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Quantitative trait loci and candidate genes for the economic traits in meat-type chicken

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Recent progress has been achieved in the identification of quantitative trait loci (QTLs) and candidate genes, and they have been found to be very important for the production of chickens with more desirable meat characteristics. The major economic traits of chicken meat production were divided into two major categories, namely growth and carcass condition. In this paper, the QTL locations and candidate genes for the above mentioned traits are reviewed. The results presented here will provide guidelines for the selection of high quality and highly productive chickens through the marker assisted selection (MAS), which should be extensively used by poultry breeders and companies.

Keywords: candidate gene; economic trait; meat-type chicken; QTL

Introduction

Chickens are one of the most common agricultural birds and are an excellent model organism for studying the development of vertebrate animals. Therefore, studies on the chicken genome have been of great value to both agriculture and medicine (Wang *et al.,* 2012a).

Economic traits are the most important issues in livestock production as they directly affect market prices. Most economic traits in livestock are multigenic, which are controlled by many genes throughout the genome and by environmental factors, and therefore, they are known as quantitative traits (Gao *et al.*, 2007; Zhu and Zhao, 2007). Of these, body weight is a popular economic trait, which is one of indicators related to the growth of the chicken. Many reports relating to the QTLs and candidate genes in relation to body weight and growth in chicken have been published. One experiment

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compared the growth and feed efficiency between the Ross 308 strain of commercial broiler and the Athens-Canadian Random bred control (ACRBC) strain, which has not been selectively bred since 1957, using similar diets to those fed in both 1957 and in 2001. They reported that there had been a three-fold decrease in the age at which a market weight of 1.8 kg was attained, and a three-fold improvement in feed efficiency between 1957 and 2001. It was estimated that 85-90% of the improvement in growth rate and feed efficiency was due to genetic selection (Havenstein *et al.*, 2003).

Carcass characteristics are important traits in broiler meat production. It goes without saying that chickens with higher growth rates and better carcass traits are the more desired chickens for the production of meat. Intensive selection efforts have reduced the age at which the market weight (1 - 2 kg live body weight) is achieved (Nadaf *et al.,* 2007). Among carcass composition traits, breast yield has increased whereas abdominal fat has reduced, creating healthier meat products for consumers and increasing profits for poultry companies (Berri *et al.,* 2001).

The QTL approach and identification of functional candidate genes have become the main molecular tools to achieve desired traits in all livestock, including chicken. Along with QTLs, identification of single nucleotide polymorphisms (SNPs) in functional candidate genes has become an effective tool for rapidly determining the association of a specific genetic variant with phenotypic traits. This review provides an overview of QTLs and candidate genes which are associated with economic traits in meat-type chicken.

QTLs for economic traits in chicken

Quantitative trait loci (QTLs) have been mapped for selection response of animal breeding programmes (Sewalem *et al.,* 2002). Whole-genome linkage in equilibrium scanning using reference populations is one of the basic methods for QTL identification (Ikeobi *et al.,* 2002). The causative genes and/or mutations for affecting economic traits can be found by tracing significant QTL regions on the chromosomes. Therefore, the causative mutations can be used as markers for the selection of economic traits if there are significant associations between QTL regions and phenotypic traits.

Previous studies reported that many QTLs were found to be associated with economic traits in chicken, such as growth and body composition, egg production, antibody response, disease resistance, and behaviour (Sasaki *et al.,* 2004; Tsudzuki *et al.,* 2007; Pinard-van der Laan *et al.,* 2009; Siwek *et al.,* 2012; Wiren and Jensen, 2011). These QTL regions provided valuable information for applying marker assisted selection (MAS) for desirable traits at an early stage.

QTL AFFECTING BODY WEIGHT AND CARCASS TRAITS IN CHICKEN

The chicken QTL database has been summarised on the National Animal Genome Research Programme (NAGRP) website (http://www.animalgenome.org/cgi-bin/QTLdb). This organisation has been gathering chicken QTL data published during the past 10+ years. Currently, this website contains 3,442 QTLs from 172 publications over the world. Those QTLs represent 286 different traits in all types of chicken. This makes it possible for researchers to compare, confirm and locate the position of both QTLs and those genes responsible for important traits in chicken production. Body weight, which is directly associated with growth rate in broiler, is a major economic trait, and evidently more than 60% of discovered QTLs are related to growth, including body weight, carcass traits etc.

