猪 *CAST* 基因的单核苷酸多态性及其对肉质性状的效应

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摘要:*CAST* 基因作为肉质性状的主要候选基因。以 80 头外来猪和 190 头地方猪为材料,在 *CAST* 基因内含子 24 上检测到两个多态性位点(A916G 和 C1633G)。在 916 位点上,长白猪和大白猪以 *A* 基因为优势基因,其频率分别为 0.88 和 1.00;莱芜猪,大薄莲猪,沂蒙黑猪和里岔黑猪以 *B* 基因为优势基因,其频率分别为 0.93, 0.97, 0.78 和 0.68。在 1633 位点上,长白猪和大白猪以 *C* 基因为优势基因,其频率分别为 0.82 和 0.79; 莱芜猪,大薄莲猪,沂蒙黑猪和里岔黑猪以 *D* 基因为优势基因,其频率分别为 1.00, 1.00, 0.88, 0.78。在试验猪种中,共检测到 6 种单倍型(*AACC*,*AACD*,*AADD*,*ABCC*,*BBCC*,*BBDD*)。单倍型分布的多重比较结果表明,外来猪种(长白猪和大白猪)与地方猪种(莱芜猪,大薄莲猪,沂蒙黑猪和里岔黑猪)比较差异极显著($P < 0.01$)。固定效应模型分析结果表明,嫩度,屠宰 45 min 后 pH 值和滴水损失单倍型间差异显著($P < 0.05$)。最小二乘分析结果表明,外来猪种与地方猪种在嫩度,屠宰 45 min 后 pH 值和滴水损失间差异显著($P < 0.05$)。*BBDD* 单倍型个体与其它单倍型个体比较,嫩度及滴水损失差异显著($P < 0.05$);*AADD*,*BBCC*,*BBDD* 单倍型个体与其它单倍型个体比较,屠宰 45 min 后 pH 值差异显著($P < 0.05$)。因此,在育种过程中将 *CAST* 基因应用于标记辅助选择,将有利于改善猪肉品质,加快育种进程。

关键词:猪;*CAST* 基因;遗传多态性;遗传效应

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Single nucleotide polymorphisms and genetic effects of *CAST* gene on meat quality traits in pigs

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Abstract: Calpastatin (*CAST*) was considered to be a candidate gene for meat quality traits. Two substitutions (A916G and C1633G) in intron 24 of porcine *CAST* gene were genotyped on a total of 270 animals, including 190 from four Chinese and 80 from two Western pig lines. At 916 site, allele *B* was the dominant gene in Laiwu Black, Dapuliang, Yimeng and the Licha Black pigs having frequencies of 0.93, 0.97, 0.78 and 0.68, respectively and allele *A* was the dominant gene in the Landrace and the Large White having frequencies of 0.88 and 1.00, respectively; At 1633 site, allele *C* was the dominant gene in the Landrace and the Large White having frequencies of 0.82 and 0.79, respectively and allele *D* was the dominant gene in the Laiwu, the Dapuliang, the Yimeng and the Licha Black pigs having frequencies of 1.00, 1.00, 0.88 and 0.78, respectively. Six haplotypes (*AACC*, *AACD*, *AADD*, *ABCC*, *BBCC*, *BBDD*) were examined in the tested pig

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breeds. The results show that: Firstly, the Landrace and the Large White breeds differed significantly ($P < 0.01$) in haplotype distribution from the Laiwu, the Dapuliang, the Yimeng and the Licha Black breeds; Secondly, association analyses between haplotypes and meat quality traits demonstrated that *CAST* haplotype was significantly associated with higher tenderness, higher pH at postmortem 45 min, and lower drip loss ($P < 0.05$); Thirdly, using least square analysis, it was seen that significant differences ($P < 0.05$) were found in the tenderness, the pH of postmortem 45 min and the drip loss between the exotic pig breeds (the Landrace and the Large White) and the native pig breeds (the Laiwu, the Dapuliang, the Yimeng and the Licha Black). Individuals of the *BBDD* haplotype had significantly higher ($P < 0.05$) tenderness and lower drip loss than those of the other haplotypes, and the pigs of the *AADD*, *BBCC*, and *BBDD* haplotypes had significantly lower ($P < 0.05$) pH of postmortem 45 min than those of the other haplotypes. The *CAST* gene can be used in marker-assisted selection to provide significant improvements for meat quality and to accelerate the breeding progress.

