continued to increase from 1 month to 3 months of age, and the average growth rate of the horns was 4.93 cm/month, and the perimeter of the horn base increased at a rate of 4.67 cm/month, so it is called the accelerated growth period. During the decelerated growth period of male small-tailed Han sheep, the average growth rate was 2.90 cm/month and the growth rate of horn basal perimeter was 0.56 cm/month. From 6 to 12 months of age, the horn growth rate tended towards stability, with an average growth rate of 2.98 cm/month and a horn basal perimeter growth rate of 1.27 cm/month. Though horn growth persisted, it slowed relative to the preceding period, resulting in a stable growth phase.

Table II. Horn index values of small-tailed Han sheep at different months of age.

Sex	Age/ Month	Sample size	Distance between base and top/(cm)	Basal perimeter/(cm)
			$\bar{x}$±SD	$\bar{x}$±SD
Male	1	10	3.45±1.606	5.40±1.647
	2	7	5.73±4.006	6.90±4.375
	3	5	13.30±3.667	14.00±3.000
	6	6	22.00±4.561	15.67±2.338
	12	7	39.86±9.686	23.29±4.821
Female	1	8	0.58±0.645	1.26±1.422
	2	10	1.24±1.326	2.30±2.052
	3	5	2.40±1.673	4.20±1.789
	4	7	4.17±2.282	5.36±2.839
	6	7	7.36±4.625	7.29±3.039
	12	10	9.00±3.528	9.00±1.491
	36	10	11.40±2.271	9.00±1.491

Growth of the horns in female small-tailed Han sheep

Table II displays the differences in horn distance between base and top and horn basal perimeter of female small-tailed Han sheep. Horn growth of female sheep follows the same pattern as the male throughout the sheep's life cycle, with adult horn distance between base and topaveraging 11.4±2.271 cm, and a horn basal perimeter of 9±1.491 cm. Additionally, based on the mean horn distance

