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Significant association of *APOA5* and *APOC3* gene polymorphisms with meat quality traits in Kele pigs

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ABSTRACT. Apolipoprotein A5 (*APOA5*) and C3 (*APOC3*) genes are involved in the PPAR lipid metabolism pathway and thus associated with elevated triglyceride levels. However, whether *APOA5* and *APOC3* genetic polymorphisms affect intramuscular fat deposition and other meat quality traits remains unknown in pigs. One hundred and seventy-one Kele pigs were sampled to investigate genetic variants in the *APOA5* and *APOC3* genes and their association with seven pork quality traits. We identified 5 single nucleotide polymorphisms (SNPs) in the promoter region of the *APOA5* gene and 17 SNPs in the *APOC3* gene. Linkage disequilibrium analysis revealed 5 complete linkage disequilibria among these 22 SNPs. We found that 10 SNPs were significantly correlated with meat quality traits, including the mutation A5/-769 in the *APOA5* gene, which was significantly associated with cooked weight percentage, and 9 SNPs in the *APOC3* gene that were significantly associated with drip loss rate, meat color value of

longissimus dorsi muscle and shear force. Therefore, these SNP markers will be useful for marker-assisted selection for improved pork quality.

Key words: *APOA5* gene; *APOC3* gene; Meat quality; Kele pig; Association analysis

INTRODUCTION

Increasing intramuscular fat (IMF) in pork has been of great interest in recent years due to the increased demand for high-quality pork with desirable nutrition and palatability. When IMF content accounts for 2-3% in pork, it has a positive effect on meat flavor, juiciness, tenderness, and water holding capability (Jiang et al., 2012). Unfortunately, long-term selection for high growth rate and lean meat in pigs during the last several decades has resulted in a significant decrease in IMF to less than 2% (Zuo et al., 2007), thus dramatically reducing meat quality.

So far, the identification of candidate genes for high IMF content has been proposed to be the most effective strategy for improved pork quality (Gerbens et al., 2000; Chen et al., 2008). Research has shown that variations in IMF content are mainly regulated via triglyceride (TG) changes (Cava et al., 1997). Greater IMF content implies a higher level of TG (Ruiz-Carrascal et al., 2000). Apolipoproteins A5 (APOA5) and C3 (APOC3), two members of the apolipoprotein family, have been identified as regulators of TG, total cholesterol, low- and high-density lipid cholesterol (Hodis and Mack, 1995; O'Brien et al., 2005). Additionally, these two genes play important roles in regulating lipoprotein metabolism-related enzyme activity, stabilizing the structure of lipoproteins and binding to lipoprotein receptor (Li et al., 2005). The TG concentration of *APOA5* KO mice was found to be three times greater than that of wild-type, while TG level of *APOA5*-overexpressing mice showed a marked decrease compared to the wild-type (Pennacchio et al., 2001). In contrast, the expression level of *APOC3* is positively correlated with serum TG concentration (Ito et al., 1990; Maeda et al., 1994). Furthermore, polymorphisms of these two genes have been reported to affect lipid deposition (Ruiz-Narváez et al., 2005; Zhang et al., 2010). Therefore, both *APOA5* and *APOC3* should be promising candidate genes for improving IMF in pigs.

Kele pigs are an indigenous pig breed in Guizhou Province located in Southwest China. The animals can live in poor conditions, but they produce high IMF pork with excellent meat palatability. As such, the Kele pig is a very famous pig breed in the Karst mountainous area. Both pig *APOA5* and *APOC3* genes are located on *Sus scrofa* chromosome 9 (SSC9) based on the current genome assembly (Build 10.2). As discussed above, these genes play an important role in the fat metabolism pathway (PPAR pathway). Thus, the objective of this study was to determine SNPs in the *APOA5* and *APOC3* genes and their effects on IMF deposition and pork quality traits in Kele pigs.

MATERIAL AND METHODS

Animal and data collection

A total of 171 clinically healthy and castrated Kele pigs were included in the present

study. The average live weight at slaughter was 104.6 ± 8.02 kg. They were raised under pasture but supplemented with concentrated feed twice daily and kept in the same environmental conditions. During the period from 25 to 60 kg, concentrated feed contained 12.97 MJ/kg metabolizable energy, 14.70% crude protein, 0.55% calcium, 0.29% available phosphorus, and 0.72% lysine; from 60 kg to slaughter weight, the pigs were fed a diet containing 12.55 MJ/kg metabolizable energy, 13.52% crude protein, 0.48% calcium, 0.26% available phosphorus, and 0.61% lysine. All pigs were slaughtered following the Chinese agricultural industry standards of NY/T825-2004. After slaughter, blood and meat samples were collected immediately.