Key Words: pigs; *CAST* gene; genetic polymorphisms; genetic effects

Meat quality traits, including tenderness, appearance, color, taste, pH, drip loss, fat content and texture are important characteristics which is affected by postmortem tenderization. The rate of postmortem proteolysis of several structurally important muscle proteins is considered to be essential for postmortem tenderization[1]. The calpain system plays an important role in postmortem tenderization of skeletal muscle as it is involved in the degradation of important myofibrillar and associated proteins[2]. Calpastatin is a Ca^{2+}-activated calpain inhibitor and influences the activity of calpain activity. Degradation of the muscle protein in postmortem muscle is associated with indices of meat tenderness[3,4]. Calcium stimulates contractions in prerigor muscle and may stimulate more rapid glycolysis and pH decline[2]. Reduced degradation of proteins that tie the myofibril to the cell membrane may allow shrinkage of the myofibril, which causes the shrinkage of the muscle cell and subsequently the increase in drip loss[5,6]. Differences in-calpain, m-calpain, and calpastatin activity may influence tenderness and water-holding capacity.

In porcine *CAST* gene, three polymorphisms were reported[7] and significant differences were found among different *CAST* genotypes in meat tenderness[10,11], backfat thickness[11,12], and longissimus muscle area[13]. The distribution of different alleles exibits breed specific[14]. Based on the function of the porcine calpastatin, *CAST* was considered to be a suitable candidate gene for pork quality. The objective of this study was to investigate the single nucleotide polymorphisms and genetic effect on meat quality of porcine *CAST* gene.

1 Materials and Methods

1.1 Materials

Longissimus dorsi muscle samples from six different pig breeds, including 42 Landrace pigs, 38 Large White pigs, 53 Laiwu pigs, 49 Dapuliang pigs, 47 Yimeng pigs and 41 Licha Black pigs were collected for the extraction of DNA and the measurements of the meat quality..

1.2 Genomic DNA extraction

Genomic DNA was isolated from 1 mg of muscle sample by overnight proteinase K digestion followed by phenol-chloroform extraction and ethanol precipitation, according to a standard protocol.

1.3 PCR-SSCP

1.3.1 Primers

Seven pairs of primers were designed from the published DNA sequence of the porcine *CAST* gene (AY522920) by using the program Primer3 (http://www.genome.wi.mit.edu/cgi-bin/primer/primer3.cgi) (Table 1).

Table 1　Primer sequences of the porcine *CAST* gene

Primer name	Amplified region	Primer sequence	Annealing temperature (℃)	Size (bp)
F1/R1	21 ~ 193	5′-CGATGTCCTGGATCAGCTTT-3′	56	173
		5′-TTTTTCCCCTTTGTGTGGAG-3′		
F2/R2	256 ~ 502	5′-TTCCATGGTCCCCATAATGT-3′	54	247
		5′-ATGATGGCAGGAAAGACTGC-3′		
F3/R3	483 ~ 659	5′-GCAGTCTTTCCTGCCATCAT-3′	58	177
		5′-TTTGCAGCCAAGTACCATGT-3′		
F4/R4	767 ~ 982	5′-TGTGTGACTGGGTCACCTTG-3′	56	216
		5′-GGATTCTTAACCCACTGA-3′		
F5/R5	1206 ~ 1372	5′-CTCAAGGACAGGGCGTTTTA-3′	58	167
		5′-ATGGCTGGTCTCTCTGTCAC-3′		
F6/R6	1482 ~ 1690	5′-TCCTGATGCTTCTGGTTCC-3′	52	209
		5′-ACGTGGGGGCATTTTCTAC-3′		
F7/R7	1780 ~ 1964	5′-AGACCCTTTGTTTTGCCTCA-3′	54	166
		5′-ATCCCTTTCTCCCAGCTTGT-3′		