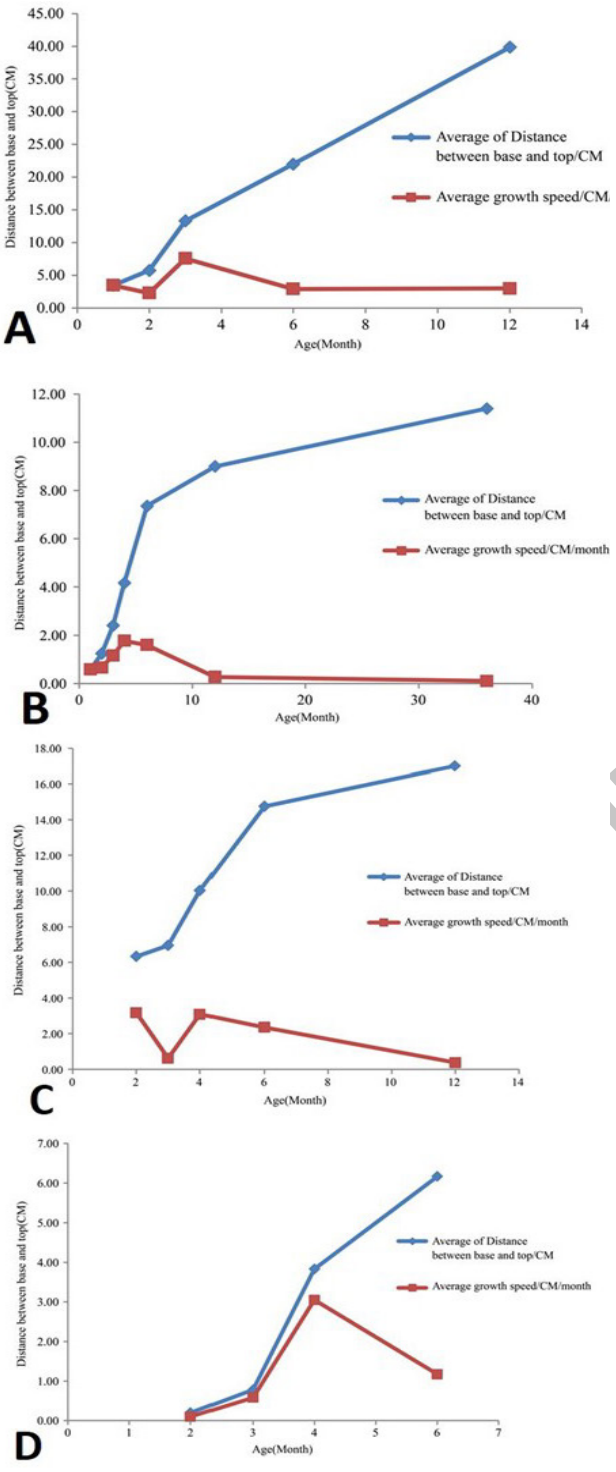

Fig. 1. Average of distance between base and top and average growth speed of horns of male (A) and female (B) small-tailed Han sheep and male Dorper×small-tailed Han sheep (C) and female Dorper×small-tailed Han sheep (D) at different months of age.

between base and top and average horn growth rate, we grouped horn growth into three categories: The accelerated growth phase (1-6 months of age), decelerated growth phase (6-12 months of age), and stable growth phase (12-36 months of age). According to Figure 1B, the average growth rate of female small-tailed Han sheep horns rose continually from 1 to 6 months of age, with the most rapid growth rate being 1.36 cm/month, alongside a growth rate of 1.22 cm/month of horn basal perimeter, marking the accelerated growth phase. During the decelerated growth phase, the average growth rate and the growth rate of horn basal perimeter were 0.27 cm/month and 0.29 cm/month, respectively. From 12 to 36 months of age, horn growth stabilized, with an average growth rate of 0.10 cm/month and a horn basal perimeter growth rate of 0.00 cm/month. Although the growth pattern of female small-tailed Han sheep horns was akin to that of males, their horn length was shorter, and they generally had slower growth rates and delayed development periods.

Growth of the horns in male Dorper×small-tailed Han sheep

Horn growth initiated from the frontal horn prominence, then gradually expanded outward from the top of the head, forming an oblique backward circular arc. Compared to small-tailed Han sheep, the male Dorper×small-tailed Han sheep's horns possess higher curvature, rougher surface, and slightly rotated downward tips. Furthermore, an increase in sheep age corresponded with a progressively apparent tendency for horns to extend downwards.

Table III. Horn index values of Dorper×small-tailed Han sheep at different months of age.

Sex	Age/ Month	Sample size	Distance between base/ (cm)	Basal perimeter/ (cm)
			$\bar{x}$±SD	$\bar{x}$±SD
Male	2	3	6.33±7.572	6.67±5.508
	3	10	6.95±6.496	6.80±5.203
	4	5	10.04±7.450	9.50±5.831
	6	4	14.75±4.856	14.00±2.449
	12	3	17.00±6.557	13.33±2.309
Female	2	2	0.20±0.000	0.50±0.141
	3	5	0.78±1.242	1.40±2.014
	4	3	3.83±3.253	4.67±3.512
	6	3	6.17±5.299	4.33±2.887

Table III illustrates the differences in horn distance between base and top and horn basal perimeter of male Dorper×small-tailed Han sheep. The adult horn distance

between base and top averaged 17±6.557 cm, while the corresponding horn basal perimeter was 13.33±2.309 cm. Male Dorper×small-tailed Han sheep experienced an average horn growth rate of 2.51 cm/month and a horn basal perimeter growth rate of 2.38 cm/month between 0 and 4 months of age. At 12 months of age, the average horn growth rate and the growth rate of horn basal perimeter were 0.87 cm/month and 0.48 cm/month, respectively, indicating a decelerated growth period. Although the small sample size prevented the stable growth period for male Dorper×small-tailed Han sheep from being observed, it can be hypothesized that such a phase would occur after the 12-month mark, following a growth pattern similar to small-tailed Han sheep. The development phases of male Dorper×small-tailed Han sheep, including the accelerated growth and decelerated growth periods, are more conveniently observed in Figure 1C.

