INTRODUCTION

Inhibin is a glycoprotein hormone belonging to the transforming growth factor-β superfamily that suppresses follicle-stimulating hormone (FSH) synthesis and secretion, follicular maturation and steroidogenesis in the female. Inhibin βA gene (INHBA) was studied as a candidate gene for the prolificacy of sheep. Single nucleotide polymorphisms of the entire coding region and partial 3’ untranslated region of INHBA were detected by PCR-SSCP in two high fecundity breeds (Small Tail Han and Hu sheep) and six low fecundity breeds (Dorset, Texel, German Mutton Merino, South African Mutton Merino, Chinese Merino and Corriedale sheep). Only the PCR products amplified by primers 3, 4 and 5 displayed polymorphisms. For primer 3, genotype CC was only detected in Chinese Merino sheep, genotype AA was detected in the other seven sheep breeds. Genotype BB was only detected in Hu sheep. Only Hu sheep displayed polymorphism. Eight or four nucleotide mutations were revealed between BB or CC and AA, respectively, and these mutations did not result in any amino acid change. For primer 4, genotypes EE, EG and GG were detected in Dorset and German Mutton Merino sheep, genotypes EE, EF and FF were detected in Chinese Merino sheep, only genotype EE was detected in the other five sheep breeds. Only Dorset, German Mutton Merino and Chinese Merino sheep displayed polymorphism. Sequencing revealed one nucleotide mutation (114G→A) of exon 2 of INHBA gene between genotype FF and genotype EE, and this mutation did not cause any amino acid change. Another nucleotide change (143C→T) was identified between genotype GG and genotype EE, and this mutation resulted in an amino acid change of serine→leucine. For primer 5, genotypes KK and KL were detected in German Mutton Merino and Corriedale sheep, genotypes KK, LL and KL were detected in the other six sheep breeds. Genotype MM was only detected in Hu sheep. All of these eight sheep breeds displayed polymorphism. Sequencing revealed one nucleotide mutation (218A→G) of exon 2 of the INHBA gene between genotype LL and genotype KK, and nine nucleotide mutations between genotype MM and genotype KK. These mutations did not alter amino acid sequence. The partial sequence (395 bp for exon 1 and 933 bp for exon 2) of the INHBA gene in Small Tail Han sheep (with genotype KK for primer 5) was submitted into GenBank (accession number EF192431). Small Tail Han sheep displayed polymorphisms only in the fragment amplified by primer 5. The Small Tail Han ewes with genotype LL had 0.53 (p<0.05) or 0.63 (p<0.05) more lambs than those with genotype KL or KK, respectively. The Small Tail Han ewes with genotype KL had 0.10 (p>0.05) more lambs than those with genotype KK.

(Regional Words : Sheep Breeds, Inhibin βA Gene, PCR-SSCP)
Merino and Corriedale sheep was 2.61, 2.29, 1.23 and 1.25, respectively (Tu, 1989). Mean litter size of Dorset, Texel, German Mutton Merino and South African Mutton Merino sheep was 1.45 (Casas et al., 2004), 1.41 (Casas et al., 2004), 2.00 (Chu et al., 2005) and 1.71 (Brand and Franck, 2000), respectively. Based on the important role of INHBA gene in reproduction, INHBA gene was considered as a possible candidate gene for the prolificacy of Small Tail Han sheep. The objectives of the present study were firstly to detect single nucleotide polymorphisms (SNPs) in coding region of INHBA gene in both two high fecundity breeds (Small Tail Han and Hu sheep) and six low fecundity breeds (Dorset, Texel, German Mutton Merino, South African Merino, Chinese Merino and Corriedale sheep) by polymerase chain reaction (PCR)-single strand conformation polymorphism (SSCP), and secondly to investigate the association between INHBA gene and high prolificacy of Small Tail Han sheep.