1.3.2　PCR Amplification

PCR was performed in a total volume of 25 μl of the following mixture: 100 ng porcine genomic DNA, 10 pmol of each primer, 200 μmol/L of each dNTP, 1.5 mmol/L $MgCl_2$, 2.5 μl buffer (10 × concentrate: 200 mmol/L Tris-HCl, pH 8.4, 500 mmol/L KCl), and 1.0 unit of *Taq* DNA polymerase. The PCR mix was incubated at 94℃ for 5 min. This step was followed by 30 cycles at 95℃ for 45 s, annealing temperature (Table 1) for 30 s, and 72℃ for 45 s. The last PCR step was 72℃ for 8 min.

1.3.3　SSCP Analysis

One microliter of each PCR product was added to 5 μl of the Loading buffer (concentrate: 98% formamide, 0.025% bromophenol blue, 0.025% xylene cyanole, and 10 mmol/L EDTA (pH 8.0)). The mixture was denatured at 98℃ for 10 min and resolved by running a 12% denaturing polyacrylamide gel. After electrophoresis, the gel was silver stained.

1.4　Phenotypic Measurement

Loin chops from each carcass were thawed under refrigeration at approximately 2℃, and then cooked simultaneously to an internal temperature of 71℃ in an electric oven broiler (Amana model ARE 80). Tenderness were assessed on 1.1-cm^3 cubes removed from the center of the broiled loin chop and evaluated on a 10-point, end-anchored category scale for tenderness. The pH of the longissimus dorsi between the fourth and the fifth ribs was measured with a glass penetration pH electrode (pHStar, SFK Technology, Inc., Kolding, Denmark) at 45 min, and 24 h postmortem. The pH probe was calibrated using 2 buffers (pH 4.0 and pH 7.0) at the temperature of the muscle at each time period and was checked after measurement on each carcass. The loin color in the transverse cut between the fourth and the fifth (back) ribs was measured on a freshly cut surface after a 10-min blooming period with the Japanese color scale (1 = pale gray to 6 = dark purple). Marble score was measured on a freshly cut surface after a 10-min blooming period using 2.45-cm thick LM chops by subjective visual assesement of the distribution and degree of fat deposit between muscle fiberes. Drip loss was measured using 2.45-cm thick LM chops. At 3 d postmortem, chops were placed in a plastic bag under atmospheric conditions at 4℃. Immediately before being placed in bags, chops were towel-dried and the initial weight of the chops was recorded. After 3 d of storage, samples were removed from their individual bags and were towel-dried and weighed. Drip loss after 3 d of

storage was calculated as a difference between final and initial weight expressed as a percentage of the initial weight.

1.5 Statistical analysis

Values of the genotype frequencies were calculated for the examined pigs and were analyzed by the χ^2 significance test. An analysis of the genotypic effects of the *CAST* gene was carried out using the GLM procedure of SPSS. The fixed model was:

$$Y_{ijkl} = u + B_i + fys_j + m_k + e_{ijkl}$$

Where, Y_{ijkl} is the observed value of lth individual from the breed i, of genotype k, in the jth farm-year-season; u is the least square means of the observed values; B_i is the effective value of the breed i; fys_j is the effective value of the jth farm-year- season; m_k is the effective value of the genotype k; and e_{ijkl} is the random residual effect corresponding to the observed value.

2 Results

2.1 Polymorphisms

The PCR products were tested by agrose gel electrophoresis for size confirmation. The PCR products amplified with the F4/R4, F6/R6 primers were shown in Fig. 1. The PCR products amplified with seven pairs of primers were subjected to SSCP analysis. Two polymorphisms were found in the PCR products amplified with the F4/R4, F6/R6 primers, as shown in Fig. 2 and Fig. 3. Homozygotes were sequenced using dye terminators on an ABI PRISM 3100 Genetic Analyzer. The Blast software was used to assemble the sequences. An A→ G transition at 916 site and a C → G transition at 1633 site were detected, as shown in Fig. 4 and Fig. 5.