Meat quality traits including pH of the longissimus dorsi muscle 24 h after slaughter (pH_{24}), drip loss rate (DLR, %), meat color value of longissimus dorsi (MCV), cooking percentage (%), shear force (kg), water moisture (%), IMF content (%), and protein content of longissimus dorsi (%) were measured according to NY/T821-2004 standards. Genomic DNA was extracted using the TIANamp Genomic DNA kit (TIANGEN, China).

Amplification and sequencing

The pig *APOA5* and *APOC3* DNA sequences available in the GenBank database (accession Nos. CU582845.2 and L00627.1) were used to design primers with the software Primer 5.0, to amplify the 5'-region of the *APOA5* gene and the complete genome sequence of the *APOC3* gene. The primer sequences are listed in Table 1. All PCR amplifications were performed in 50 μL with the following cycling parameters: initial denaturation at 94°C for 4 min, 35 cycles of denaturation at 94°C for 50 s, annealing at 58° to 63°C for 45 s, and extension at 72°C for 10 min. PCR products were used for direct sequencing by the SinoGenomax Company (Beijing, China) to detect the SNPs.

Table 1. Primer sets designed for the porcine *APOA5* and *APOC3* genes.

Gene	Position	Primer sequences	Tm (°C)	Size (bp)
APOA5	Promoter region	Forward: 5'-GTAGCCTGTGGTGGAACTG-3' Reverse: 5'-ACGCTTGCCATGATGTGC-3'	60	970
APOC3	5'-region to intron 1	Forward: 5'-TGTTGTTCCCAAGTCCAAAGA-3' Reverse: 5'-AATCAAGACGGCTGGTTTCA-3'	58	854
APOC3	Intron 1 to intron 3	Forward: 5'-TCCATGCCACCCTTCGTCTC-3' Reverse: 5'-GGGAGTAATACCCAGTCCTCGTTG-3'	63	1110
APOC3	Intron 3 to 3'-region	Forward: 5'-ATCCACAGCGGTTCTCAGTC-3' Reverse: 5'-TGGCAGGGTAGATAGGGTCAT-3'	63	983

Statistical analysis

The linkage disequilibrium (LD) among SNPs and Hardy-Weinberg equilibrium of each SNP in the porcine *APOA5* and *APOC3* genes were estimated using the Haploview 4.0 program. The effects of single genotypes on the traits studied were analyzed by the least-square method as applied in the general liner model procedure in SPSS Statistics 17.0 (USA), with the following model: $Y_{ij} = \mu + W_i + G_j + W_i \times G_j + e_{ij}$, where Y_{ij} is the observed value of a given trait, μ is the general mean, W_i is the live weight (kg), G_j is the genotype of SNP, $W_i \times G_j$ is the interaction between live weight and genotype of SNP, and e_{ij} is the residual random effect associated with the animal. $P \leq 0.05$ was considered to be statistically significant. All data are reported as means ± standard error (SE).

RESULTS

LD analysis

The sequencing results revealed a total of 22 SNPs identified in the fragments amplified, including 5 SNPs in the promoter region (from -959 to -11 bp) of *APOA5* and 17 SNPs in *APOC3*. For the *APOC3* gene, three variants were located in the promoter region, 11 in the intron regions, 2 in the exons, and one in the 3'-UTR. Only one SNP, named C3/974, resided in the coding region but did not cause an amino acid change. Analysis of the genotype data showed that there were 5 SNPs tightly linked with others (Figure 1) between A5/-769 and A5/-323, A5/-458 and C3/884, C3/813 and C3/828, and among C3/860, C3/974 and C3/1213, respectively. Therefore, the following 17 tagging SNPs were used in the association analysis: A5/-796, A5/-769, A5/-725, C3/-206, C3/-177, C3/-49, C3/168, C3/565, C3/618, C3/813, C3/860, C3/884, C3/1051, C3/1134, C3/2096, C3/2280 and C3/2405.

