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Polymorphisms in the bovine *CIDEC* gene are associated with body measurement traits and meat quality traits in Qinchuan cattle

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ABSTRACT. Previous studies have shown that the cell death-inducing DFF45-like effector-C (*CIDEC*) gene is involved in lipid storage and energy metabolism, suggesting that it is a potential candidate gene that affects body measurement traits (BMTs) and meat quality traits (MQTs). The aim of this study was to identify polymorphisms of the bovine *CIDEC* gene and analyze their possible associations with BMTs and MQTs in 531 randomly selected Qinchuan cattle aged between 18 and 24 months. DNA sequencing and polymerase chain reaction-restriction fragment length polymorphism were employed to detect *CIDEC* single nucleotide polymorphisms (SNPs). We found five SNPs: two in exon 5 (SNP1, g.9815G>A and SNP2, g.9924C>T) and three in the 3'-untranslated region (SNP3, g.13281C>T; SNP4, g.13297A>G; and SNP5, g.13307G>A). SNP1 was a missense mutation that resulted in an arginine to glutamine amino acid change, and exhibited two genotypes (GG and AG). SNP2 was a synonymous mutation that exhibited three

genotypes (CC, CT, and TT). SNP3, 4, and 5 were completely linked, and only exhibited two genotypes (CC-AA-GG and CT-AG-GA). We found significant associations between these polymorphisms and BMTs and MQTs ($P < 0.05$); GG, CT, and CT-AG-GA appeared to be the most beneficial genotypes. Therefore, *CIDEC* may affect BMTs and MQTs in Qinchuan cattle, and could be used in marker-assisted selection.

Key words: *CIDEC*; Single nucleotide polymorphism; Body measurement trait; Meat quality trait; Qinchuan cattle

INTRODUCTION

The identification of genetic markers that are positively associated with important economic traits in livestock species, such as body measurement traits (BMTs) and meat quality traits (MQTs), has the potential to significantly alter the rate of genetic improvement through the use of marker-assisted selection (MAS) (Nkrumah et al., 2004).

Beef is a nutrient-rich food, and contains high-quality protein, vitamin B, niacin, zinc, and iron. Qinchuan are yellow cattle that are indigenous to China, and exhibit a slow growth rate and an underdeveloped hind hip. It is necessary to identify important functional bovine genes by MAS, in order to accelerate the efficiency of Chinese beef cattle breeding.

Cell death-inducing DFF45-like effector-C (*CIDEC*) belongs to the CIDE family, which includes *CIDEA*, *CIDEB*, and *CIDEC/Fsp27* (Inohara et al., 1998), and is a homolog of rodent *Fsp27* (Fat-specific protein 27), which is associated with lipid and energy metabolism as well as obesity and obesity-related metabolic disturbances, such as insulin resistance and type 2 diabetes mellitus (Liang et al., 2003; Puri et al., 2007; Keller et al., 2008; Nishino et al., 2008; Toh et al., 2008). Peroxisome proliferator activated receptor-γ (*PPAR*γ) and CCAAT/enhancer-binding protein are considered to be key in regulating the transcription of *Fsp27* (Danesch et al., 1992). Similarly, *CIDEC* is predominantly expressed in adipose tissue, but has also been detected in the small intestine, heart, colon, and stomach, suggesting that *CIDEC* is not adipose tissue-specific (Liang et al., 2003; Magnusson et al., 2008). *CIDEC* allows adipocytes to adjust their metabolisms according to changes in whole-body energy availability, and facilitates lipid storage during periods of energy surplus (Magnusson et al., 2008). Li et al. (2010) suggested that *CIDEC* is essential for the formation and maturation of lipid droplets in adipocytes, and the regulation of adipocyte lipid metabolism. Recent studies have revealed that *PPAR*γ is an important regulator of the transcriptional activity of *CIDEC* during adipogenesis (Kim et al., 2008).