A total of 29 chromosomes, from GGA1 (*Gallus gallus* chromosome 1) to GGA28 and chromosome Z, have been successfully mapped in various breeds of chicken (Kerje *et al.,*

2003; Siwek *et al.,* 2004; Jacobsson *et al.,* 2005; Jennen *et al.,* 2005). Of these, major QTLs for growth-related traits have been commonly identified on GGA1 and/or GGA4. Gao *et al.* (2006) reported that two QTL regions were strongly linked to body weight and body development of a reciprocal cross of Silky Fowl and White Plymouth Rock on GGA1. The strongest evidence for QTL regions affecting body weights were located at 58.7 to 75.3 cM between *GCT0006* and *MCW0106* markers. This location was responsible for body weight at 3 to 12 weeks. Also, on the GGA1, the QTLs affecting chicken body development at 7 to 8 weeks and 10 to 11 weeks were investigated between *MCW0168* and *GCT0006* markers at 24 cM and 255 cM, respectively (*Table 1*).

In addition, QTL regions located at 497.6 cM and 501.1 cM on GGA1 significantly corresponded with growth at 56 to 70 days and body weight at 70 days were in low-weight selected (LWS) lines and high-weight selected (HWS) lines of the White Plymouth Rock chicken breed (Wahlberg *et al.,* 2009). Sheng *et al.* (2013) claimed that a QTL region located at distal end (389 - 398 cM) and midline one gene (MID1), which is involved in ubiquitin mediated proteolysis (UMP) pathway located at 296.9 cM of GGA1, were associated with growth traits in intercross populations between Chinese indigenous chickens with commercial broilers. This QTL region overlaps with previous results from a genome-wide association study (GWAS) which was conducted using another Chinese indigenous chicken breed (Xie *et al.,* 2012).

On GGA4, located at 217 cM between *MCW0122* and *LEI0062* markers, a QTL for body weight was found after cross-breeding White Leghorn and Rhode Island Red (Sasaki *et al.,* 2004). The QTLs for body weight at six and nine weeks that have a 5% genome-wide significance level were revealed at the same position of this region in different breeds of chicken (Sewalem *et al.,* 2002; Tuiskula-Haavisto *et al.,* 2002). In addition, a QTL associated with growth-related traits was verified on GGA4, located at 215 cM (Schreiweis *et al.,* 2005). Moreover, a QTL residing at 201 cM on chicken chromosome four has been associated with body weight in a crossbreed of Oh-Shamo and White Leghorn (Tsudzuki *et al.,* 2007). Wahlberg *et al.* (2009) described that QTL regions responsible for chicken average daily gain (ADG) at 42 to 56 days, body weight at 56 days, ADG at 56 to 70 days and body weight at 70 days were located on this chromosome, at 36.6 cM, 36.6 cM, 35.4 cM, and 37.8 cM, respectively (*Table 1*).

QTLs for body weight and growth were observed in differing regions from previous reports. This may be due to differences between the breeds used in the studies, which could be the main reason for the lack of confirmation of these QTLs (Gu *et al.,* 2011; Xie *et al.,* 2012). Therefore, this article aims to provide some clarity in terms of QTLs for chicken body weight. All of this QTL data will be very valuable to those who are interested in the further advancement of poultry breeding programmes.

Carcass weight is related to body weight and body size which is an economically important trait for livestock raised for meat production (Nishimura *et al.,* 2012). The intensive selection of economic traits in broilers has generated an excellent quality of carcass. A previous study crossing White Leghorn and commercial broiler chickens reported that QTL was associated with carcass traits which were found on GGA4 located at 138 - 243 cM (*Table 1*). Carcass weight (CW), wing weight (WW), and drumstick weight (DW) have 5% genome-wide significance in this location (Ikeobi *et al.,* 2004). The QTL in the same region, at 201 cM of GGA4, was revealed to have association with carcass weight in crossing between Oh-Shamo and White Leghorn chicken (Tsudzuki *et al.,* 2007). Thus, this can be used as a strong candidate region for carcass quality, even though further verification within other breeds is necessary for the identification of causative mutations.

Functional candidate genes for economic traits in chicken

Exploration of functional candidate genes is another popular approach for QTL identification. It is an effective and useful tool for quickly determining the association of a specific genetic variants with phenotypic traits (Zhu and Zhao, 2007). The candidate gene approach has been widely applied in medicine, agriculture, and other fields of life sciences, and has achieved useful results in the study of genes responsible for human health and disease, quantitative traits in animals and plants, and also evolutionary genetics. In the livestock species, especially in chickens, this method was used for decades to identify genes associated with economic traits. Below is a summary of a few candidate genes affecting economic traits in meat-type chicken.