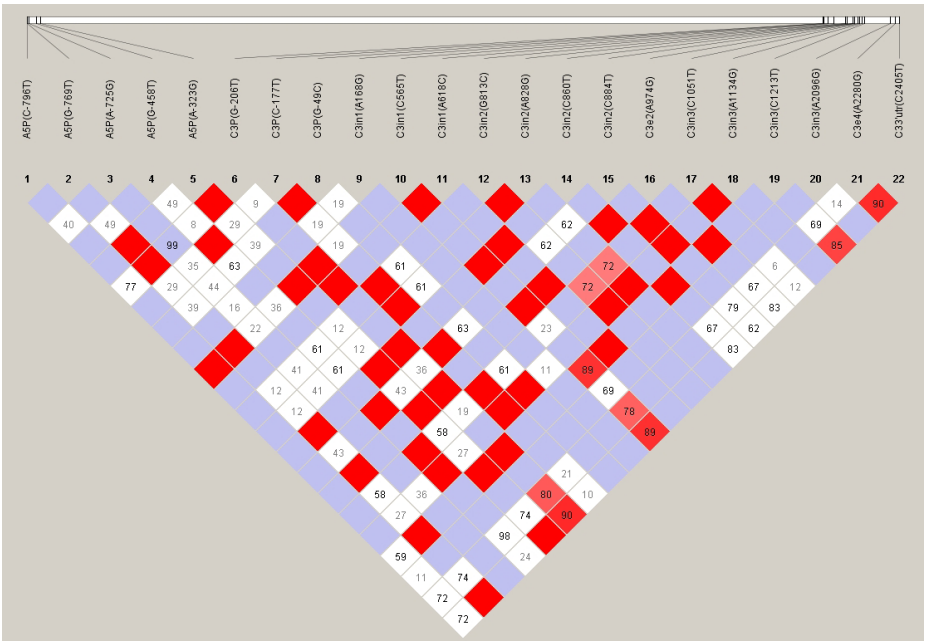

Figure 1. Linkage disequilibrium (LD) analysis in *APOA5* and *APOC3* genes. Pairwise LD relationship for 22 mutations was based on r^2 measurements.

Genotype and allele frequencies

Results for genotype and allele frequencies are presented in Table 2. Most of the SNPs were found to have only two genotypes: one homozygote and one heterozygote, and their allele frequencies showed a large difference except the one of C3/618. The results showed that almost all mutations were in agreement with Hardy-Weinberg equilibrium except C3/2280 and C3/2405 ($P < 0.05$) according to the Haploview 4.0 program.

Table 2. Distribution of genotype and allele frequencies in the resource population.

Marker	Genotype			Allele frequency		HWE P
	AA	AB	BB	A	B	
A5/-796	CC (102)	CT (48)	TT (6)	C (0.821)	T (0.179)	1.000
A5/-769	GG (102)	GT (65)		G (0.805)	T (0.195)	0.591
A5/-725	AA (150)	AG (12)		A (0.963)	G (0.037)	1.000
C3/-206	GG (54)	GT (107)	TT (6)	G (0.644)	T (0.356)	0.133
C3/-177	CC (137)	CT (24)	TT (5)	C (0.898)	T(0.102)	0.533
C3/-49	CC (151)	GC (19)		C (0.944)	G (0.056)	1.000
C3/168	GG (78)	AG (54)		G (0.804)	A (0.196)	0.760
C3/565	TT (48)	CT (96)	CC (12)	T (0.615)	C (0.385)	0.305
C3/618	CC (42)	AC (101)	AA (12)	C (0.596)	A (0.404)	0.180
C3/813	GG (133)	GC (23)		G (0.926)	C (0.074)	1.000
C3/860	TT (36)	CT (90)	CC (30)	T (0.519)	C (0.481)	0.763
C3/884	CC (138)	CT (18)		C (0.942)	T (0.058)	1.000
C3/1051	TT (132)	CT (24)		T (0.923)	C (0.077)	1.000
C3/1134	GG (114)	AG (29)		G (0.899)	A (0.101)	1.000
C3/2096	GG (132)	AG (18)	AA (6)	G (0.880)	A (0.120)	0.574
C3/2280	GG (37)	AG (125)		G (0.614)	A (0.386)	0.004
C3/2405	TT (42)	CT (120)		T (0.640)	C (0.360)	0.014

