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ORIGINAL ARTICLE

Evolution and Expression of *S100A7* Gene in Vertebrates

Husile Gong[1,4] · Ding Yang[3] · Yunxia Qi[3] · Jianghong Wu[2,3] · Wenguang Zhang[4]

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Abstract

The skin is the primary barrier between the internal organs of an organism and the environment, and it provides protection from ultraviolet (UV) radiation. According to the nocturnal bottleneck hypothesis, ungulates might have traversed to the grasslands and were exposed to UV radiation subsequent to the reduction in predation pressure. UV light exposure might have increased the *S100A7* expression. In order to test whether the UV radiation is associated with the selection pressure on *S100A7*, we acquired the complete *S100A7* DNA sequences from each of 42 vertebrate species. The results suggested that the evidence of diversifying selection in *S100A7* occurred at the end of Mesozoic era, and the site of positive selection was observed in the branch of Artiodactyla (even-toed ungulates). In addition, we found that the transcription level of *S100A7* in cashmere goat skin correlates with UV radiation. Our results indicated that *S100A7* plays a role in the signaling between the skin genes and UV radiation during evolution.

Introduction

Several *S100* genes are expressed in epithelial tissues and are involved in the epithelial defense mechanism. The *S100A7* expression was previously associated with psoriasiform hyperplasia (Al-Haddad et al. 1999). The structure and function of mouse *S100A7* are similar to those of human *S100A7* (Webb et al. 2005). The expression level of S100A7 protein is associated with the differentiation degree of keratinocytes (Martinsson et al. 2005). Moreover, *S100A7* participates in the differentiation of mammary epithelial cells (Vegfors et al. 2012).

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✉ Jianghong Wu
wujianghonglong@126.com

✉ Wenguang Zhang
nmbiatcg@aliyun.com

Extended author information available on the last page of the article

The structures of skin and appendages are maintained by the differentiation of keratinocytes (Eckhart et al. 2013).

Research demonstrated that the color of human skin experienced adaptive evolution in association with the UV radiation dose that penetrates into the epidermis (Jablonski and Chaplin 2000). UV light increased the expression level of human epidermal *S100A7* (Nuzzo et al. 2000). Previous studies of our lab found that *S100A7* is highly expressed in the normal cashmere goat skin based on transcriptome analysis (unpublished). However, the normal human skin rarely expresses *S100A7*, whereas altered expression occurs in the abnormal epidermis (Alowami et al. 2003; Moubayed et al. 2007). Changes in gene expression are considered as the genetic basis for the phenotypic variations among species (Brawand et al. 2011). The nucleic acid substitutions may affect the affinity of transcription factor during the regulation process and in turn thus the expression level of a gene (Inoue et al. 1997).

We believe that *S100A7* is responsible accounts for the variations in the skin during species divergence. We analyzed the molecular evolution across vertebrates and applied the tool codeml in phylogenetic analysis by maximum likelihood (PAML) package to detect the selection pressure on the various lineages of vertebrates. Results demonstrated that the site of positive selection was observed in the branch of Artiodactyla. Hence, we selected cashmere goat as a model to investigate the expression pattern of *S100A7* in the skin and to analyze the association between the expression levels of *S100A7* gene in cashmere goat skin and UV radiation through seasonal variation over one-year cycle.

Materials and Methods

Sequence Acquisition

To analyze the molecular evolution of *S100A7* gene in vertebrates, we downloaded the *S100A7* sequences of vertebrates, which are available online. *S100A7* gene (alias: PSOR1; $n = 39$) sequences, of species, namely *Alligator sinensis, Aquila chrysaetos, Bos taurus, Bubalus bubalis, Camelus ferus, Capra hircus, Ceratotherium simum, Cercocebus atys, Charadrius, Chrysemys picta, Condylura cristata, Cuculus canorus, Equus caballus, Geospiza fortis, Gorilla gorilla, Haliaeetus leucocephalus, Homo sapiens, Macaca mulatta, Manis javanica, Mus musculus, Myotis brandtii, Myotis davidii, Myotis lucifugus, Nomascus leucogenys, Ovis aries, Pan paniscus, Pantholops hodgsonii, Phascolarctos cinereus, Pongo abelii, Pteropus alecto, Pygoscelis adeliae, Rana temporaria, Rattus norvegicus, Sorex araneus, Sus scrofa, Trichechus manatus, Tupaia chinensis, Ursus maritimus,* and *Vicugna pacos* were obtained from GenBank. The Ensembl predicted *S100A7* sequences of *Loxdeonta africana, Lesser hedgehog,* and *Ailuropoda melanoleuca*, which were retrieved from published genomes (https://www.ensembl.org) (Supporting file 1).