**MATERIALS AND METHODS**

**Animals**

All procedures involving animals were approved by the animal care and use committee at the respective institution where the experiment was conducted. All procedures involving animals were approved and authorized by the Chinese Ministry of Agriculture.

Venous jugular blood samples (10 ml per ewe) were collected from 136 Small Tail Han ewes lambed in 2004, along with data on litter size in the first, second, or third parity (Jiaxiang Sheep Breeding Farm located in Jiaxiang County, Shandong province, China), 36 Dorset, 40 Texel and 21 German Mutton Merino (HITEK Ranch (Beijing) Ltd. Co. located in Dasunzhuang Town, Shunyi District, Beijing, China), 37 South African Mutton Merino and 31 Corriedale ewes (Qinshui Demonstration Farm located in Zhengzhuang Town, Qinshui County, Shanxi province, China), 39 Chinese Merino ewes (Ziniquan Breeding Sheep Farm located in Shihezi City, Xinjiang Uygur Autonomous Region, China), and 48 Hu ewes (Yuhang Hu Sheep Breeding Farm located in Yuhang District, Hangzhou City, Zhejiang province, China) using acid citrate dextrose as an anticoagulant. These ewes were chosen at random. Genomic DNA was extracted from whole blood by phenol-chloroform method, and then dissolved in TE buffer (10 mmol/L Tris-HCl (pH 8.0), 1 mmol/L EDTA (pH 8.0)) and kept at -20 °C. However, among these sheep breeds, the 136 Small Tail Han ewes were the progeny of 6 rams. Because the 6 rams were sold, their blood was not collected and they were not genotyped. No selection on litter size or other fertility traits was performed in the flock over previous years. Lambing seasons consisted of 3-mo groups starting with March through May as season 1 (spring), June through August as season 2 (summer), September through November as season 3 (autumn), and December through February as season 4 (winter).

**Primers and PCR amplification**

Five pairs of primers were designed according to exon 1 (GenBank accession number U16238) and exon 2 (GenBank accession number U16239) of bovine inhibin βA precursor gene (Thompson et al., 1994), and mRNA (GenBank accession number L19218) of ovine inhibin βA subunit (Fleming et al., 1995). Entire coding region (1,278 bp) and 42 bp of 3’ untranslated region (UTR) were amplified. These primers were synthesized by Shanghai Invitrogen Biotechnology Limited Corporation (Shanghai, China). Primer sequence, amplified region and PCR product size were listed in Table 1.

Polymerase chain reaction was carried out in 25 µL volume containing approximately 2.5 µL of 10×PCR buffer (50 mmol/L KCl, 10 mmol/L Tris-HCl (pH 8.0), 0.1% Triton X-100), 1.5 mmol/L MgCl2, 200 µmol/L each dNTP, 1 µmol/L each primer, 50 ng genomic DNA, and 1 U Taq DNA polymerase (Promega, Madison, WI, USA). Amplification conditions were as follows: denaturation at...
94°C for 6 min; followed by 32 cycles of denaturation at 94°C for 30 s, annealing at 55-62°C for 30 s, extension at 72°C for 30 s; with a final extension at 72°C for 10 min on Mastercycler® 5333 (Eppendorf AG, Hamburg, Germany).

SSCP detection

A volume of 1.5 µl PCR product was transferred in an Eppendorf tube, mixed with 6 µl gel loading solution containing 98% formamide, 0.025% bromophenol blue, 0.025% xylene cyanol, 20 mmol/L EDTA (pH 8.0), 10% glycerol. The mixture was centrifugalized and denatured at 98°C for 10 min, then chilled on ice for 5 min and loaded on 8% to 10% neutral polyacrylamide gels (acrylamide: bisacrylamide = 29:1). Electrophoresis was performed in 1xTris borate (pH 8.3)-EDTA buffer at 9 to 15 V/cm at 4°C overnight. After electrophoresis, the DNA fragments in the gels were visualized by silver staining, photographed and analyzed using an Alphalager™ 2200 and 1220 Documentation and Analysis Systems (Alpha Innotech Corporation, San Leandro, CA, USA).

