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The Polymorphism in 5 'Regulatory Region and Exon 13 of *PRKAG3* Gene and its Distribution Pattern in Different Goat Breeds

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ABSTRACT

Adenosine Monophosphate activated Protein Kinase (AMPK) plays a key role in cellular metabolism and regulating energy and its γ3 subunit was encoded by the *PRKAG3* gene which was regarded as the candidate gene for carcass quality trait in domestic animals and fowls. To understand *PRKAG3* gene variation and its association with carcass quality of goat breeds, the polymorphism of goat *PRKAG3* gene and its distribution patterns in different goat breeds were investigated. Five goat breeds selected were Anhui white goat, Matou, Boer, Xiangdong and Sanen dairy goat. DNA samples of all goat breeds were extracted from goat ear tissue. The polymorphisms in the 5' regulatory region and exon 13 of *PRKAG3* gene were examined using ApaI, Hpy188I, AciI and ClaI enzyme digestion, respectively and their distribution patterns were analyzed in different goat breeds. The results showed that two mutation loci in the 5' regulatory region, C-525A and C-225T, located at -525 and -225 bp upstream of the start codon of the *PRKAG3* gene and two mutation loci in the exon 13, T90C and C102T, located at 90 bp and 102 bp of the exon 13. The 525CC genotype frequencies of five goat breeds listed above were 0.8000, 0.9681, 0.6042, 0.7557 and 0.8889, respectively, while 225CC genotype frequencies corresponding to 0.7391, 0.9750, 0.8684, 0.9785 and 0.9344. The mutations at T90C and C102T didn't cause the substitution of corresponding amino acids in the AMPK protein. The muscle fat grade and carcass fat grade are lower in goat breeds with higher 525CC225CC genotype frequency while higher in the breeds with higher 525CA225CT genotype frequency ($p<0.05$). The results suggest that the lipoidosis ability of goat breeds may be associated with C-525A and C-225T loci of *PRKAG3* gene.

Key words: Goat breeds, *PRKAG3* gene, DNA polymorphism, lipoidosis, meat quality

INTRODUCTION

China has many goat breeds, native goat breeds nearly 50 and its rearing number reached 152 million in 2010, which has been playing an important role in meat supply and agricultural improvement. Due to diverse natural and geographical conditions, cultivated goat breeds in the particular habitat differ in the goat meat quality, commercial grade, meat taste, flavor and juiciness for consumer (Arain *et al*., 2010a, b; Das *et al*., 2007). Some reports showed that meat quality related to muscle fat content (Parizadian *et al*., 2011). However, in addition to the effect of nutrition level (Vahdatpour *et al*., 2008), the fat deposition ability of goat depends on the characters of goat breeds (Zhou *et al*., 2011) and associated with many fat metabolic enzymes. The molecular mechanism of fat deposition ability in goat yet remains unclear, although many molecular markers correlated with carcass fat content were found of which very few are utilized in breeding practice (Mahmoudi, 2010; Qiong *et al*., 2011; Yadav and Yadav, 2007). Compared with studies in the pig, cattle and other animal (Chen, 2010; Han *et al*., 2011; Chen *et al*., 2011a), there are few studies on the fat deposition ability in goat.

AMPK is highly conserved sensor of cellular energy and it plays a key role in cellular metabolism and regulating energy (Carling, 2004). Activation and phosphorylation of AMPK can promote glucose uptake, enhance fatty acid oxidation and inhibition of glycogen synthesis and consumption of energy in the body (Witters *et al*., 2006). AMPK is a heterotrimeric enzyme complex, consisting of one catalytic subunit (α) and two regulation subunits (β and γ) (Stapleton *et al*., 1997; Shen *et al*., 2006). γ subunit is divided into three isoforms that are γ1, γ2 and γ3 subunits encoded, respectively by the PRKAG1, PRKAG2 and *PRKAG3* gene (Hardie, 2004; Long and Zierath, 2006).