Sequence Alignment and Phylogenetic Analyses

These *S100A7* sequences of 42 vertebrate species were studied based on the coding sequences. These 42 species belong to four classes and 20 orders. ClustalW (Larking et al. 2007) and MEGA 6 (Tamura et al. 2013) were used to perform multiple sequence alignments. In this study, the species tree was constructed based on the methods described in previous publications (Murphy et al. 2001; Murphy et al. a; Meyer et al. 2003; Zhang et al. 2014) (Fig. 1).

Molecular Evolution Analyses

To estimate the rates of synonymous and nonsynonymous substitutions (*dS* and *dN*, respectively) and the *dN/dS* ratio (omega, ω), the codeml program in PAML 4 (Yang 2007) was used. Positive selection is evident where $\omega > 1$, neutral evolution where $\omega = 1$, and purifying selection where $\omega < 1$ (Nei et al. 2000). The details of parameter settings to perform codeml program were obtained from a previous study by Wu et al. (2014.

First, the model M0 (one ratio) was used to compute global *ω value* of 42 vertebrate species. Two different models of M7 (beta) and M8 (beta and *ω*) were used to test positive selection. To investigate whether the selection pressure on each branch was consistent, we used the free-ratio model to estimate the various substitution rates of each branch of the species tree. Then, the two-ratio model was used to estimate the *ω value* of specific to interested lineage. Furthermore, branch-site model A was used to estimate the sites that have evolved under positive selection in a specific lineage.

Finally, to visualize the variation in *ω* value along *S100A7*, the software SWAAP1.0.2 (Pride 2000) was used to perform the sliding window analysis. We set the window size at 60 bp (20 codons) and the step size at 9 bp (3 codons). The values were estimated by following Nei and Gojobori method (Nei et al. 1986).

Monthly Analyses of Transcription of S100A7 In Cashmere Goat Skin

The reads per kilobase of transcript per million mapped reads (RPKM) value of *S100A7* was obtained from the skin transcriptome data of cashmere goats ($n = 3$) every month for one year (unpublished Wu et al.). Then, we investigated whether a relation exists between the UV exposure and transcription level of *S100A7*. As the experimental goats were located at Tumed Zuoqi, Hohhot, China (N40°30′22.89″E110°54′47.29), the time series UV index data at 40 degrees north latitude proximity (from Dec 1, 2014 to Dec 31, 2015) were downloaded from the Tropospheric Emission Monitoring Internet Service (https://www.temis.nl/index.php). We used the Pearson method to analyze the correlation coefficients between the gene transcription and the UV index data.