Growth of the horns in female Dorper×small-tailed Han sheep

Table III illustrates the changes in horn distance between base and top and horn basal perimeter of female Dorper×small-tailed Han sheep. The average growth rate for their horns increased gradually from 0 to 4 months of age, reaching an average growth rate of 0.96 cm/month and a horn basal perimeter growth rate of 1.17 cm/month, signifying an accelerated growth period. From 4 to 6 months of age, the average growth rate decelerated to 1.17 cm/month, indicating a period of slowed growth. Although the small sample size precluded the observation of a stable growth period for female Dorper×small-tailed Han sheep, it can be inferred that their stable growth period commences after 6 months of age, with a growth pattern closely resembling that of Small-tailed Han Sheep. In comparison to male Dorper×small-tailed Han sheep, female counterparts possessed smaller horns, yet the progression periods were generally synchronous. Figure 1D conveniently depicts the accelerated and decelerated growth phases of female Dorper×small-tailed Han sheep's horns.

Comparative analysis of horn growth rate of different sheep breeds

Figure 2 visually displays the horn growth rate of small-tailed Han sheep and Dorper×small-tailed Han sheep in various stages. The results reveal that, within the same gender group, small-tailed Han sheep tend to exhibit a higher horn growth rate than that of their Dorper×small-tailed Han sheep counterparts, while within the same breed, males possess a greater growth rate compared to females. During the accelerated growth period, the average growth rate of male small-tailed Han sheep horns was 4.93 cm/month, 2.90 cm/month from the decelerated growth period, and 2.98 cm/month from the stable growth period. The average growth rate of male Dorper×small-tailed Han sheep horns was 2.51 cm/month in the accelerated growth period and 0.87 cm/month during the decelerated growth period. In terms of females, the average growth rate of Small-tailed Han sheep horns was 1.36 cm/month in the accelerated growth period, 0.27 cm/month during the decelerated growth period, and 0.10 cm/month during the stable growth period, whereas the average growth rate of female Dorper×small-tailed Han sheep horns was 0.96 cm/month during the accelerated growth period and 1.17 cm/month for the decelerated growth period.

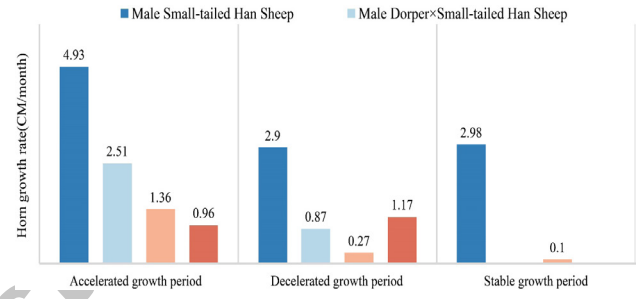

Fig. 2. Horn growth rate of small-tailed Han sheep and Dorper×small-tailed Han sheep in different periods (cm/month).

DISCUSSION

Research suggests that the phenomenon of fast-growing and curved horns in male sheep is attributed to natural and sexual selection, indicative of group competition. Male sheep with these traits exhibit a higher chance of survival as they are more predator-resistant, better at defense against attackers, and more successful in mating. Regarding genetics, the presence or absence of horns in sheep is influenced by three complex alleles located on a single locus- the dominant polled gene H, the recessive horned gene H', and the ram that expresses the horned gene h when in the presence of androgens. H is incompletely dominant to H' and h, while H' incompletely dominates H (Hu, 2019). Although the genetic mechanism of sheep horns is not fully understood, current studies suggest two loci, the polled locus on chromosome 10 and the polyhorn locus on chromosome 2 (He *et al*., 2021), which regulate this trait. Researchers have associated the *RXFP2* gene with the presence or absence of the horn trait in sheep, as per Kijas *et al*. (2012). Wang *et al*. (2014) furthermore identified *RXFP2* as a gene linked with horn deficiency in Sunit sheep through genome-wide selective signaling analysis. Besides, *RXFP2* is highly expressed

