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RESEARCH ARTICLE

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Variation of 184C→T of goat *callipyge* gene in different populations and its effect on body weight

Abstract In order to investigate its distribution in different goat populations, one SNP (184C→T, corresponding to AY850925) of goat *callipyge* (*CLPG*) gene recognized by Fork I was identified after sequencing 23 individuals from 10 breeds. PCR-RFLP was carried out according to the variation site in 584 goats of 14 populations from 11 provinces and autonomous regions in China. An interesting result was found that the Boer goat having the characteristics of double muscle had significantly higher T allele (0.2465) frequency and lower C allele (0.7535) frequency compared to other breeds. It could be inferred that the 184C→T mutation might be related to the double muscle characteristics of the Boer goat. The general linear model analysis showed that parental genotype had significant effect on the body weight of their offspring at different ages. It could be inferred that transition of 184C→T might be a paternal imprinting form, a polar over-dominance, in which only individuals that received the allele from their mother expressed the *callipyge* phenotype. The double muscle characteristics of the Boer goat might be related to its maternal genotype. More data with detailed information need to be investigated in order to confirm this assumption.

Keywords goat, *callipyge*, 184C→T, double muscle, body weight

1 Introduction

In 1983, the *callipyge* phenotype was first identified in a Dorset ram transmitting an extremely heavily muscled phenotype to some of his offspring with *callipyge* (from Greek calli-, beautiful; -pyge, buttocks) and the symbol *CLPG* was proposed for this gene (Cockett et al., 1994). The *CLPG* locus was mapped to the terminal region of the ovine chromosome 18 and exhibits a unique form of parental imprinting and polar over-dominance, in which only individuals received the allele from their sire and expressed *callipyge* phenotype (Cockett et al., 1994, 1996; Freking et al., 1998; Lien et al., 1999; Shay et al., 2001). The magnitude of expression of *callipyge* gene depended upon the location of muscles in the body, and the increased muscle mass was concentrated in the legs and loins (Jackson et al., 1997a). Lambs expressing the *callipyge* gene had higher dressing percentage, leg and conformation scores, and larger longissimus muscle areas. Their carcasses had higher protein, moisture, and ash percentages and lower fat percentage, which suggested that ram lambs expressing the *callipyge* had an advantage in retail yield and carcass conformation (Jackson et al., 1997b). Use of *CLPG* mutant allele in structured mating systems could dramatically increase the production of lean lamb (Freking et al., 1998).

It was shown that the *CLPG* phenotype of sheep resulted from the transition of 267A→G, by analyzing sheep STS (AF401294) (Freking et al., 2002; Smit et al., 2003). Similar region containing ovine *callipyge* mutation was obtained for pig (AY167895 and AY682208), horse (AY167898), cattle (AY167897), rabbit (AY167900), dog (AY167901), goat (AY884304 and AY850925), Aoudad (AY167896), Gray squirrel (AY167902), Norway rat (AY167894), and Meadow vole (AY167893) (Smit et al., 2003). The *CLPG* gene of pig and cattle was also mapped on chromosome 7 (AY682208) and 21 (Fahrenkrug et al., 2000). We analyzed the bioinformatics of partial *CLPG* gene sequences among different species and predicted its position on goat chromosome (Shen et al., 2007). Meanwhile, we found 184C→T variation site of goat *CLPG* gene and suggested that there might be a relationship between 184C→T and the trait of *callipyge* in goat (Wang et al., 2007). Boer goat is one of the most famous meat-oriented goat breeds in the world, with more obvious

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muscular hypertrophy condition at the neck, breast, shoulder, back, loin, and buttocks than other goat breeds. In this article, the 184C→T was confirmed again by sequencing. Then the distribution of this SNP in Boer goat and 13 other Chinese indigenous goat breeds, and its association with body weight at different ages were investigated for discovering its possible role in controlling the double muscle trait in goats.