Cloning and sequencing

After SSCP analysis, PCR products of different homozygous genotypes were separated on 1.0% agarose gels and recovered using GeneClean II kit (Promega). Each DNA fragment was ligated into the pGEM-T Easy vector (Promega) according to the manufacturer’s instructions. The ligation reactions were carried out in 10 µl volume containing PCR product 1 µl, pGEM-T Easy vector (50 ng/µl) 1 µl, T₄ ligase (3 U/µl) 1 µl, 2xligation buffer 5 µl, ddH₂O 2 µl. Each DNA fragment was then transformed into Escherichia coli DH5α competence cell. Positive clones of transformed cells were identified by restriction enzyme digestion. Two clones of each homozygous genotype were selected and sequenced. Each clone was sequenced for twice. The target DNA fragments in recombinant plasmids were sequenced from both directions using an automatic ABI 377 sequencer (Perkin Elmer Applied Biosystems, Foster City, CA, USA) by Shanghai Invitrogen Biotechnology Ltd. Co. (Shanghai, China).

Statistical analysis

The following fixed effects model was employed for analysis of litter size in Small Tail Han ewes and least squares mean was used for multiple comparison in litter size among different genotypes.

\[
y_{ijklm} = \mu + S_i + LS_j + P_k + G_l + e_{ijklm}
\]

Where \( y_{ijklm} \) is phenotypic value of litter size; \( \mu \) is population mean; \( S_i \) is the fixed effect of the \( i^{th} \) sire \( (i = 1, 2, 3, 4, 5, 6); LS_j \) is the fixed effect of the \( j^{th} \) lambing season \( (j = 1, 2, 3, 4); P_k \) is the fixed effect of the \( k^{th} \) parity \( (k = 1, 2, 3); G_l \) is the fixed effect of the \( l^{th} \) genotype \( (l = 1, 2, 3); \) and \( e_{ijklm} \) is random error effect of each observation. Analysis was performed using the general linear model (GLM) procedure of SAS (Ver 8.1) (SAS Institute Inc., Cary, NC, USA). Mean separation procedures were performed using a least significant difference test.

RESULTS

PCR amplification

Genomic DNA of eight sheep breeds was amplified using five pairs of primers for INHBA gene. PCR products were detected by running a 2% agarose gel electrophoresis (see Figure 1). Fragments amplified by primer 5 were not obtained in Chinese Merino sheep. The amplified products were consistent with the target fragments and had good specificity, which could be directly analyzed by SSCP.

SSCP analysis

Only the PCR products amplified by primers 3, 4 and 5

Figure 1. PCR products of five pairs of primers of ovine INHBA gene. 1, 2: primer 1; 3, 4: primer 2; 5, 6: primer 3; 7, 8: primer 4; 9, 10: primer 5.

Figure 2. SSCP analysis of PCR amplification using primer 3 in different sheep breeds. 1, 2: AA genotype; 3, 4: BB genotype; 5, 6: CC genotype.

Figure 3. SSCP analysis of PCR amplification using primer 4 in different sheep breeds. 1, 2, 11, 12: EE genotype; 3, 4: EF genotype; 5: FF genotype; 6, 7: GG genotype; 8, 9, 10: EG genotype.
displayed polymorphisms. Three genotypes (AA, BB and CC) were detected by primer 3 (Figure 2), five genotypes (EE, FF, EF, GG and EG) were detected by primer 4 (Figure 3), and four genotypes (KK, LL, KL and MM) were detected by primer 5 (Figure 4).

Sequencing of different homozygous genotypes and nucleotide mutations

In the current study, the partial sequence (395 bp for exon 1 and 933 bp for exon 2) of \textit{INHBA} gene in Small Tail Han sheep (with genotype KK for primer 5) was submitted into GenBank (accession number EF192431).