Association analysis of *APOA5* and *APOC3* gene with pork quality traits

The associations of *APOA5* and *APOC3* genetic variants with meat quality traits in Kele pigs are shown in Table 3. The results revealed that most of the SNPs significantly influenced DLR, MCV, and shear force. The A5/-769 SNP was significantly associated with cooking percentage (P = 0.034). The animals of the GG genotype had an average cooking percentage of 61.90%, i.e., 1.35% more than the GT pigs. The C3/565 variant was related to DLR and MCV in the population (P = 0.019 and P = 0.000, respectively): the CT heterozygote had 0.44% more DLR than TT pigs and 0.81% more than the CC homozygote. Pigs with the TT genotype had 0.09 more than CT pigs and 0.31 more than CC pigs of the MCV. The C3/618 site significantly affected DLR, MCV, and shear force. The animals with the CC genotype had the least DLR compared with genotypes CA and AA; the AA genotype had the least MCV, where it was 0.06 less than CC and 0.21 less than the AC genotype. The AA genotype also had the least shear force, where it was 1.13 kg less than CC and 0.51 less than the AC genotype. The SNP of C3/813 was associated with DLR, MCV, and shear force, where GG pigs had 0.96% more DLR than GC, GC had 0.18 more MCV, and 1.06 kg more shear force than did GG. The C3/860 site affected DLR and MCV, where DLR was 2.09% in CT pigs, and respectively 1.58 and 0.82% in the TT and CC pigs; CC MCV was 3.30, and the TT and CT MCV were 3.25 and 3.20, respectively. The C3/884 site was significantly associated with DLR, MCV, and shear force (P = 0.008, P = 0.000, and P = 0.019, respectively), where the CC genotype had 1.02% more DLR than CT, and CT had 0.30 more MCV and 0.68 kg more shear force than the CC genotype. The SNP of C3/1051 significantly affected DLR, MCV, and shear force (P = 0.004, P = 0.000, and P = 0.009, respectively), where genotype TT yielded pigs that had a 1.90% higher DLR and the CT pigs had a higher MCV and shear force, namely 3.38 and 4.39 kg. The variant of C3/1134 was related to MCV and shear force, where the genotype GG had 0.34 less MCV than did AG, and 0.82 kg of shear force less than AG. MCV was correlated with the C3/2280 site (P = 0.025), where the MCV of the GG pig was 3.25 and of the AG pigs 3.00. The SNP of C3/2405 was associated with DLR and MCV, where, compared with the CT genotype, the TT genotype had a lower DLR and higher MCV, where DLR was 1.81% and MCV was 3.14.

Table 3. Statistical analysis of the association of *APOA5* and *APOC3* gene polymorphisms with meat quality traits.