2 Materials and methods

2.1 Samples and DNA extraction

A total of 584 blood samples from goats of 14 populations (13 Chinese indigenous goat breeds and 1 imported goat breed, Boer goat) were collected from 11 provinces and autonomous regions in China (Table 1). The samples were divided into three groups, South (243), North (270), and Foreign (71), according to their distributions (Compiling Group of Sheep and Goat Breeds in China, 1989) (Table 1). The South group included Chengdu brown goat, Nanjiang brown goat from Sichuan Province, Guizhou white goat, and Guizhou black goat from Guizhou Province, Duan goat from Guangxi Province, Leizhou goat from Guangdong Province, and Yichang white goat from Hubei Province. The North group included Inner Mongolia cashmere goat from Inner Mongolia Autonomous Region, Liaoning cashmere goat from Liaoning Province, Taihang mountain goat and Chengde polled goat from Hebei Province, Shannan white goat from Shaanxi Province, and Jining grey goat from Shandong Province. The Foreign group had Boer goat imported from South Africa and sampled from Hebei Province. The samples were collected and stored at −70°C prior to DNA extraction, which was conducted by the Phenol extraction method.

2.2 Primer, PCR amplification, and sequencing

The primer used for amplifying goat *CLPG* gene was from that of sheep *CLPG* gene (AF401294). The forward and reverse primers were 5′-tgaaaacgtgaacccagaagc-3′ and 5′-ggcaggagagacggttaat-3′, respectively, and were synthesized by TaKaRa Biotechnology Co. Ltd. (Dalian, China). The theoretical length of an amplified goat *CLPG* gene should be 493 bp according to the sheep *CLPG* gene (AF401294).

PCR was carried out in Programmable Thermal Controller (German Biometra) with a total volume of 30 μL reaction system containing 4 μL (75 ng·μL^{-1}) of goat genomic DNA, 3 μL of 10 × PCR standard reaction buffer, 2.4 μL dNTPs (2.5 pmol·L^{-1} of each deoxynucleotide), 1.2 μL (10 pmol·L^{-1}) of each forward and reverse primer, 0.3 μL (5U·μL^{-1}) of Taq DNA polymerase (TaKaRa Biotechnology Co. Ltd., Dalian, China) and 17.9 μL of distilled water. After pre-denaturation for 3 min at 94°C, the PCR profile consisted of a denaturation step at 94°C for 45 s, an annealing step at 55°C for 45 s, and an elongation step at 72°C for 1 min for a total of 34 cycles, followed by a final extension of 10 min at 72°C. The PCR products were run on 1.5% agarose gel including 0.5 mg·mL^{-1} of

Table 1 Distribution of *CLPG* genotypes and alleles in different populations

group	breed	location (province)	num.	genotype			frequency/%	
				CC	CT	TT	C	T
north	Liaoning cashmere goat	Liaoning	71	71	0	0	1.0000^{aA}	0
	Jining grey goat	Shandong	69	64	5	0	0.9637^{aA}	0.0363
	Chengde polled goat	Hebei	55	55	0	0	1.0000^{aA}	0
	Taihang mountain goat	Hebei	33	33	0	0	1.0000^{aA}	0
	Inner Mongolia cashmere goat	Inner Mongolia	22	18	4	0	0.9091^{a}	0.0909
	Shannan white goat	Shanxi	20	20	0	0	1.0000^{aA}	0
south	Chengdu brown goat	Sichuan	54	54	0	0	1.0000^{aA}	0
	Nanjiang brown goat	Sichuan	61	56	5	0	0.9590^{aA}	0.0410
	Guizhou white goat	Guizhou	30	30	0	0	1.0000^{aA}	0
	Yichang white goat	Hubei	18	16	2	0	0.9446^{a}	0.0554
	Duan goat	Guangxi	19	17	2	0	0.9473^{a}	0.0527
	Guizhou black goat	Guizhou	25	24	1	0	0.9800^{aA}	0.0200
	Leizhou goat	Guangdong	36	35	1	0	0.9861^{aA}	0.0139
foreign	Boer goat	Hebei	71	43	21	7	0.7535^{bB}	0.2465
total			584	536	41	7	–	–

Note: The C frequency marked with different small and capital letters represents significance at 0.05 and 0.01 probability levels, respectively.

ethidium bromide, and visualized and photographed with the help of a gel automatic photographer under UV light.