For primer 3, sequencing revealed eight nucleotide mutations of exon 2 of \textit{INHBA} gene between genotype BB and genotype AA, and four nucleotide mutations between genotype CC and genotype AA (see Table 2). The deduced amino acids of the nucleotide sequences of genotypes AA, BB and CC were identical, so these mutations were silent. While comparing the deduced amino acid sequences with the sequence of ovine inhibin $\beta_A$ subunit published on GenBank (accession number NP_001009458), an amino acid change (Gln142Lys) was detected, that is, glutamine in GenBank sequences changed into lysine in the present sequences.

For primer 4, sequencing revealed one nucleotide mutation (114G→A, GGG→GGA) (see Figure 5a) of exon 2 of \textit{INHBA} gene between genotype FF and genotype EE, this mutation did not cause any amino acid change. Another nucleotide change (143C→T, TCG→TTG) was identified between genotype GG and genotype EE, this mutation resulted in an amino acid change of serine → leucine (see Figure 5b), corresponding to serine residue at 287 of amino acid sequence of ovine inhibin $\beta_A$ subunit.
published in GenBank (accession number NP_001009458).

For primer 5, sequencing revealed one nucleotide mutation (218A→G) of exon 2 of INHBA gene between genotype LL and genotype KK, and nine nucleotide mutations between genotype MM and genotype KK (see Table 3). However, these amino acid sequences of the nucleotide sequences of the three genotypes were the same, and which were identical to amino acid sequences of ovine inhibin α subunit published in GenBank (accession number NP_001009458).

### Table 3. The nucleotide mutations between three genotypes amplified by primer 5

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Nucleotide sequences 5′→3′</th>
</tr>
</thead>
<tbody>
<tr>
<td>KK</td>
<td>GCT…GCT…CAG… GTC…ATG…AAA…GCT…CCAG…ACG…AGA</td>
</tr>
<tr>
<td>LL</td>
<td>GCT…GCT…CAG… GTC…ATG…AGA…GCT…CCAG…ACG…AGA</td>
</tr>
<tr>
<td>MM</td>
<td>GCT…CAT… CGG…GCC…AGG…AGA…GTT…CTGG…ATG…AGA</td>
</tr>
</tbody>
</table>

The number indicates nucleotide site corresponding to amplified fragments in Table 1.

### Table 4. Allele and genotype frequencies of INHBA gene in eight sheep breeds

<table>
<thead>
<tr>
<th>Breed</th>
<th>Small Tail Han sheep</th>
<th>Hu sheep</th>
<th>Texel</th>
<th>Dorset</th>
<th>German Mutton Merino</th>
<th>South African Mutton Merino</th>
<th>Corriedale</th>
<th>Chinese Merino</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of samples</td>
<td>136</td>
<td>48</td>
<td>40</td>
<td>36</td>
<td>21</td>
<td>37</td>
<td>31</td>
<td>39</td>
</tr>
<tr>
<td>Primer 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Genotype</td>
<td>AA</td>
<td>1.000(136)</td>
<td>0.708(34)</td>
<td>1.000(40)</td>
<td>1.000(36)</td>
<td>1.000(21)</td>
<td>1.000(37)</td>
<td>1.000(31)</td>
</tr>
<tr>
<td>frequency</td>
<td>BB</td>
<td>0.000(0)</td>
<td>0.292(14)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
</tr>
<tr>
<td>Allele</td>
<td>A</td>
<td>1.000</td>
<td>0.708</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>frequency</td>
<td>B</td>
<td>0.000</td>
<td>0.292</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Primer 4</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Genotype</td>
<td>EE</td>
<td>1.000(136)</td>
<td>1.000(48)</td>
<td>1.000(40)</td>
<td>0.417(15)</td>
<td>0.619(13)</td>
<td>1.000(37)</td>
<td>1.000(31)</td>
</tr>
<tr>
<td>frequency</td>
<td>FF</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
<td>0.000(0)</td>
</tr>
<tr>
<td>Allele</td>
<td>E</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>0.681</td>
<td>0.762</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>frequency</td>
<td>F</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Primer 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Genotype</td>
<td>KK</td>
<td>0.471(64)</td>
<td>0.304(14)</td>
<td>0.450(18)</td>
<td>0.942(33)</td>
<td>0.905(19)</td>
<td>0.324(12)</td>
<td>0.452(14)</td>
</tr>
<tr>
<td>frequency</td>
<td>LL</td>
<td>0.220(30)</td>
<td>0.239(11)</td>
<td>0.025(1)</td>
<td>0.029(1)</td>
<td>0.000(0)</td>
<td>0.189(7)</td>
<td>0.000(0)</td>
</tr>
<tr>
<td>Allele</td>
<td>K</td>
<td>0.625</td>
<td>0.326</td>
<td>0.713</td>
<td>0.957</td>
<td>0.952</td>
<td>0.568</td>
<td>0.726</td>
</tr>
<tr>
<td>frequency</td>
<td>L</td>
<td>0.375</td>
<td>0.261</td>
<td>0.287</td>
<td>0.043</td>
<td>0.048</td>
<td>0.432</td>
<td>0.274</td>
</tr>
<tr>
<td>M</td>
<td>0.000</td>
<td>0.413</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
</tbody>
</table>