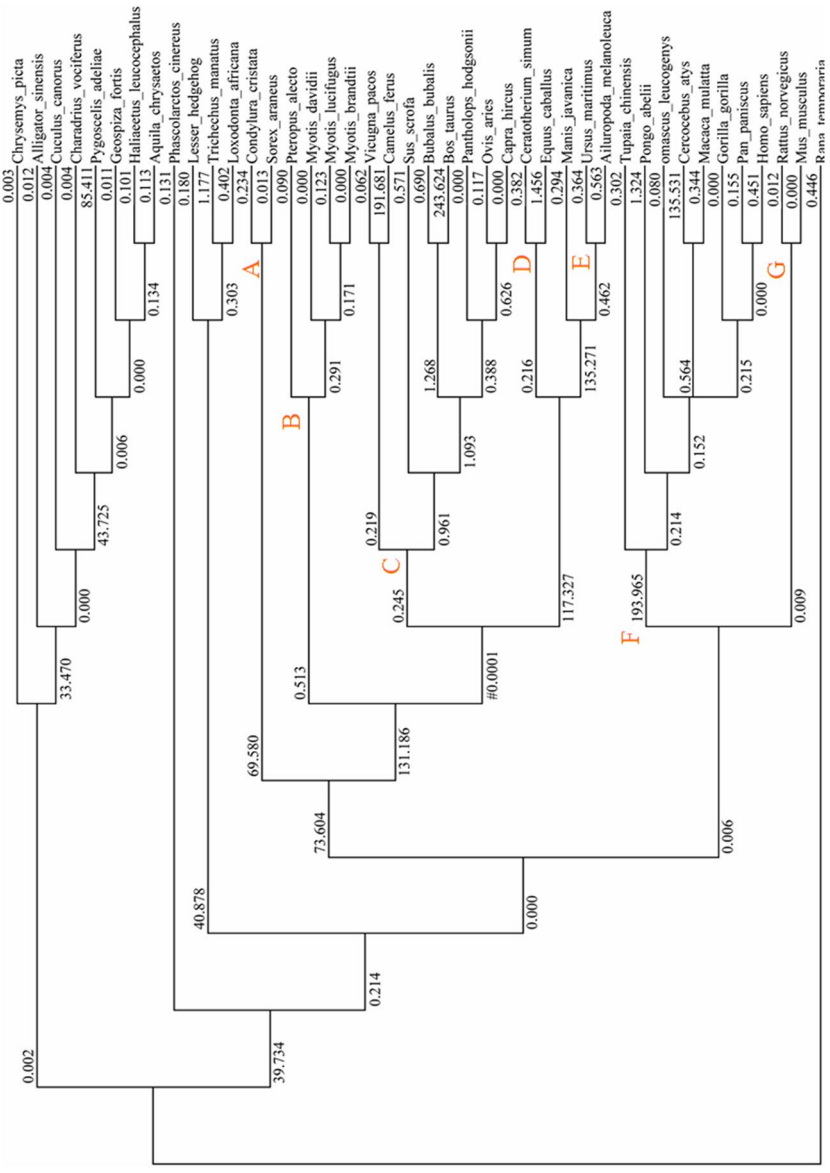

Fig. 1 Estimated ω values of distinct evolutionary lineages of vertebrates, using the phylogenetic tree topology of previous publications. The ω values of individual branches according to the free-ratio model

Results

Variation in the Rate of Molecular Evolution of S100A7 Gene

In this study, the global ω value based on the one-ratio model demonstrated that the species were under purifying selection ($\omega = 0.285$). To investigate whether the selection pressure on each branch was consistent, we utilized the free-ratio model to estimate the various ω values for each branch of the phylogenic tree. The result indicated that the free-ratio model had better fitting effect than that by the one-ratio model (Table 1; $\chi^2 = 166.86$, $P = 0$ with $df = 79$), which suggested that the ω values of *S100A7* varied among the lineages (Fig. 1). We used the two-ratio model to test the adaptive selection of each lineage separately (at least two genera) on the order of taxonomic ranks. Our results of the two-ratio model demonstrated that elevated ω values were not observed for the ancestral branches. The ω values of Primates and Chiroptera (branches marked as F, and B in Fig. 1) were compared to those of their corresponding background branches (Table 1). Our results indicated that the Artiodactyla branch (branches marked as C in Fig. 1) exhibited a significantly higher ω value compared with its corresponding background branch indicating that the selection pressures changed at the early stages of Artiodactyla divergence. However, the two-ratio model was significantly better than the one-ratio model (P = 0) (Table 1) for the ancestral branch of Rodentia (the branch marked as G in Fig. 1). The magnitude of estimated ω value of the branch of Rodentia lineage was lower than that of the other lineages (0.0089 vs. 0.3041, Table 1). These results indicated that the selection pressure on *S100A7* varied across mammal lineages.

Positive Selection of S100A7

We used the site-specific models to estimate the positive selection sites in *S100A7*. Human *S100A7* was used as a reference sequence. The results revealed that the

Table 1 Results of two-ratio model tests to estimate the selection pressure on *S100A7* in vertebrates