Marker	Genotype	pH_{24}		DLR (%)		MCV		Cook percentage (%)		Shear force (kg)		WM (%)		IMF (%)		CP (%)	
		Means ± SE	P	Means ± SE	P	Means ± SE	P	Means ± SE	P	Means ± SE	P	Means ± SE	P	Means ± SE	P	Means ± SE	P
A5/-796	CC	5.94 ± 0.25	0.793	1.71 ± 0.38	0.075	3.32 ± 0.38	0.074	61.06 ± 1.74	0.238	3.72 ± 0.86	0.726	69.67 ± 1.97	0.782	5.45 ± 0.96	0.794	20.21 ± 1.43	0.615
	CT	5.83 ± 0.21		2.40 ± 0.39		2.81 ± 0.65		62.41 ± 0.83		3.98 ± 0.52		69.42 ± 1.35		5.75 ± 1.08		19.19 ± 1.49	
	TT	5.60 ± 0.22		1.62 ± 0.55		2.50 ± 0.27		58.78 ± 0.96		3.21 ± 0.47		68.67 ± 1.54		6.85 ± 1.03		19.37 ± 1.32	
A5/-769	GG	5.89 ± 0.27	0.789	2.10 ± 0.46	0.345	2.97 ± 0.57	0.346	61.90 ± 1.63	0.034	3.82 ± 0.71	0.587	69.53 ± 1.83	0.885	5.79 ± 0.90	0.982	19.64 ± 1.46	0.689
	GT	5.92 ± 0.21		1.60 ± 0.48		3.41 ± 0.30		60.55 ± 1.47		3.71 ± 0.89		69.61 ± 1.74		5.27 ± 0.86		20.28 ± 1.48	
A5/-725	AA	5.90 ± 0.25	0.794	1.99 ± 0.36	0.626	3.12 ± 0.51	0.572	61.47 ± 1.69	0.437	3.76 ± 0.80	0.844	69.53 ± 1.84	0.939	5.67 ± 0.96	0.975	19.91 ± 1.51	0.302
	AG	5.80 ± 0.28		1.42 ± 0.29		3.25 ± 0.26		59.85 ± 1.51		3.80 ± 0.76		69.69 ± 1.43		5.30 ± 0.99		18.93 ± 0.62	
C3/-206	GG	5.98 ± 0.29	0.594	1.73 ± 0.41	0.523	3.22 ± 0.44	0.555	61.77 ± 1.79	0.454	3.77 ± 0.83	0.927	69.79 ± 2.23	0.905	5.52 ± 1.13	0.438	20.25 ± 1.42	0.486
	GT	5.88 ± 0.23		2.31 ± 0.39		2.97 ± 0.55		60.93 ± 1.74		3.80 ± 0.73		69.37 ± 1.45		6.12 ± 1.01		18.84 ± 1.18	
	TT	6.00 ± 0.18		0.61 ± 0.48		3.50 ± 0.33		61.76 ± 0.88		4.02 ± 0.55		70.10 ± 1.33		4.16 ± 0.87		21.22 ± 1.41	
C3/-177	CC	5.92 ± 0.26	0.694	2.32 ± 0.49	0.497	2.98 ± 0.49	0.285	61.41 ± 1.83	0.509	3.67 ± 0.70	0.084	69.76 ± 1.67	0.332	5.84 ± 1.42	0.316	19.83 ± 1.50	0.377
	CT	5.03 ± 0.12		0.93 ± 0.32		3.63 ± 0.48		60.49 ± 1.05		4.34 ± 0.77		68.88 ± 1.25		5.68 ± 1.07		19.97 ± 1.16	
	TT	5.70 ± 0.14		0.59 ± 0.27		3.00 ± 0.26		60.05 ± 1.02		4.62 ± 0.46		66.67 ± 1.12		3.91 ± 0.78		21.43 ± 1.45	
C3/-49	CC	5.92 ± 0.26	0.773	2.19 ± 0.51	0.761	3.00 ± 0.48	0.306	61.31 ± 1.79	0.495	3.77 ± 0.77	0.544	69.57 ± 1.75	0.689	5.78 ± 1.35	0.299	19.88 ± 1.48	0.559
	GC	5.90 ± 0.14		1.01 ± 0.34		3.67 ± 0.58		60.59 ± 1.26		4.00 ± 0.44		69.18 ± 1.35		5.47 ± 1.24		20.08 ± 1.39	
C3/168	GG	5.84 ± 0.22	0.222	2.42 ± 0.41	0.121	2.89 ± 0.59	0.154	61.11 ± 1.78	0.138	3.76 ± 0.62	0.061	69.87 ± 1.36	0.557	5.65 ± 1.72	0.591	19.62 ± 1.39	0.344
	AG	6.00 ± 0.28		1.49 ± 0.56		3.39 ± 0.33		61.98 ± 1.85		3.50 ± 0.82		69.56 ± 2.18		5.89 ± 1.32		19.94 ± 1.79	
C3/565	TT	5.98 ± 0.31	0.544	1.49 ± 0.57	0.019	3.31 ± 0.37	0.000	61.76 ± 1.91	0.561	3.62 ± 0.75	0.420	67.79 ± 3.29	0.817	5.56 ± 1.35	0.982	20.30 ± 1.51	0.813
	CT	5.85 ± 0.22		1.93 ± 0.29		3.22 ± 0.41		61.20 ± 1.81		3.76 ± 0.80		69.47 ± 1.56		5.54 ± 0.96		19.85 ± 1.55	
	CC	5.80 ± 0.28		1.12 ± 0.31		3.00 ± 0.71		60.27 ± 2.11		3.62 ± 0.67		69.36 ± 1.01		5.51 ± 0.90		20.30 ± 1.31	