In 2009, a female patient was found to be homozygous for a single nucleotide polymorphism (SNP) involving a G to T transversion in *CIDEC* exon 6, which caused a Glu 186 X nonsense mutation in the CIDE-C domain that has been identified as an autosomal recessive form of familial partial lipodystrophy (Rubio-Cabezas et al., 2009). In addition, it is noteworthy that *CIDEC* hepatic expression levels positively correlate with the body mass index (Hall et al., 2010).

Considering the importance of *CIDEC* in energy and lipid metabolism, as well as in metabolic disorders, it may be an attractive candidate gene for BMTs and MQTs in cattle. Therefore, in this study we aimed to detect polymorphisms in the bovine *CIDEC* gene, and evaluate their associations with BMTs and MQTs in Qinchuan cattle. The results of this study further our knowledge of the functions of *CIDEC*, and are useful for future studies into this topic.

MATERIAL AND METHODS

DNA samples and data collection

Blood samples from 531 randomly selected individuals aged between 18 and 24 months from a breeding Qinchuan cattle population were used to analyze *CIDEC* allelic frequencies. BMTs were measured as previously described (Gilbert et al., 1993), including body length (BL), withers height (WH), hip height (HH), rump length (RL), hip width (HW), chest depth (CD), heart girth (HG), and pin bone width (PBW). Ultrasound backfat thickness (UBT) and ultrasound loin muscle area (ULA) were measured to evaluate MQTs (Brethour, 1994; Hamlin et al., 1995). A single person was appointed to measure each of the ten traits, in order to minimize systematic error.

Genomic DNA samples were extracted from the blood samples using a standard phenol-chloroform method (Müllenbach et al., 1989), and subsequently stored at -80°C.

Polymerase chain reaction (PCR) and DNA sequencing

Based upon the bovine *CIDEC* gene sequence (AC_000179), primers were designed to amplify fragments of *CIDEC* exon 5 and the 3'-untranslated region (UTR) using the PRIMER 5 software (Table 1). PCR amplifications were performed in a 20-μL reaction mixture containing 50 ng DNA, the primers (10 pM each), 0.20 mM dNTPs, 2.5 mM $MgCl_2$, and 0.5 U *Taq* DNA polymerase (TaKaRa, Dalian, China). The PCR protocol was as follows: 95°C for 5 min, 35 cycles of denaturing at 94°C for 30 s, annealing at Tm °C (Table 1) for 30 s, and extension at 72°C for 30 s, with a final extension at 72°C for 10 min. The products for sequencing were first electrophoresed on 1.5% agarose gels (containing 200 ng/mL ethidium bromide), and then purified using an Axygen™ kit (BMI Fermentas, Glen Burnie, MD, USA), and sequenced in both directions in an ABI PRIZM 377 DNA sequencer (Perkin-Elmer). The DNASTAR software package was used to analyze the sequence maps.

Table 1. Primers used to amplify the bovine *CIDEC* gene.

Amplified region		Primer	Tm (ºC)	Size (bp)
Exon 5	Primer A	F: 5'-TGGCAGCCCCCATCAGAAC-3' R: 5'-GTATCCAGATTCCACCAGCAG-3'	64.2	516
3'-UTR	Primer B	F: 5'-GCAGGCATTTAGAAGAGGC-3' R: 5'-TGAGGGAGATGTAGGAAGGT-3'	57.7	332

Tm = melting temperature.

Genotyping *CIDEC* alleles by PCR-restriction fragment length polymorphism (PCR-RFLP)

Five novel SNPs were found in the bovine *CIDEC* gene by DNA sequencing, two in exon 5 (SNP1, g.9815G>A, Figure 1A and B; and SNP2, g.9924C>T, Figure 2A, B, and C) and three in the 3'-UTR (SNP3, g.13281C>T; SNP4, g.13297A>G; and SNP5, g.13307G>A; Figure 3A and B). It is worth noting that SNP3, 4, and 5 were completely linked (data not shown).

Finally, SNP1, 2, and 5 were chosen for further genotype detection by RFLP; aliquots (10 μL) of the PCR products were digested with 10 U *Eco*88I, *Msp*I, and *Msp*I, respectively (TaKaRa) at 37°C for 16 h, following the instructions provided in the supplier's manual. The digested products were detected by electrophoresis on a 1.5% agarose gel stained with ethidium bromide.