Model	Np	l	ω_0 [a]	ω [a]	Model compared	$2\Delta l$	P
A. One ratio: ω_0	82	− 8702.47	0.28516	$= \boldsymbol{\omega_0}$			
B. Free ratio	161	− 8619.04			B versusA	166.86	0
C. Two ratios: ω_0, ω_A	83	− 8702.43	0.2868	0.2657	C versusA	0.08	0.7772
D. Two ratios: ω_0, ω_B	83	− 8702.23	0.2896	0.2473	D versusA	0.48	0.488
E. Two ratios: ω_0, ω_C	83	− 8696.75	0.2563	0.4809	E versusA	11.44	0.001
F. Two ratios: ω_0, ω_D	83	− 8701.64	0.2794	0.4129	F versusA	1.66	0.1976
G. Two ratios: ω_0, ω_E	83	− 8700.81	0.2776	0.5200	G versusA	3.32	0.0684
H. Two ratios: ω_0, ω_F	83	− 8701.42	0.2755	0.3880	H versus A	2.1	0.147
I. Two ratios: ω_0, ω_G	83	− 8686.63	0.3041	0.0089	I versus A	31.68	0

[a] $\omega(\omega_A, \omega_B, \omega_C, \omega_D, \omega_E, \omega_F, \omega_G)$ and ω_0, are the ratios of branches A, B, C, D, E, F, G, and other branches, respectively (see Fig. 1)

Table 2 Models of variation in *S100A7* sequences of 42 vertebrate species

Model	*np*	*lnL*[a]	Estimates of parameters[b]	Positively selected sites[c]
Free-ratio	161	− 8619.04	$k = 1.8409$	
M7 (beta)	83	− 8462.10	$k = 1.79667$	Not allowed
			$p = 0.80809$ $q = 1.09317$	
M8 (beta and ω)	85	− 8458.72	$k = 1.83696$	**23R,0.986***
			$P_0 = 0.83169$ ($P_1 = 0.16831$)	
			$p = 0.95088$ $q = 1.87404$	
			$\omega = 1.32933$	

[a]Log-likelihood value

[b]k estimate of transition/transversion rate ratio

[c]Positive selection sites are identified at the cutoff $P > 90\%$ and those with 95% are shown in boldface, the asterisk indicates that the posterior probability is > 95%

model M8 was better than the model M7 ($2\Delta l = 6.72$, $df = 2$, $P 0.05$) and one site (23R, $P = 0.981$) was found to be under positive selection (Table 2). The test 2 of branch-site model A was used to check the positively selected sites on *S100A7* of Artiodactyla, Rodentia, and Carnivora of vertebrate lineages (Table S1). Moreover, the results indicated that 23 R (0.986*) of *S100A7* is under positive selection ($\chi^2 = 4.4$, $df = 1$, $P = 0.0359$) on the ancestral branch leading to Artiodactyla (Supporting file 2), which was consistent with the result of site-specific models.

Sliding window analysis was used to compare substitution ratios between each of the species and Artiodactyla clade. The region with accelerated evolutionary rates was located in the loops between two EF-hand domains. The ω ratio of this *S100A7* region on Artiodactyla lineage was > 1, which is significantly higher than that of other vertebrates, Moreover, $\omega > 1$ means that the region of Artiodactyla *S100A7* is under positive selection. In addition, the N-terminal EF-hand motif is more variable than that of the C-terminal EF-hand in Artiodactyla (Fig. 2).

Correlation of the Transcription of S100A7-with the UV Index Variation

The RPKM value of *S100A7* was estimated using the skin transcriptome data of cashmere goats. Transcription value data were obtained for each individual goat for contained 13 months dating from 1 December 2014 to 31 December 2015. *S100A7* exhibited a high transcription level between June and July. The seasonal transcription pattern of *S100A7* was correlated to UV radiation index with a Pearson correlation coefficient of 0.88 ($P < 0.001$) (Fig. 3).

