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Genetic Association and Expression of *JHDM1A* Gene Related to Meat pH in Commercial Pigs

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ABSTRACT

An experiment was conducted to study the association and expression of *JHDM1A* gene as a candidate gene for meat quality. The polymorphism was genotyped by the polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) using restriction enzyme on a total of 300 muscle samples of [Duroc × (Large White × Landrace)] pigs. Results showed that *JHDM1A* gene was significantly associated with meat pH 45 min post-mortem (p.m.) ($p<0.05$). Allele frequencies for G and C were 0.53 and 0.47. The genotype frequencies for GG, GC, and CC were 0.24, 0.58, and 0.18, respectively. The Quantitative Reverse Transcription Polymerase Chain Reaction (qRT-PCR) study were analyzed between low and high pH 45 min p.m. groups (n=10 per group) according to the association result. *JHDM1A* expression was higher in animals with a low post-mortem meat pH 45 min ($p<0.05$). Therefore, polymorphism and expression in the porcine *JHDM1A* gene might be the important candidate genes to improve meat quality traits in terms of meat pH.

Keywords: JHDM1A gene; single nucleotide polymorphism; gene expression; meat quality

INTRODUCTION

Meat quality is considered an important trait in the economics of farm animals. It has been reported that meat quality has low heritability controlled by multiple genes and the management system. The advances in molecular genetics research have led to identifying genes, or genetic markers for meat quality traits (Piórkowska *et al.*, 2018; Gao *et al.*, 2007). The loss of fluid from meat called "drip loss" will affect the economic, sensory, and meat quality (Jennen *et al.*, 2007). The key factor that has an influence on drip loss is the dramatic pH decline during the high temperature of carcass and protein denaturation. Low muscle pH is involved in reduced water-holding capacity (Scheffler & Gerrard, 2007). The development of databases of animal-genome sequences provides information that can be used to identify the function and position of candidate genes responsible for complex traits such as meat quality traits (Davoli & Braglia, 2007).

The *JHDM1A* (JmjC domain-containing histone demethylase 1A) is the first JmjC domain-containing protein including histone demethylase activity that selectively to remove mono- and di-methylation from histone H3K36. Previous studies implicated the relation of H3K36 demethylases with cell proliferation, senescence, and apoptosis (Fukuda *et al.*, 2011). The lysine demethylase 2A (*JHDM1A*) gene plays a crucial role through histone H3K36 demethylation modification on gene silencing, cell growth, cell cycle, and cancer development (He *et al.*, 2008; Peng *et al.*, 2011). *JHDM1A* gene was associated with meat quality such as drip loss, lactic acid content in meat, fiber type ratio, and shear force (Peng *et al.*, 2011). The same position of SNP on C224G has been associated with carcass quality traits in terms of backfat thickness (Han *et al.*, 2014). *JHDM1A* was located on a region of pig chromosome 2 (SSC2) (https://www.ncbi.nlm.nih.gov/gene/?term=JHDM1A+sus). The chromosomal region of *JHDM1A* was incorporated with several Quantitative Trait Loci (QTL) related to pH

value (Liu *et al.*, 2007; Große-Brinkhaus *et al.*, 2010) and drip loss (Liu *et al.*, 2007). Identifying genomic regions are providing biological meanings of more specific gene products and builds associated gene networks related to the interesting traits (Campos *et al.*, 2020). Quantitative trait loci and genome-wide association studies have played an important role in identifying candidate genes and animal characterization. The utilization of animal genotyping technologies and gene identification methods, many functional genes and genetic variants associated with economically important phenotypic traits have been identified and annotated. The identification of genomic regions, genes associated with phenotypic traits, and description of gene function are some of the applied research activities to understand the genetics of livestock species (Gebreselassie *et al.*, 2020).

According to the role of *JHDM1A* gene that is correlated to cell growth, cell cycle, and apoptosis. Detection of single nucleotide polymorphisms (SNPs) and description of gene function via gene expression are some of the applied research activities to understand the genetics of pigs. Therefore, the aim of this research was to study the genetic association and expression of porcine *JHDM1A* gene with meat quality traits to be used as a potential marker for meat quality in the future.