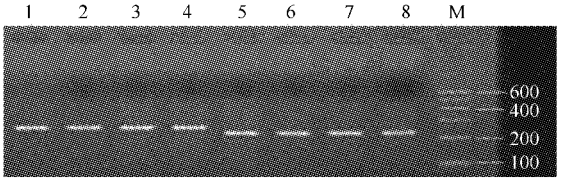

Fig. 1 PCR products amplified with the F4/R4 and F6/R6 primers
1,2,3,4: PCR products of the F4/R4 primers; 5,6,7,8: PCR products of the F6/R6 primers
M:100 bp DNA Marker

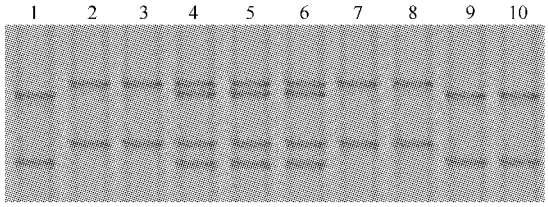

Fig. 2 SSCP result of the PCR product amplified with the F4/R4 primers (12% PAGE)
1, 9,10:genotype *AA*; 4,5,6:genotype *AB*; 2,3,7,8:genotype *BB*

2.2 Genotype and allele frequencies

Genotype and allele frequencies were different among the six pig breeds (Table 2). At 916 site, allele *A*, which is the dominant gene in the Landrace, and the Large White, had a frequency of 0.88, and 1.00, respectively, whereas allele *B*, which is the dominant gene in the Laiwu, the Dapuliang, the Yimeng and the Licha Black pigs, had a frequency of 0.93, 0.97, 0.88 and 0.68, respectively. At 1633 site, allele *C*, which is the dominant gene in the Landrace, and the Large White, had a frequency of 0.82, and 0.79; allele *D*, which is the dominant gene in the Laiwu, the Dapuliang, the Yimeng and the Licha Black pigs, had a frequency of 1.00, 1.00, 0.88 and 0.78, respectively. The results of the multi comparison showed that the haplotype distribution was significantly different ($P < 0.01$) between the exotic (the

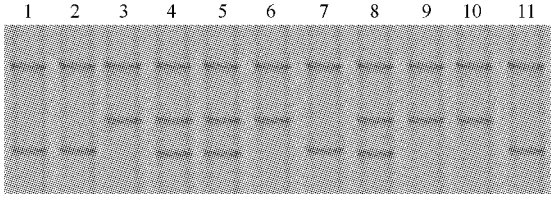

Fig. 3 SSCP result of the PCR product amplified with the F6/R6 primers (12% PAGE)
1,2,7,11: genotype *CC*; 4,5,8: genotype *CD*; 3,6,9,10: genotype *DD*