Human *PRKAG3* gene contains 13 exons and 12 introns (Park *et al*., 2003). *PRKAG3* is specifically expressed in skeletal muscle (Yu *et al*., 2003). Milan *et al*. (2000) and Ciobanu *et al*. (2001) found that Arg200/Gln200 mutation of *PRKAG3* protein in Hampshire pig reduced AMPK activity and increased skeletal muscle glycogen content, while the Val199/Ile199 mutations decreased skeletal muscle glycogen content (Mallick *et al*., 2006), which thereby influenced the meat quality. *PRKAG3* gene mutations in human and mouse resulted in an increase of lipid peroxidation which affected the metabolism of skeletal muscle (Barnes and Zierath, 2005). Some reports found that the polymorphisms of cattle *PRKAG3* gene related to the protein activity, meat quality traits and disease resistance (Roux *et al*., 2006; Yu *et al*., 2005). At present, the polymorphism of goat *PRKAG3* gene and its association with meat quality has not been reported. In this study, the polymorphisms in 5' regulatory region and exon 13 of goat *PRKAG3* gene was detected and the polymorphic distribution in five goat breeds and its association with meat quality were analyzed.

MATERIALS AND METHODS

Samples: Genomic DNA samples were extracted form the ear tissues of five goat breeds using DNA extraction kit, stored at 4°C. The five goat breeds were Sanen dairy goat (Sanen) from Northwest Sci-Tech University of Agriculture and Forestry (Shanxi, China), Xiangdong from Xiangdong black goat sheepstud of Changsha (Hunan, China), Matou from Matou goat breed conservation field of Shimen County (Hunan, China) and Anhui white goat (Anbai) and Boer from Boda Feidong sheepstud (Anhui, China).

Assessment of goat meat grade: The Muscle Fat Grade (MFG) of five goat breeds were estimated according to the fat of goat longissimus muscle and less than 1.0% in the muscle as level 1, then each additional 0.5% to improve a grade, respectively. The Carcass Fat Grade (CFG) were assessed

based on the fat content of goat carcass and less than 10.0% in the carcass as level 1, then each additional 1.0% to improve a grade, respectively.

Primers: Based on the sequences of bovine *PRKAG3* gene (GenBank DQ082736), four pairs of primers were designed using the primer premier 5.0 program (http://www. premierbiosoft. com) in which primer P5-900 and PE-13 were employed for the amplification of the fragment containing 5' partial regulatory region and exon 13 of goat *PRKAG3* gene and primer P5-600 and P5-350 for PCR-RFLP analysis of the 5' regulatory region. The primers were synthesized by Shanghai Bioengineering Inc. (Shanghai, China).

P5-900: Upstream primer 5'GTTGGCTCTAGGAGACGCAG3'
Downstream primer 5' ATACACAGAGAAAATCGTGGTCA3'
P5-600: Upstream primer 5' CGTCAAGGTGATTCTCAGGACT3'
Downstream primer 5'CGAGTGCGCAACACTGTATCT3'
P5-350: Upstream primer 5'TTTCCTCCTTTGGCACCTGAC3'
Downstream primer 5'CGAGTGCGGCACACTGTATCT3'
PE-13: Upstream primer 5' ATTCTTAGTATCAACCTCATCAGC3'
Downstream primer 5'GAGCCTACCTGAACAAGAGC3'

PCR conditions and procedures: PCR was carried out using 25 μL PCR amplification kits: 1.0 μL (10 μM) of each primer, 2.5 μL of 10×PCR buffer with Mg^{2+}, 2.0 μL dNTP (2.5 mM), 0.5 μL (5 units μL^{-1}) Taq DNA polymerase (Beijing Trans Gen Biotech Co., Ltd. China), 1.0 μL genomic DNA (50 ng μL^{-1}) and 17 μL double-distilled H_2O. Amplification conditions were: initial denaturation of 5 min at 94°C; 35 cycles of 94°C for 30 sec, 30 sec at 57°C for primer P5-900 (35 sec at 59°C for primer P5-600, 58°C for primer P5-350 and 55°C for primer PE-13, respectively), 72°C for 1 min, followed by 72°C extension for 10 min. The PCR products were detected using 1.5% agarose gel electrophoresis.