MATERIALS AND METHODS

Animals and Phenotypes

All pig muscles were randomly collected from a local meat supplier. Genomic DNA and phenotypic data were obtained from muscles of the commercial breed [Duroc × (Large White × Landrace)] (n=300) population in Thailand. The muscle samples were immediately taken from the *Longissimus lumborum* between $13^{th}/14^{th}$ rib to evaluate meat quality and the muscle samples were kept at -20 °C for DNA isolation and -80 °C for mRNA expression until subsequent analysis. Meat quality traits analyzed in this study include drip loss, thawing loss, cooking loss, meat pH at 45 min p.m., meat pH at 24 h p.m., shear force, and meat color. pH-values were measured by using a spear-type electrode (pH Spear, Eutech Instruments, Singapore) in the *Longissimus lumborum* between $13^{th}/14^{th}$ rib. The pH meter was calibrated by using buffers 4.20 and 7.10, using the temperature of the chops. Drip loss (2 muscles per animal) was scored based on a bag method with a size-standardized sample from *Longissimus lumborum* collected at 24 h p.m. that was weighed, suspended in a plastic bag, held at 4 °C for 48 h, and thereafter re-weighed (Honikel *et al.*, 1986). To determine cooking loss, a loin cube was taken from the *Longissimus lumborum*, weighed, placed in a polyethylene bag, and incubated in water at 75 °C for 50 min. The bag was then immersed in flowing water at room temperature for 30 min and the solid portion was re-weighed. Thawing loss was determined similarly after at least 24 h freezing at −20 °C. The samples were frozen in a blast freezer, kept at −20 °C. Thawing methods were carried out at 4±1 °C in refrigeration overnight. Drip loss, cooking loss, and thawing loss were calculated as a percentage of weight loss based on the start weight of a sample. The color of the meat was measured by a Minolta chromameter (Minolta Camera Co., Osaka, Japan). The samples were placed on trays and measured the meat surface after exposing to the air for 30 min at 4 °C in the refrigerator. The results were expressed as L*(lightness) value. Shear force values were determined by a Texture Analyzer TA-XT2 (Texture Technologies Corp., Scarsdale, NY, USA) on 12.5-mm-diameter cores drilled from the boiled samples (5 replicates/sample) previously cooled to room temperature. Shear force value was expressed as Newtons (N). The mean values and standard deviation are represented in Table 1.

DNA Extraction, PCR Reaction, and Analysis of Mutation

The muscle tissues were immediately collected after slaughtering and kept in liquid nitrogen for DNA isolation. DNA was isolated from skeletal muscle tissue by using AxyPep Multisource Genomic DNA Minipep Kit (Axygen Scientific, Inc., USA). The single nucleotide polymorphism in the porcine *JHDM1A* gene was genotyped for the samples. Primers used for genotyping are depicted in Table 2. Polymerase chain reactions (PCR) were performed in a 20 μL volume containing 2 μL of genomic DNA, 1 × PCR buffer (with 1.5 mM $MgCl_2$),

Table 1. Descriptive statistics of meat quality traits of pigs

Traits	Mean±SD (*n*=300)
Drip loss (%)	2.84±1.34
Thawing loss (%)	4.16±2.25
Cooking loss (%)	30.16±4.14
pH45 [a]	6.64±0.31
pH24 [a]	5.86±0.22
Shear force (N)	60.21±6.22
Meat color	43.81±10.73

Note: [a]meat pH45, pH24 values at 45 min and 24 h post-mortem, respectively.

Table 2. Primers sequence for *JHDM1A* and *TBP* genes

Gene	Primer sequence	Application	Tm (°C)	Product	Enzyme	Reference
JHDM1A	Fw: 5′-CCCAGACTGAGCAGGAACC-3′	Genotyping	61.5	348 bp	MBoI	Peng *et al*. (2011)
	Rw: 5′-GGACACCACGAGGAGAACC-3′					
JHDM1A	Fw: 5′-CGACGACGCTATGAAGATGA-3′	qRT-PCR	60	163 bp	-	-
	Rw: 5′-GCCACCACGCTGGATATACT-3′					
TBP	Fw: 5′- GATGGACGTTCGGTTTAGG -3′	qRT-PCR	60	124 bp	-	Kayan *et al*. (2013)
	Rw: 5′- AGCAGCACAGTACGAGCAA -3′					