Statistical analysis

Genotypic frequencies, allelic frequencies, Hardy-Weinberg equilibrium, gene homozygosity, gene heterozygosity, effective allele numbers, and the polymorphism information content (PIC) were statistically analyzed according to previous studies (Nei and Roychoudhury, 1974; Nei and Li, 1979). Associations between the SNP-marker genotypes of *CIDEC* and body measurement and meat quality traits (BL, WH, HH, RL, HW, CD, HG, PBW, UBT, and ULA) were analyzed using the SPSS software (version17.0), according to the following linear model:

$$Y_{ijk} = \mu + G_i + A_j + \varepsilon_{ijk}$$

where Y_{ijk} is the measurement of the trait, μ is the overall mean for each trait, G_i is the genotype effect, A_j is the fixed effect of age, and ε_{ijk} is the random error.

RESULTS

Genetic polymorphisms of *CIDEC* and chi-square test

As previously described in this paper (see Material and Methods), five SNPs were detected in the bovine *CIDEC* gene. At the SNP1 site, which resulted in a missense mutation of arginine to glutamine, two genotypes were present, namely GG and AG (Figure 1A and B). SNP2 was a synonymous mutation with three genotypes, namely CC, CT, and TT (Figure 2A, B, and C). SNP3, 4, and 5 were completely linked and had two genotypes, namely CC-AA-GG and CT-AG-GA (Figure 3A and B).

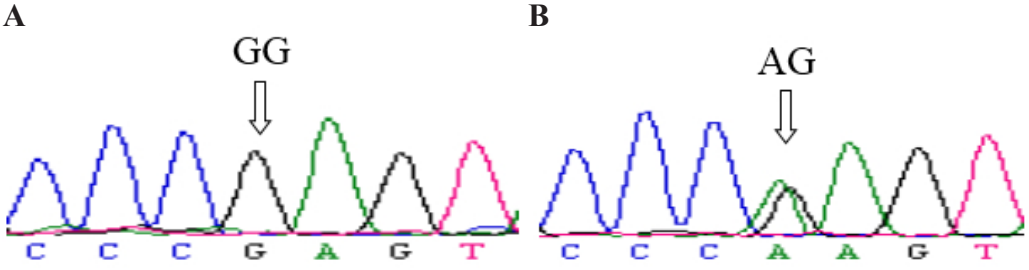

Figure 1. A. and **B.** Sequencing map of SNP1 in the bovine *CIDEC* gene exon 5 (9815-bp locus).