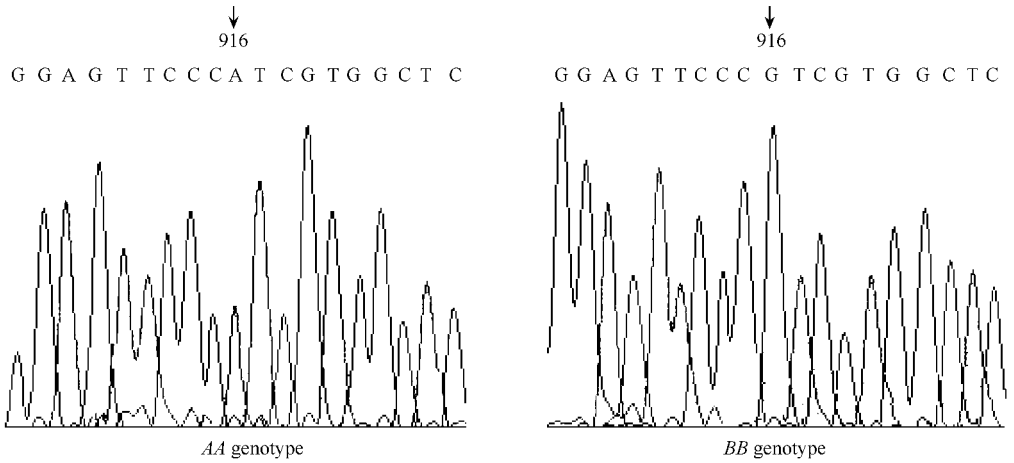

Fig. 4　Sequence comparison of *AA* and *BB* genotypes of porcine *CAST* gene at 916 site

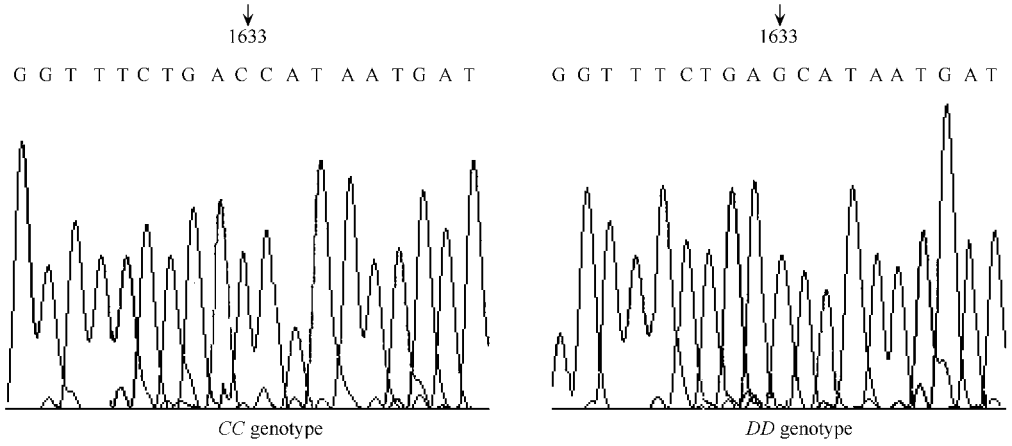

Fig. 5　Sequence comparison of *CC* and *DD* genotypes of porcine*CAST* gene at 1633 site

Landrace, and the Large White) and the indigenous pig breeds (the Laiwu, the Dapuliang, the Yimeng and the Licha Black pigs) (Table 3).

Table 2　Genotype frequency in the different pig breeds

Site	Genotype & Gene frequencies	Landrace	Large White	Laiwu	Dapuliang	Yimeng Black	Licha Black
916	*AA*	0.88(37)	1.00(38)	0	0	0.07(4)	0.15(6)
	AB	0	0	0.13(7)	0.06(3)	0.30(17)	0.34(14)
	BB	0.12(5)	0	0.33(46)	0.94(46)	0.63(35)	0.51(21)
	A	0.88	1.00	0.07	0.03	0.22	0.32
	B	0.12	0	0.93	0.97	0.78	0.68
1633	*CC*	0.71(30)	0.76(28)	0	0	0.13(7)	0.22(9)
	CD	0.21(9)	0.11(4)	0	0	0	0
	DD	0.07(3)	0.13(6)	1.00(53)	1.00(49)	0.88(49)	0.78(32)
	C	0.82	0.79	0	0	0.13	0.22
	D	0.18	0.21	1.00	1.00	0.88	0.78

Note: The number of samples were shown in parentheses

2.3　Effects of the different haplotypes

The haplotypic effects of the *CAST* gene were summarized in Table 4. Significant differences ($P < 0.05$) were

found among the different *CAST* haplotypes for the tenderness, the pH of postmortem 45 min and the drip loss, but not for the color score, the marbling score and the pH of postmortem 24 h.