in horn tissue, according to Wang *et al*. (2019), with its protein binding with ligand relaxin and regulating horn development, while a decline in RXFP2 inhibits bony horn core formation. Nevertheless, the EEF1A1-like insertion of 1833 bp in the flanking 3' region of *RXFP2*, described by Wiedemar and Drögemüller (2015), may be associated with the polled phenotype in sheep. However, subsequent researchers have refuted the notion that this insertion alone determines polled in sheep (Lühken *et al*., 2016; Simon *et al*. 2022; Kalds *et al*., 2022). To date, no concrete evidence exists to support any such linkage between EEF1A1-like insertion and the polled phenotype. Although *RXFP2* has a significant correlation to horn size and shape in sheep, the pathway underlying the divergence in phenotype remains unclear. To shed light on the matter, Pan *et al*. (2020) examined the *INSL3* gene's tissue expression patterns in sheep. The findings suggested that male sheep exhibited greater *INSL3* expression in their horn tissue than female sheep. Notably, researchers identified four SNPs potential loci that were significantly distributed in horn groups, which suggested a possible link between *INSL3* and horn growth differences between male and female sheep. Hence, *INSL3* may have a role in determining the presence or absence of horns. According to Greyvenstein *et al*. (2016), the 4-horn trait in sheep can be traced back to the 131-133 Mb region of chromosome 2. The study highlighted the HOXD gene cluster as a probable causal variant gene in 4-horned sheep. Similarly, Ren *et al*. (2016) localized the multi-horned trait QTL segment adjacent to the HOXD gene cluster on chromosome 2, designating it as a possible candidate gene for the 4-horned sheep trait (Sun *et al*., 2021). In a hermaphroditic population of Dall sheep, Hoefs *et al*. (1982) observed horn aberrations in individual specimens. Meanwhile, Chen (2016) deployed iTRAQ protein expression profiling to identify differential proteins in two-horn, aberrant horn, and polyhorn combinations and outlined potential signaling pathways that influence the development of horn aberrations. Zhou *et al*. (2021) discovered through past research that genes like *OTOP3*, *OLIG1*, *RXFP2*, *B3GLCT*, *SOX10*, *SNAI1*, and *TFAP2A* could modulate neural crest cells differentiation and migration. As these cells play a critical part in regulating sheep horn growth, the authors suggested that the neural crest cell signaling pathways during craniomaxillofacial skeleton development might be closely tied to sheep horn development. Furthermore, Kijas *et al*. (2016) noted a significant relationship between sheep horn and eyelid development, highlighting that eyelid deformities could influence horn development. Wang (2019) found that highly expressed sheep horn tissue-specific genes are recruited from bone, skin, testis, and brain tissues, implying that sheep horn development is reliant on bone, skin, and nerve tissue development. In addition to dietary considerations, LaSharr *et al*. (2019) suggested that factors such as flock migration, hunting, flock density, and diseases can all impact horn size. Morrissey *et al*. (2021) also concluded that when hunting pressure intensifies, sheep horn growth tends to decrease. These findings highlight the complexity involved in investigating the genetic mechanisms underlying sheep horns.

Over time, sheep farming has grown in scale, eliminating the need for sheep to defend themselves from predators and compete for breeding rights. The utilization of sheep horns in combat might adversely affect livestock product quality, such as meat and fur. With large-scale farming, horns prove to be a disadvantage, and breeding new sheep breeds has become a priority for breeders. Although the molecular mechanisms underlying sheep horn development remain uncertain, this study suggests that segmenting sheep horn growth at different periods could reveal the essential genes that control this process. As a result, this experiment delivers crucial data for studying sheep horn growth mechanisms, along with a reference point for future molecular investigations and gene selection in sheep breeding.

CONCLUSION

The study of sheep horn growth across both genders indicated that various breeds and sexes undergo unique and shared growth patterns. Typically, sheep horn development can be divided into three stages: An accelerated growth period, a decelerated growth period, and a stable growth period. The speed of sheep horn growth differs across various breeds, with male horns generally growing at a faster rate and to larger sizes than females during the same time frame. Comparatively, female small-tailed Han sheep exhibit generally slower horn growth rates during the lagging development period than their male counterparts. In the case of Dorper×small-tailed Han sheep, males and females typically undergo the same growth stages; however, the latter's horns tend to have a smoother surface and curve less drastically.

DECLARATIONS

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Statement of conflict of interest

The authors have declared no conflict of interest.

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