THYROID HORMONE RESPONSIVE SPOT 14

Thyroid Hormone Responsive Spot 14 (THRSP), referred to as the 'spot14' gene, encodes a small acidic protein that is rapidly induced by thyroid hormone (T^3) and dietary carbohydrate in liver. This protein, which acts in hepatocytes, was discovered in earlier studies on the activity of thyroid hormone (TH) (Seelig *et al.,* 1981; Jump *et al.,* 1984; Kinlaw *et al.,* 1995), and the THRSP gene has been used as a model for the regulation of *de novo* lipogenesis for many years. A discrepancy of THRSP mRNA content in tissue affects its ability to synthesise lipids. The expression of THRSP correlates with a sensitivity of both lipogenesis and insulin. Specifically, the level of THRSP mRNA in white, brown adipose tissues, and in the liver is elevated when *de novo* fatty acid synthesis is induced by dietary and hormonal stimulations (Breuker *et al.,* 2010).

The polymorphism of THRSP gene was discovered in the putative protein coding region of the duplicated chicken THRSPα (9 bp) and THRSPβ (6 or 12 bp) genes. Polymorphism in the THRSP locus has been associated with abdominal fat traits in crossing broiler and Leghorn chicken populations (Wang *et al.,* 2004). In addition, the A213C SNP and 9 bp insertion-deletion (indel) of the thyroid hormone responsive spot 14α (THRSPα) gene was found to be tightly linked with body weight (BW), which implied that THRSPα gene has an important effect on the growth of chickens (Cao *et al.,* 2007). Moreover, d'Andre Hirwa *et al.* (2010) reported that the A197835978G and G197836086A SNPs, and 9 bp indel of THRSPα gene were associated with body weight and carcass traits in crossbred chicken between White Recessive Rock and Xinghua (*Table 2*). Hence, this gene should be related to important economic traits in meat-type chickens.

ORNITHINE DECARBOXYLASE

Ornithine decarboxylase (ODC) is a pyridoxal-5'-phosphate dependent enzyme that presents a critical step in the synthesis of polyamines, particularly putrescine, spermidine and spermine (Kern *et al.,* 1999). Polyamines, small organic polycations, are essential for stabilising DNA structure, the DNA double strand-break repair pathway and as antioxidants. Therefore, ODC is an essential enzyme for cell growth. This gene also plays a key role in diverse biological processes, such as differentiation, transformation, and apoptosis in mammals (Pendeville *et al.,* 2001).

In chicken muscle, the higher mRNA expression of the ODC gene was followed by higher enzyme activity in chicken lines genetically selected for both rapid growth rate and egg production. The ODC mRNA levels and enzyme activity in broiler lines were significantly higher than those of White Leghorn line. These results suggest that the ODC gene may play an important role in cell growth (Johnson *et al.,* 1995). The QTL study in Shamo and White Plymouth Rock cross chicken, the QTLs on chromosome 3 (GGA3)

located at 263 - 456 cM were strongly correlated with growth and carcass traits (Uemoto *et al.,* 2009). This region is adjacent to where the ODC gene resides, at 267.4 cM on chromosome three. Two haplotypes, haplotype W (A_CC) derived from White Plymouth Rock, and haplotype S (GCCCGTT) derived from Shamo, were distinguished as being constructed by four different SNPs, including g.-638A>G SNP, g.-465C>T SNP, g.-353C>T) SNP, and a 4-bp indel mutation (g.-633_-632ins) (*Table 2*). The significance relationship between haplotypes and growth and carcass traits was measured in body weight at 3 weeks (BW3), BW6, BW9, carcass weight (CW), average daily gain (ADG), breast muscle weight (BMW), and tight muscle weight (TMW), where haplotype W (A_CC) have positive effects on all traits (Uemoto *et al.,* 2011).

PRD1-BF1-RIZ1 HOMOLOGOUS CONTAINING 16

The PRD1-BF1-RIZ1 homologous domain containing 16 gene (abbreviated as PRDM16) acts as a transcription co-regulator, which controls the development of brown adipocytes in brown adipose tissue (BAT) and manages a bidirectional cell fate switch between skeletal myoblasts and brown fat cells. It should bind to peroxisome-proliferator-activated receptor-c (PPAR-c) and is thought to activate its transcriptional function to encourage brown adipogenesis (Seale *et al.,* 2008).