0.25 mM of dNTP, 5 pM of each primer, and 0.1 U of Taq DNA polymerase (Fisher Scientific Ltd.). The PCR was performed under the following condition: initial denaturing at 95 °C for 5 min followed by 35 cycles of 30 sec at 95 °C, 30 sec at an annealing temperature of each primer pair (Table 2), 1 min at 72 °C, and a final elongation of 10 min at 72 °C. Genotyping of the samples was performed by PCR-RFLP. The PCR product was checked on 1.5% agarose gel before digestion by using a restriction enzyme (MBoI enzyme) for *JHDM1A* gene (Table 2). After digestion, PCR-RFLP products were resolved on 3% agarose gel. The fragments were visualized under ultraviolet light. The sizes and number of the fragments were analyzed using molecular analyst software (Bio-Rad).

mRNA Expression of *JHDM1A*

Total RNA was isolated from the *Longissimus lumborum* muscle base on low and high pH 45 min p.m. muscle groups (n=10 per group) by using QIAamp RNA Mini Kit (Qiagen, France) according to manufacturer recommendations. The concentration and purity of the extracted RNA was measured using the NanoDrop spectrophotometer. The purity of the RNA extract was measured, showing an A260/A280 ratio ranging from 1.80 to 2.10. Real-time PCR analysis was run using MyGo Pro® real-time PCR instrument (IT-IS Life Science Ltd, Middlesbrough, UK), and using QuantiNova SYBR Green RT-PCR Kit (Qiagen, Hilden, Germany) for real-time reaction. The Real-time PCR master mix consisted of 10 µl of 2X QuantiNova SYBR Green RT-PCR Master Mix, 1 µL of each 10 µM (0.5 µM) forward and reverse primer, 0.2 µL of QN SYBR Green RT Mix, 5 µL of template, and 2.8 µL of nuclease-free water, the total volume was 20 µL. A two-step amplification program was used where pre-denaturation occurred at 95 °C for 2 min, followed by 40 cycles of denaturation at 95 °C for 5 sec and annealing and extension at 60 °C for 10 sec and 72 °C for 15s, with collection of fluorescence signal at the end of each cycle. Melting analysis was performed from 60 °C to 97 °C at 0.1 °C/s. Real-time PCR amplifications were performed in a duplicate of each sample and each standard. The expression level was calculated from the ratio of Cq values of target gene with housekeeping gene *TATA sequence binding protein* (*TBP*). PCR Primers were designed using the Primer3 software and are shown in Table 2.

Statistical Analysis

Allele and genotype frequencies were determined by using the following formulas (Pahuja *et al.*, 2020). Allele frequencies formulation was $p + q = 1$ where the alleles will be G and C. Genotype frequencies formulation was $p^2 + 2pq + q^2 = 1$ where the genotypes will be GG, GC, and CC. The association of the genotypes with meat quality traits was calculated using the variance of quantitative traits. The statistical analysis was used by a generalized linear model with SAS (var. 9.2, SAS Inst. Inc., Cary, NC). The model was as follow (Kayan *et al.*, 2013):

$$Y_{ij} = \mu + Genotype_i + YS_l + e_{ij}$$

where Y_{ij} is the observation of meat quality; µ is the population mean; $Genotype_i$ is the effect of i-th genotype (i = GG, GC, and CC); YS_l is the effect of l-th date of slaughtering (l = 1 for day 1 of slaughtering until to 6 for day 6 of slaughtering) and e_{ij} is the random residual error. The least-square mean values of the genotypes were adjusted by the Tukey-Kramer correction. The additive effect was estimated as half of the difference between the 2 homozygous groups: a = 1/2(BB-AA) where A and B means the first and the second allele of the analyzed markers, respectively. The dominance effect was estimated as the difference between the heterozygous group and the average of the 2 homozygous groups: d = AB-1/2(AA+BB). The estimates of effects were tested by *t*-test on significant deviation from zero (Davoli *et al.*, 2017).

Differences between qRT-PCR were analyzed by t-tests. The statistically significant differences were considered at $p<0.05$.