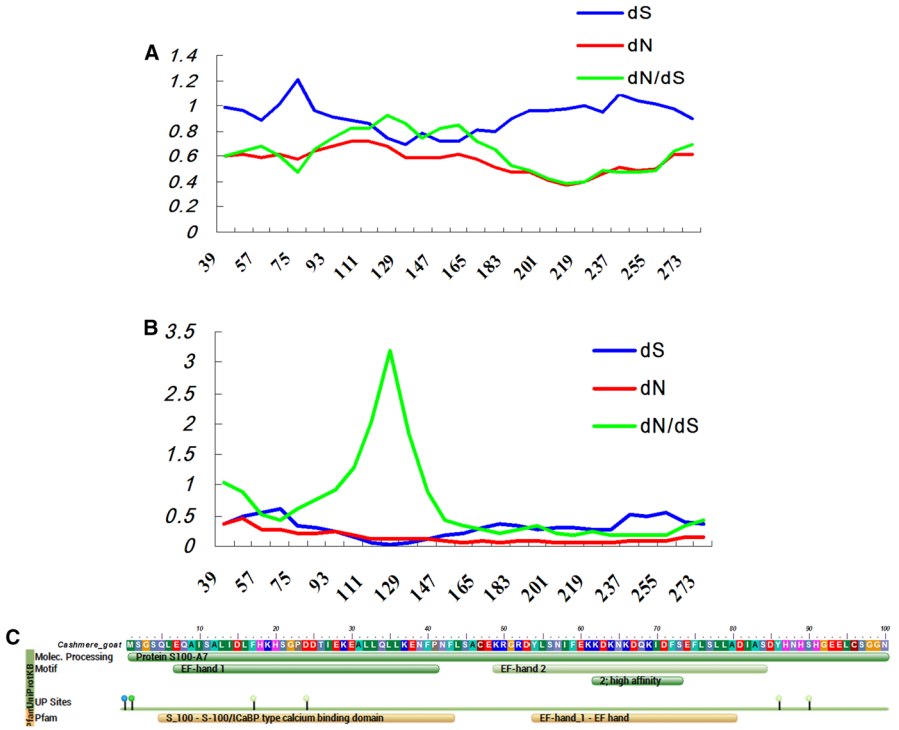

Fig. 2 Sliding window analysis of ω values. Estimates are based on Nei–Gojobori method and are depicted across the protein-coding regions of *S100A7*. For the estimations of **a** 42 species chosen in this study and **b** 8 species of Artiodactyla lineage, we set the window at 60 bp and step at 9 bp. **c** The structure of S100A7 protein in cashmere goat

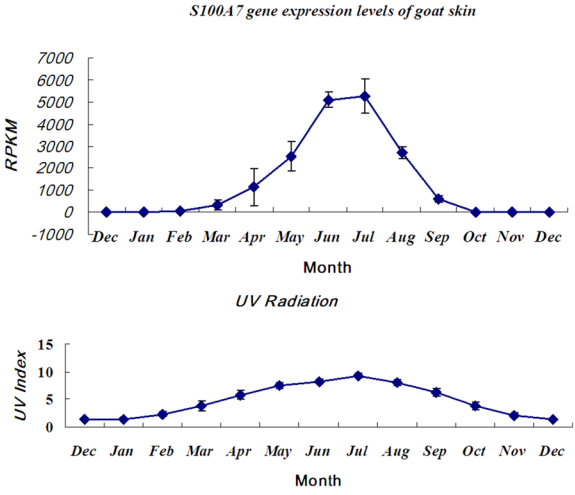

Fig. 3 The *S100A7* expression levels of cashmere goat skin and the UV index data of the experimental goat location

Discussion

As the early eutherian mammals faced predation risk owing to the presence of diurnal reptiles (e.g., dinosaurs) during the Mesozoic era, their activities were limited to night (Gerkema et al. 2013). The diversification of mammals might have occurred shortly prior to the late Mesozoic era. The skin is the primary interface between the internal and external regions of the organism. It acts as a protective barrier as well as perceives environmental changes, such as temperature, pressure, and UV radiation. The genes related to the skin structure and vision might evolve novel functions to adapt to the diverse habitats (Wu et al. 2014).