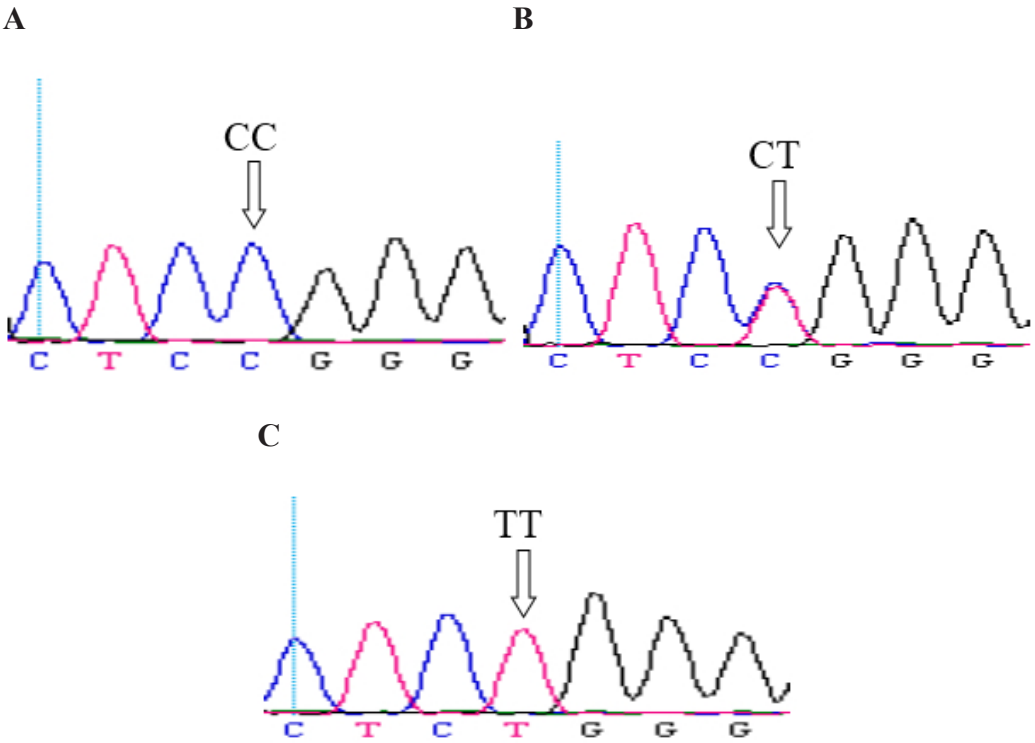

Figure 2. A.-C. Sequencing map of SNP2 in the bovine *CIDEC* gene exon 5 (9924-bp locus).

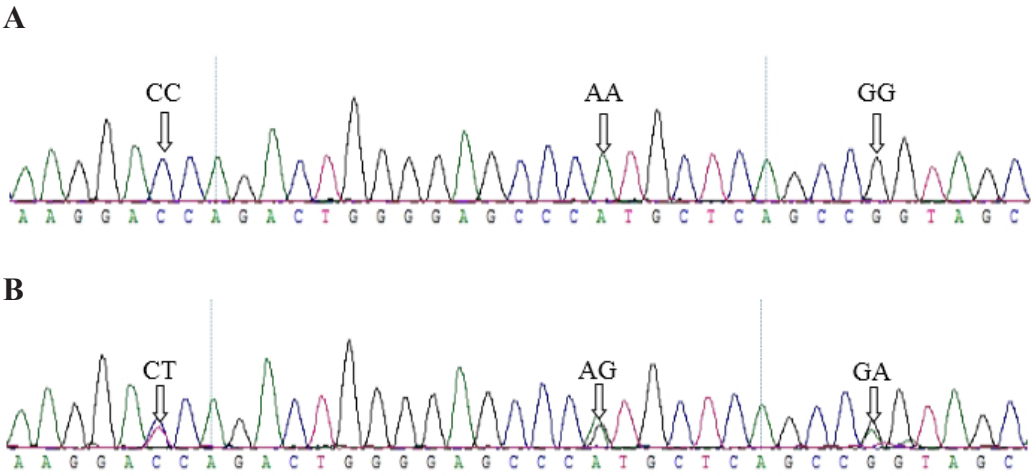

Figure 3. A. and **B.** Sequencing map of SNP3-SNP4-SNP5 in the bovine *CIDEC* gene 3'-untranslated region (13281-, 13297-, and 13307-bp locus).

The products of Primer A were digested with *Eco*88I endonuclease to genotype SNP1, and the electrophoretic pattern obtained revealed two fragments (358 and 158 bp) for genotype GG and three fragments (516, 358, and 158 bp) for the heterozygote AG (Figure 4). SNP2 was genotyped by the *Msp*I endonuclease, and the resulting electrophoretic pattern revealed two fragments (267 and 247 bp) for genotype CC, three fragments (516, 267, and 247 bp) for CT, and one 516-bp fragment for TT (Figure 5). It should be pointed out that the difference between the 267- and 247-bp fragment lengths was extremely small; consequently, they were difficult to separate, but this did not affect the identification of the genotypes of this SNP. The 332-bp products of Primer B were digested with *Msp*I to genotype SNP3-SNP4-SNP5, which revealed two fragments (274 and 58 bp) for genotype CC-AA-GG and three (332, 274, and 58 bp) for CT-AG-GA (Figure 6).