Polymorphism analysis: PCR products digested with ApaI (Fermentas China Co., Ltd.) and Hpy188I (New England BioLabs), ClaI (Fermentas China Co., Ltd.) and AciI (Fermentas China Co., Ltd.) endonucleases and then electrophoresed on 3% agarose gel for genotyping polymorphisms. The gene frequencies of the different goat breeds were analyzed statistically. Allele gene frequencies (Chen *et al*., 2011b), p and q, was calculated by p = D+0.5H and q = 1-p, respectively where D and H represent homozygote and heterozygote genotype frequencies, respectively. The gene frequencies of two hnkage SNP loci were calculated by Zhou *et al*. (2011).

Statistical analysis: The 5' regulatory region was subjected to promoter and transcription factors binding loci prediction in Signal scan (http://www-bimas.cit.nih.gov/molbio/signal/). The correlation coefficients between the genotypes and the levels of MFG and CFG were calculated and evaluated for p = 0.05 significant relationship using student's t-test.

RESULTS

Sequence analysis of the promoter region and exon 13: PCR amplification fragment lengths of primer P5-900, P5-600, P5-350 and PE-13 were 889, 596, 351 and 314 bp in Fig. 1, respectively. Based on the sequencing results of mixed DNA samples (Fig. 2), two mutation sites, C-525A and C-225T located at -525 and -225 bp upstream of the start codon of the *PRKAG3* gene, respectively, were detected. The promoter region of *PRKAG3* gene was assessed for potentially functional

(P5-900)gttggctctaggagacgcagaaaacagcacacacagcggaacgaggggacagtggctcctgcgcaccttggatctacctccact
ggtacaaacaggtgtctgtcacactggagacaagtgcaagcccaccacacgc(P5-600)cgtcaaggtgattctcaggact
ccccacctgcctgaaccatccagttccagctccttcacctagggaacgggccCctggg(AP-2)acttgaatagtgacatctgggcacacact
gaccactctctcagtaccacccacaaacctcttagccccaacctgctagccggctgcaacctgccctttctaattccagcaccacccatgacccaggtttgtacaaggaaga
gcgttcagctcaactgcctctgtt(P5-350)tttcctcctttggcacctgacaaagataagaggggctct
cagaggagaaaccccagggctctaaaagacccccctcctcccacgccagcgcccaccctcccccacagcagggtccttctctcccatcatTgg(NF-
Y)acacgcaggaggcacacagaaccaggcatcaagattccaagtgtacccctccttcacctccccagcagccccccaggctt
cagggctggagcagctgcgcgggtggaccccttcctccccagtgcccgacacccaatcagagagaacctgatccgggagggcagggtgccaggggccgggcccagaata
gtgctgcccagatacagtgttgcgcactcg(P5-600,P5-350)ctcATGGAGCCCCGCCG
AGCTGAAGCACGCTCTGCCCAGGgtaccggggtcccgggggctgggagctggggcagctgaggccacagggctgagagcaccctgccgcatggata
tgtgcgtgcatgtggatatgtttgaccacgattttctctgtgtat(P5-900)------(PE-13)attcttagtat
caacctcatcagctgctctagccacatggcgccgccccctcactgagcctctgtggacccacagGTGCACCGGCTGGTGCTCGTGGATGAAACCC
AGCACCTCCTGGGCGTGGTGTCCCTCTCCGACATCCTCCAAGCTCTAGTGCTCAGCCCTGCTGGCATCGACG
CCCTCGGGGCCTGAgaacatcgcagtcctcacgctcgggccaccttccacacctggaagccagtgaagggagccgggactcggccttcacctccaccacccccctt
ttgtgggttctgctcttgttcaggtaggctc(PE-13)