Table 3 χ^2 test of the haplotypes in the different pig breeds

Breeds	Landrace	Large White	Laiwu	Dapuliang	Yimeng Black
Large White	0.453				
Laiwu	20.432**	23.773**			
Dapuliang	21.317**	19.413**	0.312		
Yimeng Black	17.469**	20.804**	1.473	0.978	
Licha Black	18.301**	19.744**	0.574	1.074	0.418

Note: Values with * * differ at $P < 0.01$

Table 4 Effects of the source of variation on the meat quality

Sources	*df*	*F*-value					
		Tenderness	pH[1]	Color score	Marbling score	pH[2]	Drip loss(%)
Breeds	5	11.381*	14.072*	13.221*	14.237*	19.433**	16.738**
Fys	4	2.078	4.332	0.447	3.201	6.033	4.738
Haplotypes	5	12.381*	12.793*	4.752	9.032	0.762	13.032*

Fys Farm-year-season; Values with * differ at $P < 0.05$; Values with * * differ at $P < 0.01$; pH[1] and pH[2] values tested at postmortem 45 min and 24 h, respectively

Using least square analysis, it was shown that significant differences($P < 0.05$) are found in the tenderness, the pH of postmortem 45 min and the drip loss between the exotic pig breeds (the Landrace and the Large White) and the native pig breeds(the Laiwu, the Dapuliang, the Yimeng and the Licha Black) (Table 5).

Table 5 Least square means and standard errors for the measured traits of the different pig breeds

Traits	Landrace	Large White	Laiwu	Dapuliang	Yimeng Black	Licha Black
Tenderness	$7.82^a \pm 0.219$	$7.42^a \pm 0.173$	$4.08^b \pm 0.021$	$4.32^b \pm 0.155$	$5.47^b \pm 0.209$	$6.01^b \pm 0.028$
pH 1	$5.88^a \pm 0.173$	$5.89^a \pm 0.411$	$5.41^b \pm 0.063$	$5.37^b \pm 0.331$	$5.55^b \pm 0.138$	$5.57^b \pm 0.041$
Color score	3.03 ± 0.112	3.02 ± 0.152	3.02 ± 0.009	2.98 ± 0.073	3.01 ± 0.210	2.99 ± 0.091
Marbling score	3.13 ± 0.125	3.15 ± 0.228	3.09 ± 0.271	2.99 ± 0.412	3.16 ± 0.029	3.09 ± 0.187
pH 2	5.33 ± 0.012	5.30 ± 0.431	5.34 ± 0.812	5.33 ± 0.412	6.32 ± 0.093	5.33 ± 0.112
Drip loss(%)	$1.60^a \pm 0.321$	$1.55^a \pm 0.215$	$1.07^b \pm 0.092$	$1.11^b \pm 0.132$	$1.17^b \pm 0.072$	$1.14^b \pm 0.119$

a,b within a row, means without a common superscript letter differ($P < 0.05$)

The least square means and the standard errors of the tenderness, the pH of postmortem 45 min and the drip loss were analyzed by the GLM procedure using SPSS and were summarized in Table 6. Significant differences($P < 0.05$) were found in the tenderness between the pigs of the *BBDD* haplotypes and the pigs of the other haplotypes; Significant differences($P < 0.05$) also existed in the tenderness compared the pigs of *AADD* and *BBCC* haplotypes with the pigs of *AACC*, *AACD*, and *ABCC* haplotypes. Compared the pigs of *AADD*, *BBCC*, and *BBDD* haplotypes

Table 6 Least square means and standard errors for the measured traits of the different haplotypes

Traits	Haplotypes					
	AACC(60)	*AACD*(21)	*AADD*(20)	*ABCC*(11)	*BBCC*(26)	*BBDD*(132)
Tenderness	$6.73^a \pm 0.202$	$7.19^a \pm 0.153$	$4.90^b \pm 0.091$	$6.98^a \pm 0.091$	$5.33^b \pm 0.207$	$3.85^c \pm 0.116$
pH 1 min	$5.79^a \pm 0.175$	$5.88^a \pm 0.302$	$5.18^b \pm 0.217$	$5.96^a \pm 0.121$	$5.21^b \pm 0.106$	$5.25^b \pm 0.092$
Drip loss(%)	$1.38^a \pm 0.125$	$1.34^a \pm 0.216$	$1.29^a \pm 0.052$	$1.27^a \pm 0.018$	$1.30^a \pm 0.038$	$0.98^b \pm 0.217$