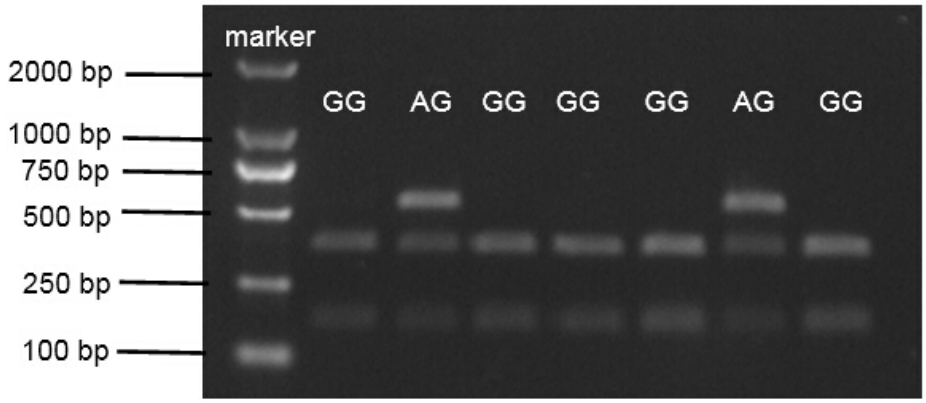

Figure 4. Polymerase chain reaction-restriction fragment length polymorphism electrophoresis patterns of the bovine *CIDEC* gene exon 5 (9815-bp locus).

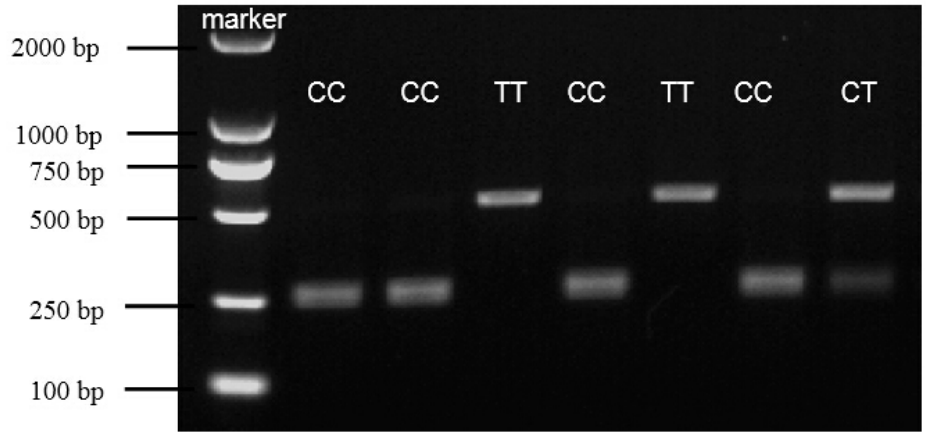

Figure 5. Polymerase chain reaction-restriction fragment length polymorphism electrophoresis patterns of the bovine *CIDEC* gene exon 5 (9924-bp locus).

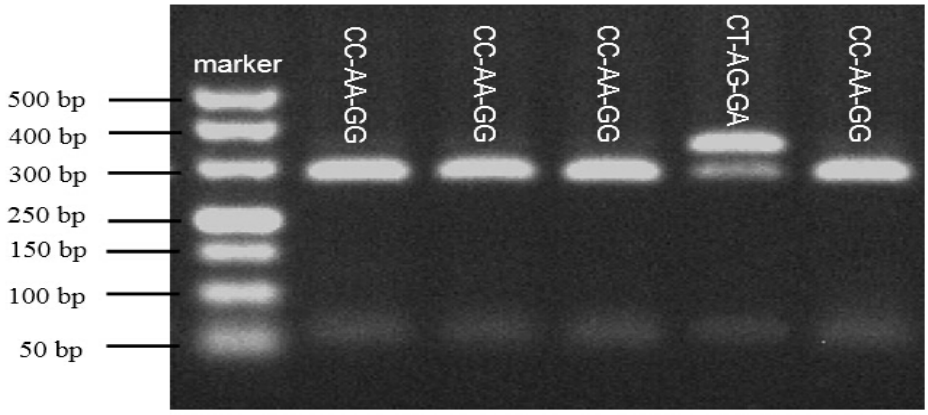

Figure 6. Polymerase chain reaction-restriction fragment length polymorphism electrophoresis patterns of the bovine *CIDEC* gene 3'-UTR (13307-bp locus).