A total number of 23 goats from 10 breeds (five Boer goats, three Chengdu brown goats, three Nanjiang brown goats, three Leizhou goats, three Jining grey goats, three Liaoning cashmere goats, and three Chengde polled goats) were amplified first for sequencing in order to screen SNPs. The PCR products were sequenced by Shanghai Sangon Biological Engineering & Technology services Co. Ltd. (Shanghai, China).

2.3 PCR-RFLP of goat *CLPG* and genotype determination

In order to identify the SNP of goat *CLPG* gene, 23 sequenced individuals were aligned by BioEdit software (Version 7.0) with two Tibetan goat sequences (AY850925 and AY884304). The transition of 184C→T was defined after aligning and checking for sequencing results (A, C, D, and E in Fig. 1). The PCR-RFLP was carried out according to the variation site (184C→T). Fork I (TaKaRa Biotechnology Co. Ltd., Dalian, China) recognizing GGATG and cutting at positions 194 and 444 was selected according to the variation, using Webcutter 2.0 (http://users.unimi.it/~camelot/tools/cut2.html). The digestion solution with a total volume of 10 μL containing 6.5 μL of PCR products, 0.3 μL (5 U·uL^{-1}) of Fork I, 1.2 μL of distilled water, 1.0 μL 0.1% BSA, and 1.0 μL of 10 × buffer, was incubated at 37°C for 2 h in the Programmable Thermal Controller. The genotype was detected by running digested products on 1.5% agarose gel including 0.5 mg·mL^{-1} of ethidium bromide. Homozygote CC was defined when base C was present at position 184, forming GGACG but not recognized by Fork I, and forming 444 bp and 49 bp (B in Fig. 1, invisible on agarose gel for 49 bp fragment, same as below), homozygote TT was defined when base T was present at position 184 forming GGATG, recognized by Fork I, forming 250 bp, 194 bp, and 49 bp, and heterozygote CT was defined when C and T were both present at the same position on the homologous chromosome, forming 444 bp, 250 bp, 194 bp, and 49 bp.

2.4 Statistical analysis of the relationship between 184C→T and body weight

A total of 247 individuals (131 males and 116 females) including 71 Boer goats and another 176 upgrading offspring of the Boer goat to Tangshan dairy goat with body weight records and identified genotypes of *CLPG* gene using PCR-RFLP mentioned earlier were collected

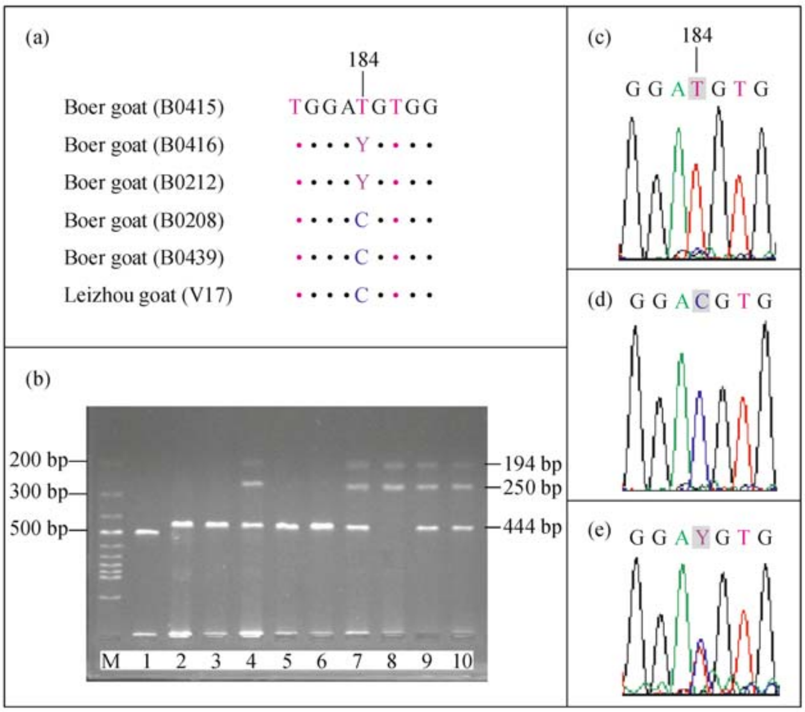

Fig. 1 Alignment of varied individuals, SNP identification and PCR-RFLP by Fork I