Fig. 1: Sequence characters of promoter region and exon 13 of goat *PRKAG3* gene. The primers with same names in the brackets are a pair of primers and the region between upstream and downstream primers is the DNA sequence. The capital letters are the sequences of exon 1 and exon 13 of *PRKAG3* gene, respectlvely. The atTgg sequence was binding motif for NF-Y transcription factors and the ccCctggg sequence for AP-2 transcription factors, in which capital letters, T and C, are mutation sites. While replacing the nucleotide at both sites, T→C and C→A, the binding sites for NF-Y and AP-2 disappeared

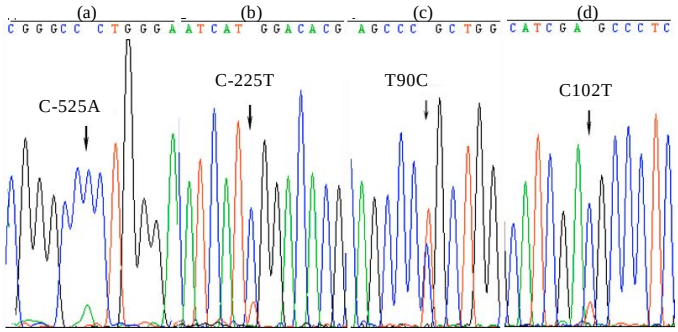

Fig. 2: The mutation sites in the promoter region and exon 13 of goat *PRKAG3* gene. C-525A and C-225T locate at -525 and -225 bp upstream of the start codon of the *PRKAG3* gene, respectively. T90C and C102T locate at 90 bp and 102 bp in the exon13 of the *PRKAG3* gene, respectively

sequence elements by comparison with paralogous promoter sequences. ATTGG sequence at C-225T was the binding motif of NF-Y transcription factor and CCCCTGGG sequence at C-525A was that of AP-2 transcription factor, while the binding site disappeared after T→C and C→A at C-225T and C-525A, respectively.

In exon 13, T90C and C102T mutant sites located at 90 bp and 102 bp of the exon 13 of the *PRKAG3* gene were detected, respectively, which were only synonymous mutations for the protein.

Table 1: The genotype and allele frequencies of *PRKAG3* gene at C-525A, C-225T, T90C and C102T sites in different goat populations

		Anbai	Matou	Boer	Xiangdong	Sanen
Sample size		150	94	48	176	72
Genotype	525CC	0.8000	0.9681	0.6042	0.7557	0.8889
	525CA	0.1733	0.0319	0.3750	0.2443	0.1111
	525AA	0.0267	0	0.0208	0	0
Allele gene	525C	0.8867	0.9840	0.7917	0.8778	0.9444
	525A	0.1133	0.0160	0.2083	0.1222	0.0556
Sample size		92	80	38	93	61
Genotype	225CC	0.7391	0.9750	0.8684	0.9785	0.9344
	225CT	0.2391	0.0250	0.1316	0.0215	0.0656
	225TT	0.0217	0	0	0	0
Allele gene	225C	0.8587	0.9875	0.9342	0.9892	0.9672
	225T	0.1413	0.0125	0.0658	0.0108	0.0328
Sample size		87	80	40	62	57
Genotype	90TT	0.5172	0.6500	0.5250	0.7419	0.7018
	90TC	0.4828	0.2625	0.4500	0.2419	0.2281
	90CC	0	0.0875	0.0250	0.0161	0.0702
Allele gene	90T	0.7586	0.7813	0.7500	0.8629	0.8158
	90C	0.2414	0.2188	0.2500	0.1371	0.1842
Sample size		118	94	40	104	62
Genotype	102CC	0.9237	0.8404	0.8750	0.9712	0.9839
	102CT	0.0763	0.1596	0.1250	0.0288	0.0161
Allele gene	102C	0.9619	0.9202	0.9375	0.9856	0.9919
	102T	0.0381	0.0798	0.0625	0.0144	0.0081

Polymorphisms of the promoter region and exon 13 in different goat breeds: Incision of the PCR product by ApaI, Hpy188I, AciI and ClaI, respectively, revealed that four polymorphism sites consisted of three genotypes, repectively.