The genetic diversity and population genetic characteristics of each locus are presented in Tables 2 and 3. A chi-square test indicated that the genotype distributions of SNP2 and SNP3-SNP4-SNP5 were in Hardy-Weinberg equilibrium ($\chi^2 < \chi_{0.05}^2$), except for the SNP1 mutation ($\chi_{0.05}^2 < \chi^2 < \chi_{0.01}^2$). According to the PIC, the experimental Qinchuan cattle population exhibited a medium level of polymorphism at SNP2 and low levels of polymorphism at SNP1 and SNP3-SNP4-SNP5.

Table 2. Genotypic and allelic frequencies (%) of *CIDEC* gene single nucleotide polymorphisms (SNPs) in Qinchuan cattle.

SNP	Observed genotype (number)	Total	Frequency		χ^2 (HWE)
			Genotype	Allele	
SNP1	GG (N = 423)	531	0.7966	G = 0.8983	6.8053
	AG (N = 108)		0.2034	A = 0.1017	
SNP2	CC (N = 282)	531	0.5311	C = 0.7232	0.8709
	CT (N = 204)		0.3842	T = 0.2768	
	TT (N = 45)		0.0847		
SNP3-SNP4-SNP5	CC-AA-GG (N = 466)	531	0.8776	C-A-G = 0.9388	2.2570
	CT-AG-GA (N = 65)		0.1224	T-G-A = 0.0612	

HWE = Hardy-Weinberg equilibrium; $\chi_{0.05}^2 = 5.991$, $\chi_{0.01}^2 = 9.21$.

Table 3. Population genetic characteristics of *CIDEC* gene single nucleotide polymorphisms (SNPs) in Qinchuan cattle.

SNP	Gene homozygosity	Gene heterozygosity	Effective allele number	Polymorphism information content (PIC)
SNP1	0.8173	0.1827	1.2236	0.1660
SNP2	0.5996	0.4004	1.6678	0.3202
SNP3-SNP4-SNP5	0.8851	0.1149	1.1298	0.1083

PIC > 0.5 indicates a high level of polymorphism, 0.25 < PIC < 0.5 indicates a moderate level of polymorphism, and PIC < 0.25 indicates a low level of polymorphism.

Associations between polymorphisms and BMTs and MQTs

Associations between the *CIDEC* polymorphisms and eight BMTs (BL, WH, HH, RL, HW, CD, HG, and PBW) and two MQTs (UBT and ULA) for the five SNPs are presented in Tables 4, 5, and 6.

In light of the information in Table 4, an association analysis of the polymorphisms with BMTs and MQTs at SNP1 revealed that the mean values of animals with the genotype GG were significantly higher than those with the genotype AG for BL, CD, and HG ($P < 0.01$). In addition, there were significant differences in RL and ULA between the two genotypes ($P < 0.05$). No association was found between any genotype and the other traits. Therefore, we believe that the missense mutation at the SNP1 locus may affect BMTs and MQTs in cattle, and could be used for MAS.

Table 4. Associations between SNP1 genotypes of the *CIDEC* gene and body measurement and meat quality traits in Qinchuan cattle.

Trait (means ± SE)		Genotype	
		GG	AG
Body measurement trait	BL (cm)	134.445 ± 0.752^{A}	130.111 ± 1.264^{B}
	WH (cm)	120.916 ± 0.484	120.311 ± 1.076
	HH (cm)	123.603 ± 0.428	123.000 ± 0.950
	RL (cm)	42.206 ± 0.245^{a}	41.028 ± 0.561^{b}
	HW (cm)	38.837 ± 0.339	38.931 ± 0.648
	CD (cm)	59.291 ± 0.415^{A}	56.729 ± 0.797^{B}
	HG (cm)	164.131 ± 1.028^{A}	158.069 ± 1.971^{B}
	PBW (cm)	18.553 ± 0.183	18.431 ± 0.425
Meat quality trait	UBT (cm)	0.920 ± 0.021	0.873 ± 0.038
	ULA (cm^2)	47.609 ± 0.960^{a}	42.531 ± 1.802^{b}

^{a,b}Means with different superscripts were significantly different ($P < 0.05$). ^{A,B}Means with different superscripts were significantly different ($P < 0.01$). SE = standard error.