The numbers in the parentheses are the individuals that belong to the respective genotypes.

For primer 5, genotypes KK and KL were detected in German Mutton Merino and Corriedale sheep, genotypes KK, LL and KL were detected in other six sheep breeds. Genotype MM was only detected in Hu sheep. All of these eight sheep breeds displayed polymorphism.

Based on sequencing results, primer 3 had 10 DNA variations, primer 4 had two DNA variations, and primer 5 had 9 DNA variations. In total of the 21 mutations, 17 DNA variations were originated from the Hu breed, five DNA variations were originated from other breeds (two mutations 24T→C and 282T→C of them were the same as those in the Hu breed) were found in the Chinese Merino breed, and one SNP was detected in the Texel breed. Only Dorset and German Mutton Merino sheep, genotypes EE, EF and FF were detected in Chinese Merino sheep, only genotype EE was detected in other five sheep breeds. Only Dorset, German Mutton Merino and Chinese Merino sheep displayed polymorphism.

The frequencies of 12 genotypes and 9 alleles in eight sheep breeds were presented in Table 4.

For primer 3, genotype CC was only detected in Chinese Merino sheep, genotype AA was detected in other seven sheep breeds. Genotype BB was only detected in Hu sheep. Only Hu sheep displayed polymorphism.

For primer 4, genotypes EE, EG and GG were detected in Dorset and German Mutton Merino sheep, genotypes EE, EF and FF were detected in Chinese Merino sheep, only genotype EE was detected in other five sheep breeds. Only Dorset, German Mutton Merino and Chinese Merino sheep displayed polymorphism.

These results indicated that the polymorphisms in coding region of INHBA gene were rather abundant among sheep. Only Hu sheep displayed polymorphism. Seven sheep breeds. Genotype BB was only detected in Hu sheep. Only Hu sheep displayed polymorphism.

For primer 4, genotypes EE, EG and GG were detected in Dorset and German Mutton Merino sheep, genotypes EE, EF and FF were detected in Chinese Merino sheep, only genotype EE was detected in other five sheep breeds. Only Dorset, German Mutton Merino and Chinese Merino sheep displayed polymorphism.

For primer 5, genotypes KK and KL were detected in German Mutton Merino and Corriedale sheep, genotypes KK, LL and KL were detected in other six sheep breeds. Genotype MM was only detected in Hu sheep. All of these eight sheep breeds displayed polymorphism.
Influence of fixed effects on litter size in Small Tail Han sheep

Sire significantly influenced litter size in Small Tail Han sheep (p<0.01). Both lambing season and parity significantly influenced litter size in Small Tail Han sheep (p<0.05). The INHBA genotype significantly influenced litter size in Small Tail Han sheep (p<0.05).