Genotype and allele frequencies of the four sites in different goat populations were shown in Table 1. 525C gene frequencies of the Matou, Sanen, Xiangdong, Anbei and Boer were 0.9840, 0.9444, 0.8778, 0.8867 and 0.7917, respectively. 525AA genotype was not found in the Matou, Sanen and Xiangdong. From Table 1, the frequencies of 225CC genotype were higher than 0.93 in the Matou, Sanen and Xiangdong. 225TT genotype was only detected in the Anbai and lower. 90T was advantage alleles in the five goat populations at T90C site. The frequency of 90TT genotype in Xiangdong was higher (0.7419) and that in Boer lower (0.5250). 102C was advantage allele at C102T site. The frequencies of allele 102C in all goat populations were higher than 0.92. All goat populations of the four sites were in Hardy-weinberg equilibrium ($p>0.05$).

The genotype and haplotype frequencies of C-525A and C-225T linkage sites were shown in Table 2. The 525CC225TT, 525CA225TT, 525AA225CC and 525AA225CT were not detected. The 525CC225CC was preponderant genotype and the frequency was higher than 0.69 for all goat breeds, next the 525CA225CT genotype for Anbei (0.1628) and Boer (0.1316) and followed by the 525CA225CC genotype for Boer (0.1053) and Xiangdong (0.1196). The haplotype frequency of 525C225C was higher than 0.79.

Association of the polymorphisms with goat lipoidosis ability: The correlation coefficients between goat lipoidosis ability and genotype frequencies were shown in Table 3. The MFG and CFG were lower in goat breeds with higher 525CC225CC genotype frequency, whlie higher in the

Table 2: The genotype and haplotype frequencies of C-525A and C-225T linkage of goat *PRKAG3* gene

Goat breeds	Anbai	Matou	Boer	Xiangdong	Sanen
Sample size	86	79	38	92	57
Genotype freqnency					
525CC225CC	0.6970	0.9747	0.7632	0.8587	0.8772
525CC225CT	0.0814	0	0	0.0109	0
525CA225CC	0.0349	0	0.1053	0.1196	0.0526
525CA225CT	0.1628	0.0253	0.1316	0.0109	0.0702
525AA225TT	0.0233	0	0	0	0
Haplotype freqnency					
525C225C	0.7965	0.9810	0.8487	0.9266	0.9211
525C225T	0.0814	0.0063	0.0329	0.0082	0.0175
525A225C	0.0581	0.0060	0.0855	0.0625	0.0439
525A225T	0.0640	0.0063	0.0329	0.0027	0.0175

Table 3: The association of the genotypes with goat lipoidosis ability

	525CC225CC	525CC225CT	525CA225CC	525CA225CT	525AA225TT
Muscle fat grade	-0.7935*	0.4335	0.2286	0.8111*	0.4641
Carcass fat grade	-0.7564*	0.3665	0.1559	0.8490*	0.4180

*$p<0.05$

breeds with higher 525CA225CT genotype frequency ($p<0.05$). The heterozygous at C-525A and C-225T resulted in the increase of goat lipoidosis ability.

DISCUSSION

There have been some reports about the polymorphisms of *PRKAG3* gene and their genetic effects on meat quality in ruminant animals. Lu (2009) found 9 polymorphic loci of the *PRKAG3* gene in 7 sheep breeds, the distribution of which differed. Some polymorphic sites have been detected in the 5' regulatory region and exon 3, 9, 10 and 11 in the foreign and local chicken breeds (Zhao *et al*., 2006). Many mutation sites were found in the exons of pig *PRKAG3* gene (Ciobanu *et al*., 2001; Lindahl *et al*., 2004). In the present study, we have also found 4 polymorphic loci in the 5' regulatory region and exon 13 of *PRKAG3* gene in native goat breeds of China. These results showed that the polymorphism of *PRKAG3* gene was rich in many animals.