At the SNP2 locus (Table 5), there were highly significant differences between the CT and CC genotypes with CD, HG, UBT, and ULA, and between the CT and TT genotypes with CD ($P < 0.01$). Individuals with the CT genotype had significantly higher mean values than those with the TT genotype for BL, WH, HW, HG, PBW, and ULA ($P < 0.05$). In most cases, the CT genotype had the highest mean value, and may be the most beneficial genotype.

Table 5. Associations between SNP2 genotypes of the *CIDEC* gene and body measurement and meat quality traits in Qinchuan cattle.

Trait (means ± SE)		Genotype		
		CC	CT	TT
Body measurement trait	BL (cm)	133.098 ± 0.884	135.007 ± 1.089^{a}	129.933 ± 2.177^{b}
	WH (cm)	120.316 ± 0.590	122.033 ± 0.752^{a}	118.167 ± 1.295^{b}
	HH (cm)	123.319 ± 0.515	124.151 ± 0.662	121.450 ± 1.363
	RL (cm)	41.782 ± 0.309	42.478 ± 0.381	40.800 ± 0.611
	HW (cm)	38.745 ± 0.398	39.493 ± 0.511^{a}	36.667 ± 0.873^{b}
	CD (cm)	58.122 ± 0.462^{A}	60.180 ± 0.672^{B}	56.433 ± 1.050^{A}
	HG (cm)	161.144 ± 1.204^{A}	166.353 ± 1.553^{aB}	158.233 ± 2.961^{b}
	PBW (cm)	18.442 ± 0.229	18.890 ± 0.276^{a}	17.433 ± 0.556^{b}
Meat quality trait	UBT (cm)	0.874 ± 0.024^{A}	0.976 ± 0.033^{B}	0.845 ± 0.030
	ULA (cm^2)	44.875 ± 1.120^{A}	49.969 ± 1.460^{aB}	41.856 ± 2.396^{b}

BL = body length; WH = withers height; HH = hip height; RL = rump length; HW = hip width; CD = chest depth; HG = heart girth; PBW = pin bone width; UBT = ultrasound backfat thickness; ULA = ultrasound loin muscle muscle area. ^{a,b}Means with different superscripts were significantly different ($P < 0.05$). ^{A,B}Means with different superscripts were significantly different ($P < 0.01$).

The results of an association analysis between the polymorphisms in the *CIDEC* 3'-UTR and the BMTs and MQTs are presented in Table 6. HG, UBT, and ULA were significantly different between CT-AG-GA and CC-AA-GG ($P < 0.01$), and individuals with the CT-AG-GA genotype had significantly higher mean values for HW and CD ($P < 0.05$). Therefore, the CT-AG-GA genotype could be a valuable molecular marker for selecting desired BMTs and MQTs in Qinchuan cattle.

Table 6. Associations between SNP3-SNP4-SNP5 genotypes of the *CIDEC* gene and body measurement and meat quality traits in Qinchuan cattle.

Trait (means ± SE)		Genotype	
		CC-AA-GG	CT-AG-GA
Body measurement trait	BL (cm)	133.137 ± 0.708	136.651 ± 1.711
	WH (cm)	120.545 ± 0.477	122.593 ± 1.159
	HH (cm)	123.220 ± 0.425	125.361 ± 0.936
	RL (cm)	41.830 ± 0.246	42.954 ± 0.555
	HW (cm)	38.624 ± 0.327^{a}	40.535 ± 0.668^{b}
	CD (cm)	58.478 ± 0.398^{a}	60.884 ± 0.985^{b}
	HG (cm)	161.933 ± 0.982^{A}	169.884 ± 2.400^{B}
	PBW (cm)	18.437 ± 0.183	19.186 ± 0.433
Meat quality trait	UBT (cm)	0.892 ± 0.019^{A}	1.042 ± 0.059^{B}
	ULA (cm^2)	45.688 ± 0.896^{A}	53.001 ± 2.534^{B}

^{a,b}Means with different superscripts were significantly different ($P < 0.05$). ^{A,B}Means with different superscripts were significantly different ($P < 0.01$). For abbreviations, see Table 5.