Note: Means with different superscripts within the same traits among the different haplotypes differ significantly ($P < 0.05$)

with the pigs of *AACC*, *AACD*, and *ABCC* haplotypes, significant differences ($P < 0.05$) were found in the pH of postmortem 45 min. Significant differences ($P < 0.05$) were also found between the individuals of *BBDD* haplotypes and the others.

3 Discussion

The calpain system plays an important role in postmortem tenderization of skeletal muscle. The known role of calpastatin as a calpain inhibitor and association results between the identified substitutions (A916G and C1633G) and a number of relevant meat quality traits in several different commercial pig lines suggested that *CAST* might be responsible for the observed phenotypic variation. Six haplotypes (*AACC*, *AACD*, *AADD*, *ABCC*, *BBCC*, *BBDD*) were examined in the tested pig breeds. It is interesting to note that the distribition of genotype frequencies between the examined Chinese and Western pig breeds was markedly different. This may explain why the large difference in meat quality exist between the Chinese and western pig breeds: large differences ($P < 0.05$) exist in tenderness, pH at postmortem 45 min, and drip loss between the western pigs (the Landrace and the Large White) and the Chinese pigs (the Laiwu, the Dapuliang, the Yimeng and the Licha Black) (Table 5). In the previous study by Cheng[14], significant differences are found among different pig breeds with regard to the genotype frequencies of the *CAST* gene, which is in accordance with our results. Therefore, it may be suggested that the differences between the exotic pig breeds and the Chinese indigenous pig breeds with regard to the meat quality traits are related to the genotypes of the *CAST* gene, which results from the long-term selection.

In the previous studies by Koohmaraie[2,8], Huff-Lonergan[3,4], Kristensen[5], Rowe[6], Parr[9], and Kocwin-Podsiadla[10] show that *CAST* gene affects the meat quality by affecting the degradation of the muscle protein in postmortem muscle, which is in consistent with our results. Haplotype effects were analyzed and significant differences ($P < 0.05$) were found among the different *CAST* haplotypes with regard to the tenderness, the pH of postmortem 45 min and the drip loss (Table 4). The haplotype analysis showed important differences between the effects of haplotype *BBDD* and other haplotypes for tenderness ($P < 0.05$) and drip loss ($P < 0.05$). For pH at postmortem 45 min, significant differences were revealed between the effects of *AADD*, *BBCC*, *BBDD* haplotypes and other haplotypes. Haplotype *BBDD* was demonstrated to be the favorable haplotype, and it was associated with higher tenderness, higher pH at postmortem 45 min, and lower drip loss (Table 6).

In conclusion, two genetic transitions of the porcine calpastatin gene were firstly detected in this study, and this results suggest that these genetic variation may be associated with significant variation in meat quality traits, including tenderness, pH, drip loss and other commercially important pork quality traits. It remains to be further demonstrated whether the effects are caused by these variation alone or by their linkage disequilibrium with the causative mutations. These identified genetic polymorphisms can be used in breeding programs to improve overall meat quality and, there by the economic value for the pork supply chain and quality products for consumers.

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更 正

《生态学报》第 28 卷第 5 期 2320～2328 页,王长云,刘海燕,邵长伦,等作者文章的文题更正为“软珊瑚和柳珊瑚化学防御物质研究进展”、“Research progress on chemical defensive substances from soft corals and Gorgonians”。中英文摘要中“软珊瑚(*Sinularia flexibilis*)更正为软珊瑚,柳珊瑚(*Plexaura homomalla*)更正为柳珊瑚”,“soft corals(*Sinularia flexibilis*)更正为 soft corals, gorgonians(*Plexaura homomalla*)更正为 gorgonians”。谨向作者与读者深表歉意。