The evolutionary analyses of *S100A7* revealed various patterns of selection among 42 vertebrate species. The results of one-ratio model indicated that *S100A7* was under purifying selection in most of the vertebrates suggesting its important function to maintain the structure of skin. Positive selection is unlikely to affect all the gene sites over prolonged time. Therefore, in the one-ratio model, the ratio averaged for over all the sites and its value was always < 1 for all the lineages. Contrarily, various different branches of vertebrates exhibited variable evolutionary rates and were under distinct patterns of selection. The results of two-ratio model tests were consistent with those of free-ratio model, indicating that the change in selection pressure varied among mammals such as Rodentias and Artiodactyla. The Artiodactyla branch exhibited a significantly higher evolutionary rate compared to that of other vertebrates, whereas the Rodentia a significantly lower ω value than that of the corresponding background branches. In addition, the ω value of Chiroptera lineage demonstrated a slightly lower evolutionary rate than that of the corresponding background branches but the variation was not significant. Chiroptera and Rodentia belong to nocturnal animal groups (Gerkema 2013); however, a few types of bats in the tree-roosting are often exposed to UV radiation during the daytime. The pigmentation genes of these bats undergo an adaptation to the environmental pressures (UV radiation) (Kermott and Timm 1988). Rodents that maintain the nocturnal activity might have lost UV protection mechanisms in their skin. However, subsequent to the reduction in the predation pressure, ungulates might have migrated to grasslands and were exposed to UV radiation. Therefore, in this study, we speculate that the *S100A7* might have evolved a novel function to adapt to the UV radiation. The seasonal variations in UV radiation might facilitate a biorhythm in living organisms and animal migration (Lennox 2016).

The results of site-specific model analyses revealed that a site of the *S100A7* (**23R, $P = 0.981$**) was under positive selection. Branch model tests and SWAAP results confirmed the site-specific analysis results suggesting positive selection on Artiodactyla S100A7 genes. The positively selected region occurs at the loops between two EF-hand domains and the linker helix of N-terminal EF-hand (Brodersen et al. 1998). These changes might affect the angle between the two helices in order to perform their diverse biological functions (Yap et al. 1999). In this study, we found that the transcription level of *S100A7* in the cashmere goat skin was strongly correlated with UV radiation. *S100A7* belongs to the antimicrobial peptide that could be induced by the UV radiation in a dose-dependent

manner in vitro and in vivo (Glaser et al. 2009). UV radiation as well as retinoic acid could stimulate normal human keratinocytes to secrete S100A7 protein; however, they inhibit the keratinocyte differentiation that is dependent on the reduced expressions of keratin 1, keratin 10, involucrin, and loricrin and an increased expression of abnormal differentiation markers (keratin 6 and keratin 16) (Son et al. 2016). All these genes are very important to maintain the normal function of the skin and appendages.

Moreover, our previous study demonstrated that Hoxc13/β-catenin genes are seasonally expressed in cashmere goat skin (WU et al. 2012). Zhou et al. reported that *S100A7* can regulate the β-catenin signaling to inhibit the tumor progression (Zhou et al. 2008). As β-catenin is essential for the hair follicle cell cycle and correlates with the hair follicle activity in cashmere goat skin (WU et al. 2012), *S100A7* might play an important role in regulating the cashmere growth cycle. These results indicate that the seasonal variation in UV radiation might regulate the *S100A7* expression in order to modulate the cashmere growth and adaptability of cashmere goat skin.

Conclusion

We speculate that *S100A7* might have influenced the structure of integument in order to perceive UV radiation during the species divergence after the extinction of dinosaurs. The selection pressure on *S100A7* varied with respect to the various lineages of vertebrates. Our results demonstrated positive selection on *S100A7* in the Artiodactyla branch. Cashmere goats were selected as a model to investigate the transcription pattern of *S100A7* in the Artiodactyla skin. We observed that the transcription levels of *S100A7* in cashmere goat skin were correlated with the seasonal variation in the UV index. Artiodactyla skin might evolve a new biological function to adapt to the environment with intense UV radiation.

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Compliance with Ethical Standards

Conflict of interest All the authors listed have declared that no competing interests exist. The authors declare that the grant, scholarship, and/or funding do not lead to any conflict of interest. In addition, the authors declare that there is no conflict of interest regarding the publication of this manuscript.

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Affiliations

Husile Gong[1,4] · Ding Yang[3] · Yunxia Qi[3] · Jianghong Wu[2,3] · Wenguang Zhang[4]

Husile Gong
huslee@163.com

Ding Yang
yangding81@126.com

Yunxia Qi
qi_yunxia@163.com

1 College of Life Science, Inner Mongolia University for Nationalities, Tongliao 028000, China

2 College of Animal Science and Technology, Inner Mongolia University for Nationalities, Tongliao 028000, China

3 Inner Mongolia Academy of Agricultural & Animal Husbandry Sciences, Hohhot 010031, China

4 College of Animal Science, Inner Mongolia Agricultural University, Hohhot 010018, China