The least squares means and standard errors for litter size of different genotypes of INHBA gene in Small Tail Han sheep were given in Table 5. The Small Tail Han ewes with genotype LL had 0.53 (p<0.05) or 0.63 (p<0.05) lambs more than those with genotype KL or KK, respectively. The Small Tail Han ewes with genotype KL had 0.10 (p>0.05) lambs more than those with genotype KK.

DISCUSSION

Polymorphisms of INHBA gene in sheep

A TaqI polymorphism at the ovine INHBA locus had been identified (Hiendleder et al., 1992). Jaeger and Hiendleder (1994) identified polymorphisms in the coding regions and regulatory elements of ovine INHBA gene. Leyhe et al. (1994) revealed two TaqI alleles (1.9 kb and 1.5 kb) of ovine INHBA gene, and found that the four sheep breeds (Rhoenschaf, Merinolandschaf, East Friesian Milksheep and Romanov) with different reproductive performance differed significantly (p<0.001) in TaqI allele frequencies. Hiendleder et al. (1996a) reported two TaqI alleles at the ovine INHBA locus.

The present study identified 21 new nucleotide polymorphisms in the entire coding region and partial 3' UTR of ovine INHBA gene, only one of which disrupted the protein product among eight sheep breeds, and another amino acid change was detected between the investigated sheep and ovine amino acid sequence from GenBank. These polymorphisms determined 12 genotypes and 9 alleles in eight sheep breeds. What is cause that leads to such a high rate of mutation in INHBA gene without changing the amino acid sequence in these sheep breeds deserves further study.

In the current study, 17 of 21 SNPs were from the Hu breed. The Hu sheep breed is a special local breed in China.

Table 5. Least squares means and standard errors for litter size of different genotypes of INHBA gene in Small Tail Han sheep

<table>
<thead>
<tr>
<th>Primer</th>
<th>Genotype</th>
<th>No. of samples</th>
<th>Litter size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primer 5</td>
<td>KK</td>
<td>64</td>
<td>1.90±0.15</td>
</tr>
<tr>
<td></td>
<td>KL</td>
<td>42</td>
<td>2.00±0.17</td>
</tr>
<tr>
<td></td>
<td>LL</td>
<td>30</td>
<td>2.53±0.20</td>
</tr>
</tbody>
</table>

Least squares means with different superscripts for the same pair of primer differ significantly (p<0.05).

Relationship of INHBA gene with prolificacy of sheep

As inhibin plays an important role in FSH regulation and acts as a growing factor in ovary, it was proposed as a candidate gene for reproductive performance (Xue et al., 2004). Leyhe et al. (1994) and Hiendleder et al. (1996a) reported that the frequency of the TaqI allele A of INHBA gene coincided with the average litter size in each sheep breed examined. Average litter size was 1.10, 1.44, 1.48, 1.76, 3.00, whereas the frequency of the TaqI allele A was 0.0, 0.20, 0.29, 0.35, 0.65, respectively, in wild sheep, Merinolandschaft, Rhoenschaf, East Friesian Milksheep and Romanov. Jaeger and Hiendleder (1994) analyzed 1,000 lambing records and found that INHBA gene had obvious genetic effect on litter size of sheep. Hiendleder et al. (1996b) reported that INHBA gene had significant influence on ovine litter size. Animal model analysis of 1,562 litters of 389 Merinolandschafe ewes showed that the substitution effect of INHBA gene reached 0.04 lambs (0.25σλ), and the analysis of 620 litters of 155 East Friesian Milksheep ewes indicated that the substitution effect of INHBA gene reached 0.09 lambs.

ACKNOWLEDGMENTS

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