RESULTS

Genotype, Allele Frequencies, and Association Analysis of *JHDM1A* gene

The SNP in *JHDM1A* gene was located in the g.224G>C. PCR-RFLP patterns of *JHDM1A* alleles were as follows: genotype GG resulted in one fragment (348 bp) while the CC genotype resulted in two fragments (189 and 159 bp). Allele frequencies G and C were 0.53 and 0.47. The genotype frequencies for GG, GC, and CC were 0.24, 0.58, and 0.18, respectively (Table 3). This study revealed that there was a significant association between SNP with meat pH 45 min p.m. ($p<0.05$) (Table 4). The polymorphism was not significantly different with drip loss, thawing loss, cooking loss, meat pH 24 h p.m., shear force, and meat color. The animals of the genotype GG showed the highest pH 45 min p.m. and the genotype GC was the lowest pH 45 min p.m. (Table 4). The polymorphism of *JHDM1A* gene showed dominant effect on pH 45 min p.m. ($p<0.01$) (Table 4).

mRNA Expression of *JHDM1A* Gene

This study revealed the abundance of *JHDM1A* transcript with divergent meat pH 45 min p.m. The mRNA expression was significantly different between low and high pH min p.m. groups ($p<0.05$) (Figure 1). The normalized expression level of *JHDM1A* gene was higher in the low post-mortem muscle pH 45 min.

Table 3. Genotype and allele frequencies of *JHDM1A* gene in the commercial pigs

Genotype	Commercial pigs (*n*=300)	Allele	Commercial pigs (*n*=300)
GG	0.24	G	0.53
GC	0.58	C	0.47
CC	0.18		

Table 4. Least square means (LSM) and standard errors (SE) for meat quality traits across genotype of *JHDM1A* gene in the commercial pigs

Traits	Genotype (Ls mean ±SE)[1]			p-Value	Effect (mean ±SE)	
	GG	GC	CC		Additive	Dominance
Drip loss (%)	2.80 (0.18)	2.89 (0.10)	2.99 (0.20)	0.560	-0.09±0.14	0.01±0.17
Thawing loss (%)	4.47 (0.25)	4.11 (0.14)	4.30 (0.28)	0.316	0.09±0.20	0.28±0.24
Cooking loss (%)	30.16 (0.16)	30.14 (0.09)	29.98 (0.18)	0.485	0.09±0.13	-0.07±0.15
pH45[c]	6.67 (0.03)[b]	6.58 (0.02)[a]	6.66 (0.04)[ab]	0.029	0.01±0.03	0.08±0.03**
pH24[c]	5.84 (0.02)	5.87 (0.01)	5.89 (0.03)	0.295	-0.02±0.02	0.00±0.02
Shear force (N)	58.64 (0.04)	59.43 (0.03)	59.13 (0.05)	0.256	-0.02±0.04	-0.05±0.04
Meat color	43.96 (0.20)	43.88 (0.11)	43.98 (0.22)	0.624	-0.01±0.16	0.09±0.19

Note: Different letters denoting significant difference between groups: [a,b]*p<0.05; **p<0.01. [c]meat pH45, pH24 value at 45 min and 24 h post-mortem respectively.

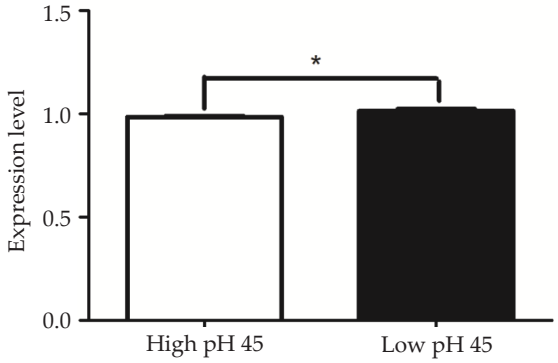

Figure 1. Normalized expression level of *JHDM1A* gene transcript in *Longissimus lumborum* in pig between high and low meat pH 45 min p.m. (n=10 per group). The expression level was expressed as the ratio of Cq values of *JHDM1A* gene with housekeeping gene *TATA sequence binding protein* (TBP). *The mRNA expression was significantly different between low and high pH min p.m. groups (p<0.05).

The abundance of *JHDM1A* transcript of low and high pH 45 min p.m. groups were 1.01±0.01 and 0.98±0.01, respectively.