AMPK acts as a metabolic master switch regulating several intracellular systems including the cellular uptake of glucose, the β-oxidation of fatty acids and the biogenesis of glucose transporter 4 and mitochondria (Thomson *et al*., 2007). Li *et al*. (2009) found that the polymorphism of *PRKAG3* gene and its association with beef meat tenderness, fleshcolor and some amino acids. The T2885C of two polymorphic sites in intron 4 of cattle *PRKAG3* gene significantly related to meat tenderness. In addition, the mutation of cattle *PRKAG3* gene resulted in change of bovine muscle glycogen content and pH value (Immonen *et al*., 2000). Lu (2009) confirmed that the meat color scores and pH values among genotypes of the sheep *PRKAG3* gene significantly differ. In the chicken *PRKAG3* genes, the 1744 genotype significantly affected on the water content and crude protein content of chicken meat ($p<0.01$) and rate of the chest ($p<0.05$) (Zhou, 2008; Yin *et al*., 2011). The mutation of pig *PRKAG3* gene was significantly associted with carcass quality (Lindahl *et al*., 2004). Amino acid substitutions at some important places of *PRKAG3* protein, I199V, G52S and T30N, might improve the quality of pork and reduce muscle glycogen content (Ciobanu *et al*., 2001). Obviously, the polymorphism of *PRKAG3* gene causes the diversity of AMPK

function, which results in change of the animal meat quality. Present investigation indicated that the heterozygous at C-525A and C-225T in the 5' regulatory region of goat *PRKAG3* gene resulted in the increase of goat lipoidosis ability ($p<0.05$), while the two mutational sites in exon 13 showed the codon non-random usage (Zhang *et al*., 2007) which prefers to uese the CCU for Pro and GAC for Asp.

AP-2 transcription factor binds to GC-rich sequences (Bosher *et al*., 1996). The *cis*-acting DNA sequences 5'-(G/C)CCCA(G/C)(G/C)(G/C)-3' and the palindromic sequences 5'-GCCNNNGGC-3' are considered as consensus AP-2 binding sites (Eckert *et al*., 2005; Debieve *et al*., 2011). The AP-2 is highly involved in the development and function of the central nervous system. Thus, AP-2 has been identified as an important regulator of gene expression during embryonic development of many neural tissues including the midbrain, hindbrain, spinal cord, cranial and dorsal root ganglia (Pfisterer *et al*., 2002). The CCAAT box is one of the most common elements in the promoters of candidate genes with important functions in animal metabolism (Hirwa *et al*., 2011), found in the forward or reverse orientation (ATTGG). The frequency of CCAAT boxes appears to be relatively higher in TATA-less promoters, particularly in the reverse ATTGG orientation (Mantovani, 1998). NF-Y transcription factor binging to the box plays an important role in the regulation of coordinate and tissue-specific gene expression (Dolfini *et al*., 2012). Present investigation found two mutational sites involved in AP-2 binding site at C-525A and NF-Y binding site at C-225T. It is interesting that Matou, Xiangdong and Sanen have higher AP-2 frequency and lower NF-Y frequency in the binding site of transcription factor and lower levels in MFG and CFG. These imply that *PRKAG3* gene influences goat lipoidosis ability via regulating the development and function of goat central nervous system and itself expression level.

CONCLUSION

According to the results of this study, C-525A and C-225T of goat *PRKAG3* gene are two SNP loci affacting MFG and CFG levels of goats. The muscle fat content and carcass fat content are lower in goat breeds with higher 525CC225CC genotype frequency, whhe higher in the breeds with higher 525CA225CT genotype frequency. C-525A and C-225T loci may be associated with the lipoidosis ability of goat breeds.

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