C3/618	CC	5.88 ± 0.18	0.800	0.99 ± 0.37	0.011	3.14 ± 0.56	0.001	60.42 ± 1.67	0.306	4.18 ± 0.71	0.039	68.81 ± 1.24	0.492	5.67 ± 0.87	0.706	20.26 ± 1.14	0.480
	AC	5.91 ± 0.28		1.99 ± 0.40		3.29 ± 0.36		61.68 ± 1.63		3.56 ± 0.71		69.67 ± 1.94		5.72 ± 0.74		19.87 ± 1.61	
	AA	5.70 ± 0.14		2.10 ± 0.04		3.08 ± 0.28		61.14 ± 4.02		3.05 ± 0.56		70.65 ± 0.08		3.60 ± 0.56		20.45 ± 2.16	
C3/813	GG	5.89 ± 0.27	0.795	1.88 ± 0.32	0.009	3.20 ± 0.40	0.000	61.41 ± 1.95	0.748	3.55 ± 0.67	0.022	69.72 ± 1.71	0.297	5.55 ± 0.86	0.961	20.02 ± 1.55	0.632
	GC	5.88 ± 0.15		0.92 ± 0.23		3.38 ± 0.48		60.71 ± 0.73		4.61 ± 0.56		68.38 ± 1.68		5.49 ± 1.04		20.05 ± 1.27	
C3/860	TT	6.00 ± 0.36	0.453	1.58 ± 0.24	0.001	3.25 ± 0.27	0.001	61.92 ± 2.22	0.222	3.42 ± 0.76	0.124	69.70 ± 2.63	0.157	5.46 ± 3.72	0.979	20.54 ± 1.56	0.399
	CT	5.86 ± 0.21		2.09 ± 0.11		3.20 ± 0.41		61.48 ± 1.73		3.68 ± 0.70		69.79 ± 1.40		5.70 ± 2.11		19.64 ± 1.55	
	CC	5.83 ± 0.21		0.82 ± 0.25		3.30 ± 0.57		60.00 ± 1.15		4.15 ± 0.86		68.43 ± 1.25		5.18 ± 1.32		20.55 ± 097	
C3/884	CC	5.89 ± 0.26	0.560	1.85 ± 0.10	0.008	3.20 ± 0.39	0.000	61.42 ± 1.87	0.626	3.63 ± 0.71	0.019	69.67 ± 1.79	0.258	5.55 ± 2.45	0.754	19.97 ± 1.56	0.476
	CT	5.90 ± 0.14		0.83 ± 0.12		3.50 ± 0.50		60.35 ± 1.24		4.31 ± 0.94		68.28 ± 0.37		6.32 ± 1.67		20.46 ± 0.75	
C3/1051	TT	5.90 ± 0.26	0.789	1.90 ± 0.59	0.004	3.20 ± 0.40	0.000	61.48 ± 1.89	0.347	3.59 ± 0.69	0.009	69.81 ± 1.70	0.174	5.51 ± 2.48	0.975	19.90 ± 1.56	0.237
	CT	5.83 ± 0.15		0.77 ± 0.19		3.38 ± 0.48		60.27 ± 1.02		4.39 ± 0.78		67.88 ± 0.86		5.12 ± 1.82		20.70 ± 0.78	
C3/1134	GG	5.86 ± 0.2	0.528	1.91 ± 0.37	0.118	3.16 ± 0.37	0.016	61.40 ± 1.95	0.345	3.58 ± 0.71	0.041	69.67 ± 1.79	0.136	5.66 ± 2.64	0.952	19.94 ± 1.52	0.490
	AG	5.88 ± 0.15		0.86 ± 0.32		3.50 ± 0.50		60.40 ± 0.93		4.40 ± 0.68		68.44 ± 1.47		5.33 ± 1.81		20.26 ± 1.20	
C3/2096	GG	5.87 ± 0.22	0.316	2.08 ± 0.61	0.154	3.16 ± 0.50	0.658	61.21 ± 1.83	0.919	3.68 ± 0.68	0.354	69.73 ± 1.45	0.515	5.15 ± 1.89	0.138	19.89 ± 1.48	0.875
	AG	5.93 ± 0.12		1.42 ± 0.03		2.83 ± 0.29		61.28 ± 2.07		4.38 ± 0.28		67.95 ± 3.16		8.92 ± 3.53		19.84 ± 1.24	
	AA	6.00 ± 0.23		3.70 ± 0.66		2.50 ± 0.14		61.90 ± 1.14		4.98 ± 0.65		71.04 ± 1.12		5.22 ± 1.15		19.89 ± 1.12	
C3/2280	GG	5.83 ± 0.15	0.789	1.49 ± 0.50	0.061	3.25 ± 0.42	0.025	61.16 ± 1.82	0.930	3.87 ± 0.72	0.285	69.01 ± 2.49	0.329	6.48 ± 3.72	0.175	20.30 ± 1.36	0.539
	AG	5.91 ± 0.23		2.25 ± 0.65		3.00 ± 0.55		61.30 ± 1.77		3.83 ± 0.73		69.64 ± 1.50		5.51 ± 1.97		19.72 ± 1.40	
C3/2405	TT	5.86 ± 0.15	0.801	1.81 ± 0.24	0.047	3.14 ± 0.48	0.009	61.56 ± 1.84	0.704	4.01 ± 0.78	0.365	69.49 ± 2.48	0.728	5.86 ± 3.52	0.385	19.83 ± 1.30	0.696
	CT	5.90 ± 0.23		2.18 ± 0.46		3.03 ± 0.55		61.17 ± 1.76		3.78 ± 0.70		69.51 ± 1.48		5.68 ± 2.01		19.86 ± 1.45	