DISCUSSION

In a previous study, the polymorphism of the *JHDM1A* gene had a highly significant association with drip loss percentage, muscle fiber type II Ratio, shear force, and lactate content. The mRNA expression of *JHDM1A* gene can be observed in various tissues with high expression levels in the lung and kidney, and with moderate expression levels in the heart, liver, and skeletal muscle, respectively (Peng *et al.,* 2011). In this study, the polymorphism of the *JHDM1A* gene was significantly associated with pH 45 min p.m. in our sample population. The expression level of *JHDM1A* gene was higher in the low post-mortem meat pH 45 min p.m. Meat quality is a complex trait. Meat quality attributes also obtained significant correlations with pH, positively with water holding capacity and negatively with cooking loss and L* color (Moreno *et al.,* 2020). It is clear that early post-mortem events, a rate of pH decline, proteolysis, and protein oxidation are influences on the ability of meat to retain water in muscle fiber (Mateescu *et al.,* 2017; Pegolo *et al.,* 2020). One of the natural biochemical processes occurring after the death of the animal is post-mortem acidification which is direct of pH decline in muscle (the accumulation of lactic acid due to anaerobic glycolysis of glycogen) (Le *at al.,* 2020). There has been no evidence study to support the direct role of *JHDM1A* gene on pH in muscle. Our study was the first to highlight the possible role of *JHDM1A* gene on pH in muscle via metabolic pathways e.g., proteolysis and gluconeogenesis pathways. Several studies have elucidated that the roles of *JHDM1A* expression in skeletal muscle are related to cell proliferation and apoptosis (Peng *et al.,* 2011; Kawakami *et al.,* 2015). Stress is one of the reasons that cell apoptosis is induced. In addition, the apoptosis onset period may lead to the loss of water from muscle cells by increasing protein denaturation via the proteolysis pathway (Plastow & Bruce, 2014). The onset of apoptosis might be associated with drip loss and pH at 45 min post-mortem. During the conversion of muscle into meat, the rapid metabolism will increase the lactate accumulation in the muscle that may cause the cell to undergo apoptosis conditions (Gao *et al.,* 2020). The apoptosis condition has been observed when the pH of muscle falls from 7.2 to 5.7 within 90 min (Nilsson *et al.,* 2006).

Furthermore, the function of physiological and biochemical in different pig breeds may indicate different for changing process of the muscle into the meat (Oskoueian *et al.,* 2016). Another role of *JHDM1A* gene was associated with the gluconeogenesis pathway and resulted in a decreased expression of gluconeogenic genes (Zhang *et al.,* 2019). The previous studies reveal that blood glucose was related to a change in pH muscle (Akşit *et al.,* 2006; Koomkrong *et al.,* 2017). Blood glucose was related to a change in pH muscle (Akşit *et al.,* 2006). Blood glucose level had a negative relationship with pH 45 min post-mortem. The high blood glucose level group presented lower pH values at post-mortem in animals, and consequences decreased the water holding capacity in meat (Choe *et al.,* 2009). Moreover, high glucose has the effects of inducing apoptosis, increasing glycogen accumulation, and inhibiting protein synthesis on muscle cells (Liu *et al.,* 2021). Meat quality is affected by the energy stored in the form of glucose and glycogen in the muscle at the slaughtering period and the rate

of decline in metabolism in post-mortem (Savenije *et al.*, 2002). The degradation of glycogen in post-mortem via glycogenolysis and glycolysis pathways for providing ATP and lactic acid to the muscle cell and resulting in the decreased pH by lactate accumulation in the muscle (Daskalova, 2019; Scheffler & Gerrard, 2007). This study revealed the evidence role of *JHDM1A* gene based on meat pH as well.

CONCLUSION

The major findings of the present study were the association and expression of *JHDM1A* gene with meat pH. These results imply that *JHDM1A* gene might be the important candidate gene to improve meat pH. The functional of *JHDM1A* genes should be performed in further study to provide a better understanding of the molecular mechanism of meat pH.

CONFLICT OF INTEREST

Asep Gunawan serves as an editor of the Tropical Animal Science Journal, but has no role in the decision to publish this article. We also certify that there is no conflict of interest with any financial organization regarding the material discussed in the manuscript.

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