Note: (a) represents the alignment of varied individuals. (b) represents the result of PCR-RFLP by Fork I. M refers to DNA marker. Lane 1 illustrates PCR products of *CLPG*. Lanes 2, 3, 5 and 6 illustrate genotype CC with bands of 444 bp and 49 bp (invisible). Lanes 4, 7, 9 and 10 illustrate genotype CT with bands of 444 bp, 250 bp, 194 bp and 49 bp (invisible). Lane 8 illustrates genotype TT. (c), (d) and (e) are SNP identification for genotype TT, CC and CT (Y), respectively.

from the Boer goat farm in Qinhuangdao City, Hebei Province. According to birth types, all the individuals were sorted into single birth (66), twin births (139), and triplet births (42). The body weight records were marked at birth, and in one week, two weeks, three weeks, one month, two months, three months, and four months, respectively.

The statistical objective was to investigate the effect of paternal genotype, maternal genotype, interaction of paternal and maternal genotype, and individual genotype on body weight at different ages. According to the data type, some other factors also affected the dependent variable and body weight. Therefore, the general linear model, $Y = \mu + B + S + T + P + M + P{*}M + G + e$, was selected according to the data type, where the cardinals B, S, T, P, M, $P{*}M$ and G, and the fixed factors, represent the effect of breed type (Boer goat and its upgrading offspring), sex (male and female), birth type (single, twin, or triplet birth), paternal genotype, maternal genotype, interaction of paternal and maternal, and genotype of individuals. μ and e represent the population mean and error. SPSS software (version 13.0) was used to analyze the genotype effect.

The chi-square test for crosstables or Fisher's exact test was performed to analyze differences in allele frequencies between two populations using SPSS software (version 13.0).

3 Results

3.1 SNP of goat *CLPG* gene and its distribution in different populations

The substitution of 184C→T was detected according to the alignment of 23 sequenced individuals with two Tibetan sequences from GenBank (AY850925 and AY884304). Genotyping results using PCR-RFLP with Fork I for individuals from different populations are listed in Table 1. The results indicated that the transition of 184C→T was monomorphic in Liaoning Cashmere goat, Chengde polled goat, Taihang Mountain goat, Shannan white goat, Chengdu brown goat, and Guizhou white goat. The populations which were polymorphic at 184C→T were all in the Hardy-Weinberg equilibrium. The gene frequency did not display a significant difference among Chinese indigenous goat breeds, but it was significant ($P < 0.05$ or $P < 0.01$) between Chinese indigenous goat breeds and the Boer goat imported from South Africa.

3.2 Genotype effects of goat *CLPG* gene on body weight at different ages

The general linear model was significant ($P < 0.01$) for body weight at different ages, and the adjusted R squared of the model ranged from 0.964 to 0.981 (Table 2). In this model, the effect of the individual on body weight at different ages was not significant ($P > 0.05$, Table 2). The effect of breed and sex on body weight was significant ($P < 0.01$, $P < 0.05$, Table 2) from birth to two weeks, but were not significant from three weeks to four months ($P > 0.05$, Table 2). It showed that the effect of breed and sex on body weight decreased with an increase in age. It could also be seen from Table 2 that there was a significant effect of birth type, genotype of paternal and maternal genotype, and the interaction of paternal and maternal genotype ($P < 0.01$, $P < 0.05$, Table 2). The pair wise comparisons between estimated marginal means of body weight at different ages from paternal, maternal, and individual genotypes are listed in Table 3, and the interaction between paternal and maternal genotype is shown in Table 4.