DISCUSSION

With the development of molecular breeding technology in recent years, MAS has become an effective way for breeders to mark and identify quantitative trait loci (QTLs) in order to improve domestic animals' economically important traits and breeding efficiency (Wu et al., 2005). Candidate genes are crucial tools for investigating and localizing target genes that affect quantitative traits, by determining the relative magnitudes of polymorphic effects (Rothschild and Soller, 1997). Previous studies have followed the candidate gene approach with respect to milk production (Zhou and Dong, 2012), growth (Zhang et al., 2013), physiological processes (Wang et al., 2013), and meat quality (Liu et al., 2012; Fu et al., 2013).

The *CIDEC* gene plays important roles in regulating energy availability (Magnusson et al., 2008), lipid metabolism (Kim et al., 2008; Li et al., 2010), and the body mass index (Hall et al., 2010), and its polymorphisms may be used to investigate human partial lipodystrophy and 'ketosis-prone' insulin-resistant diabetes (Rubio-Cabezas et al., 2009). The present study provides evidence that *CIDEC* may also influence BMTs and MQTs. We found five *CIDEC* SNPs in this study, and associations between these and eight BMTs (BL, WH, HH, RL, HW, CD, HG, and PBW) and two BMTs (UBT and ULA) were analyzed in 531 Qinchuan cattle.

SNP1 was a missense mutation that resulted in a change from arginine to glutamine, and exhibited GG and AG genotypes. SNP2 was a synonymous mutation, and exhibited CC, CT, and TT genotypes. Importantly, SNP3, 4, and 5 were completely linked, and only exhibited two genotypes (CC-AA-GG and CT-AG-GA). The absence of a third genotype at the SNP1 and SNP3-SNP4-SNP5 mutations may be because a third genotype does not exist in Qinchuan cattle, or because the sample size was too small. SNP3, 4, and 5 were in complete linkage disequilibrium, which may have been related to the short distances between them.

SNP1 was associated with BL, RL, CD, HG, and ULA, and the GG genotype appeared to be the most beneficial genotype; the replacement of arginine with glutamine may affect the function of the protein produced by *CIDEC*. SNP2 was associated with BL, WH, HW, CD, HG, PBW, UBT, and ULA, and the CT genotype was the most beneficial. This synonymous mutation may indirectly affect messenger RNA splicing, stability, structure, as well as protein folding. These changes might have a significant effect on altering the structure, function, or expression levels of proteins (Hunt et al., 2009). SNP3-SNP4-SNP5 was associated with HW, CD, HG, UBT, and ULA, and the CT-AG-GA genotype was the most beneficial. The 3'-UTR is known to play crucial roles in the post-transcriptional regulation of gene expression, including nucleocytoplasmic transport (Köhler and Hurt, 2007), stability (Borrmann et al., 2001; Kamiyama et al., 2007), translation efficiency (Kindler et al., 2005; Piccone et al., 2009), and subcellular localization (Narsai et al., 2007; Thomsen et al., 2010). In addition, the binding sequence of the molecular regulator miRNA is usually located in the 3'-UTR (Grillo et al., 2010). Therefore, mutations in the 3'-UTR of the *CIDEC* gene might modulate the gene's expression levels, through a mechanism that is yet to be discovered.

In conclusion, based on the results obtained in this study, it can be inferred that *CIDEC* mutations affect the BMTs and MQTs of Qinchuan cattle. Further studies should be conducted that investigate the mechanism involved, and the significance of the polymorphisms to BMTs and MQTs of cattle in different populations, and with larger sample sizes.

Conflicts of interest

The authors declare no conflict of interest.

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