pH_{24} = pH 24 h after slaughter; DLR = drip loss rate; MCV = meat color value; WM = water moisture; IMF = intramuscular fat content; CP = protein content.

DISCUSSION

In recent years, improving IMF content has become one of the most important breeding objectives in pigs, because IMF is positively correlated with pork quality. Both *APOA5* and *APOC3* genes have been mapped to SSC9, which harbors quantitative trait loci (QTL) for HDL45 and TG45 in the range of 33 cM (Gallardo et al., 2008). It is well known that *APOA5* and *APOC3* can regulate TG concentration and subsequently affect fat deposition, so they were chosen as candidate genes in the present study to investigate their associations with fat deposition and meat quality in Kele pigs (Talmud et al., 2004). In human research, an LD was detected between the *APOA5* (-C1131T) and *APOC3* (C-428T) genes, which showed an association with increased insulin and glucose levels, prior to and after an oral glucose tolerance test (Waterworth et al., 2005; Miller et al., 2007; Niculescu et al., 2010). In the present study, there was a complete LD between *APOA5* and *APOC3* (T-458G and C884T), and they were significantly correlated with DLR, MCV, and shear force in Kele pigs, indicating that the two genes could have a linkage relationship in the process of regulating TG level.

APOA5 is a key fat transfer factor in the PPAR signal pathway, and functions in the regulation of TG level and fat deposition. In humans, several variants in the *APOA5* gene (-1131T>C, c.56C>G, c.553G>T, and -3A>G) have been identified to be related to significant changes in TG level (Talmud et al., 2004). In chicken, 7 mutations were demonstrated to affect abdominal fat weight, percentage of abdominal fat yield, and liver weight (Yao et al., 2008). Furthermore, 12 SNPs were detected in the crossbred pigs of Landrace sire x Yorkshire, and the mutation of C1834T in the 3'-region yielded a strong association with average back fat thickness and leaf fat. In this study, the mutation G-769T was detected in the promoter region of the *APOA5* gene and it was associated with cooking percentage. The promoter region contains the regulatory *cis*-acting element of eukaryotic gene expression, and plays a key role in the gene expression strength and specificity (Xu et al., 2012). However, whether or not the G-769T causes gain or loss of regulatory binding sites needs to be further investigated. Current research on *APOC3* also revealed that it affects TG level. In humans, reports showed that people with the alleles -455C, -482T, and *Sst*I have a higher TG level and a higher risk of coronary heart disease than normal (Shoulders et al., 1991; Maeda et al., 1994). In the present study, we demonstrated that 9 SNPs in the pig gene were associated with meat quality phenotypes, namely DLR, MCV, and shear force.

In conclusion, our present research provided evidence that the *APOA5* and *APOC3* genes are responsible for QTLs located on SSC9 related to HDL45 and TG45 in pigs. We propose that the different genotypes of *APOA5* and *APOC3* can affect pork quality traits by regulating blood TG level. However, the detailed mechanisms involved in these processes need to be further investigated in the future.

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