4 Discussion

It has been known that the *CLPG* phenotype of sheep results from the transition of 267A→G, by analyzing the sheep STS (AF401294) (Freking et al., 2002; Smit et al., 2003). It can be seen from Table 1 that the populations with polymorphic at 184C→T were all in Hardy-Weinberg equilibrium, and most of the Chinese indigenous goat

Table 2 The effects (P values) of the model and factors included in the model

trait	model	B	S	T	P	M	$P{*}M$	G	R^2
BW0/kg	0.000	0.000	0.025	0.000	0.013	0.003	0.040	0.451	0.977
BW1/kg	0.000	0.001	0.030	0.000	0.043	0.008	0.011	0.234	0.979
BW2/kg	0.000	0.004	0.031	0.000	0.041	0.006	0.046	0.367	0.981
BW3/kg	0.000	0.108	0.213	0.000	0.046	0.008	0.039	0.556	0.978
BW4/kg	0.000	0.084	0.436	0.000	0.033	0.014	0.044	0.415	0.975
BW8/kg	0.000	0.653	0.220	0.004	0.046	0.031	0.036	0.591	0.969
BW12/kg	0.000	0.970	0.200	0.008	0.035	0.038	0.041	0.601	0.964
BW16/kg	0.000	0.430	0.133	0.003	0.038	0.044	0.038	0.455	0.971

Note: BW0–4, 8, 12 and 16 represent body weight at birth, in one week, two weeks, three weeks, one month, two months, three months, and four months, respectively. The same definition is shown in Tables 3 and 4.

Table 3 Pair wise comparisons between estimated marginal means of body weight at different ages from paternal, maternal and individual genotypes

trait	effect of paternal genotype		effect of maternal genotype		effect of individual genotype	
	CC	CT	CC	CT	CC	CT
BW0/kg	3.61±0.10 (148)^{a}	3.17±0.16 (43)^{b}	3.13±0.23 (73)^{A}	3.65±0.11 (66)^{B}	3.43±0.15 (123)	3.57±0.18 (36)
BW1/kg	5.96±0.31 (138)^{a}	4.02±0.31 (38)^{b}	4.48±0.31 (70)^{A}	5.18±0.30 (58)^{B}	4.53±0.19 (118)	5.02±0.22 (35)
BW2/kg	6.96±0.29 (133)^{a}	5.05±0.32 (38)^{b}	5.34±0.32 (69)^{A}	6.17±0.28 (58)^{B}	5.48±0.23 (118)	6.03±0.26 (35)
BW3/kg	7.17±0.37 (131)^{a}	6.36±0.41 (37)^{b}	6.22±0.42 (68)^{A}	7.30±0.36 (58)^{B}	6.55±0.30 (118)	6.97±0.33 (35)
BW4/kg	8.95±0.46 (131)^{a}	7.86±0.52 (37)^{b}	7.81±0.52 (68)^{a}	8.99±0.45 (58)^{b}	7.68±0.37 (118)	8.45±0.42 (35)
BW8/kg	13.20±0.84 (131)^{a}	11.42±0.90 (37)^{b}	11.41±0.92 (66)^{a}	13.21±0.78 (53)^{b}	12.06±0.63 (115)	13.02±0.72 (35)
BW12/kg	16.28±1.20 (125)^{a}	14.09±1.31 (33)^{b}	14.92±1.17 (61)^{a}	16.95±1.15 (47)^{b}	15.81±0.91 (109)	16.98±1.01 (33)
BW16/kg	20.73±1.34 (108)^{a}	17.31±1.54 (26)^{b}	18.32±1.62 (50)^{a}	20.97±1.28 (42)^{b}	18.99±1.05 (95)	19.80±1.64 (30)

Note: The figures in parentheses are the numbers of individual observations. The different capital and small letters in the same row of paternal, maternal and individual genotype represent significance at 0.01 and 0.05 probability levels, respectively.

Table 4 Interaction between paternal and maternal genotype

trait	mating type			
	CC(*P*)×CC(*M*)	CC(*P*)×CT(*M*)	CT(*P*)×CC(*M*)	CT(*P*)×CT(*M*)
BW0/kg	3.49±0.14 (41)^{b}	3.72±0.12 (43)^{b}	2.46±0.24 (33)^{a}	3.58±0.19 (11)^{b}
BW1/kg	5.01±0.29 (41)^{b}	5.26±0.25 (43)^{b}	3.28±0.35 (31)^{a}	5.08±0.33 (11)^{b}
BW2/kg	5.92±0.35 (40)^{b}	6.20±0.29 (43)^{b}	4.36±0.41 (31)^{a}	6.04±0.39 (11)^{b}
BW3/kg	6.81±0.47 (40)^{b}	7.52±0.37 (43)^{b}	5.13±0.52 (31)^{a}	7.08±0.50 (11)^{b}
BW4/kg	8.52±0.57 (40)^{b}	9.37±0.47 (42)^{b}	6.19±0.66 (31)^{a}	8.62±0.64 (11)^{b}
BW8/kg	12.26±1.04 (40)^{a}	15.14±0.84 (42)^{b}	11.55±1.14 (31)^{a}	12.28±1.09 (11)^{a}
BW12/kg	14.02±1.49 (37)^{a}	18.74±1.20 (38)^{b}	13.32±1.62 (30)^{a}	14.36±1.65 (10)^{a}
BW16/kg	18.39±1.72 (33)^{a}	22.07±1.09 (36)^{b}	17.25±2.11 (29)^{a}	18.38±2.23 (10)^{a}

Note: The capital letter *P* and *M* represent paternal and maternal, respectively. The different small letters in the same row represent significance at 0.05 probability level.

breeds had higher significant frequencies of C, from 0.9446 to 1.0000, but the Boer goat had a lower significant frequency of C (0.7535) and a higher frequency of T (0.2465). It is also known that the Boer goat from South Africa is a famous meat-oriented goat breed in the world, with more obvious muscular hypertrophy conditions at the neck, breast, shoulder, back, loin, and buttocks compared with other goat breeds. Therefore, it can be inferred that the transition of 184C→T may be related to the muscular hypertrophy of the Boer goat.

Our results of general linear model analysis showed that paternal genotype, maternal genotype, and their interactions affected their body weights significantly at different ages ($P < 0.01$, $P < 0.05$, Table 2). Table 3 shows that the effect of paternal genotype (CC) was significantly higher than that of CT ($P < 0.05$), whereas, the effect of maternal genotype (CT) was significantly higher than that of CC ($P < 0.01$, $P < 0.05$). Meanwhile, it is also seen from Table 4 that the interaction between paternal genotype (CC) and maternal genotype (CT), CC(*P*) × CT(*M*) was significantly higher ($P < 0.05$) than that of CT(*P*) × CC (*M*) from birth to one-month-old, and significantly higher ($P < 0.05$) than that of other combinations, CC(*P*) × CC (*M*), CT(*P*) × CC(*M*), and CT(*P*) × CT(*M*). Therefore, the CC(*P*) × CT(*M*) is the best combination among the four kinds of mating.

This phenomenon was similar to sheep parental imprinting form, a polar over-dominance, in which only individuals having received the allele from their sire expressed the *callipyge* phenotype (Cockett et al., 1994, 1996; Freking et al., 1998; Lien et al., 1999; Shay et al., 2001) . It could be inferred that the transition of 184C→T might be a paternal imprinting form, a polar over-dominance, in which only individuals having received the allele from their mothers expressed the *callipyge* phenotype, the double muscle characteristics of the Boer goat might be related to the maternal genotype. However, the difference between the sire or dam CC genotype and CT genotype was so complicated that further analysis could hardly be done to date because only few individuals could be recognized for its allele in genotype from the parent.

Unfortunately, only several TT genotypes were observed in the Boer goat. Hence, another task needs to be done, that is, selecting special genotype individuals to mate with each other, to determine the offspring genotype easily, and to determine from which allele it comes. Fortunately, we are carrying out phenotype recording and genotyping of the *CLPG* gene of individual Boer goats to confirm the findings mentioned above. On the other hand, although there is a very low frequency of T allele in the Chinese indigenous goat breeds, it can be increased through genotyping and selection as T allele proved to be related to muscular hypertrophy.

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