In animals, enhancement of BAT is correlated with lean and healthy phenotypes in rat (Ghorbani *et al.,* 1997). On the other hand, the lack of BAT function in mice is associated with obesity and metabolic disease (Lowell *et al.,* 1993). Based on these functions, an association study between PRDM16 gene with growth and fat-related traits in livestock would be very interesting, especially for investigations in broilers. An association study using Chinese native chicken crossing Gushi (representing slow-growing Chinese native chickens) and Anka (representing fast-growing broilers) has been linked with growth, fatness and meat quality. In detail, the c. 1433 G>A SNP had positive effects on body weight and body size, whereas GG genotype was favourable for growth and fatness (Han *et al.,* 2012). This gene has been located at 12 cM on chromosome 21 (GGA21), the upstream of QTL position (17.84 cM), which is significantly associated with growth in the White Leghorn chicken line (Dorshorst *et al.,* 2011).

FAT MASS AND OBESITY ASSOCIATED GENE

The fat mass and obesity associated gene (FTO) encodes fat mass and obesity-associated proteins with a novel C-terminal alpha-helical domain and an N-terminal double-strand beta-helix domain, which is conserved in Fe (II) and alpha-ketoglutarate-dependent dioxygenase family (Gao *et al.,* 2010). In humans, FTO is the first gene found to have a role in human obesity, and exhibits energy balance functions (Do *et al.,* 2008). The identified SNP in intron 1 of FTO gene in human is closely linked to obesity related traits, while the deletion of FTO allele in mice has generated immediate postnatal retardation, resulting in shorter body length, lower body weight, and lower bone mineral density than control mice, where body composition (fat mass, total tissue mass, and fat content) was relatively normal (Gao *et al.,* 2010). In chicken, FTO gene expression has been examined in both broilers and layers. This gene is highly expressed in chicken hypothalamus, liver, visceral fat and cerebellum, which are known to be involved in energy balance (Wang *et al.,* 2012b). Significant correlations were determined between this gene and growth, body composition, and fatness traits, in F2 populations crossing between Xinghua and Recessive White Rock chicken lines in China (Jia *et al.,* 2012).

OTHER CANDIDATE GENES

Identified functional candidate genes related to economic traits in chicken include

pituitary-specific positive transcription factor 1 (PIT1), high mobility group AT-hook 2 (HMGA2), pro-opiomelanocortin (POMC) and agouti-relatedprotein (AGRP), acetyl-COA carboxylase α (ACACA) and others (*Table 2*).

PIT1, a pituitary-specific transcription factor, plays an important role in pituitary development and hormone expression. Protein expressed by this gene is responsible for high affinity DNA binding with genes encoding for growth hormone (Mukherjee and Porter, 2012). A previous study revealed that variations in this gene were correlated with body weight, growth and body composition in different stages (Nie *et al.,* 2008). This gene is located on chicken chromosome one, where the QTL location was detected for body weight (Sewalem *et al.,* 2002). Another functional candidate gene for body weight in the QTL region is HMGA2. This gene is involved in diet-induced obesity, acts as a transcriptional regulating factor, and appears to have a function in proliferation and differentiation during the development of cells (Cattaruzzi *et al.,* 2007). Three SNPs, namely rs13849341, rs15231472 and rs13849381, were strongly associated with body weight, as determined in a reciprocal crossing between White Plymouth Rock and Silky Fowl chickens (Song *et al.,* 2011). In addition, the POMC gene encodes a polypeptide hormone precursor, which is known as prohormone convertase, was identified on chromosome three at 303.3 cM. A recent study of chickens, synonymous mutations (C495T) in the coding region of the gene, was significantly correlated with body weight. Furthermore, AGRP and ACACA genes were strongly associated with body weight (Tian *et al.,* 2010; Bai *et al.,* 2012).

Conclusions

This review discusses the QTL regions and candidate genes which have been correlated with economic traits of interest in meat-type chicken. The QTL regions in GGA1 and GGA4 were reported to be strongly associated with body weight and carcass-related traits in various breeds of chicken. In addition, candidate genes were determined to have positive associations with economic traits in meat-type chicken. This article represents the current status of QTLs and candidate genes for meat-type chicken, which will provide the guidelines for poultry breeders attempting to create chicken breeds with improved performance.

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Table 1 QTL locations affecting growth and carcass traits in chicken.

Trait	Chr. No.	Position (cM)*	*P*-Value (Pg^a/Pc^b)	Chicken Breed/Line	Reference
BW21; BW28; BW35; BW42; BW56; BW63; BW70; BW77; BW84; G49-56; G70-77	1	72.7; 70.9; 75.3; 68.3; 58.7; 71.5; 71.5; 71.5; 62.2; 24; 255.3	0.05[a]	Silky Fowl x White Plymouth Rock	Gao *et al.* (2006)
G56-70; BW70		497.6; 501.1		White Plymouth Rock	Wahlberg *et al.* (2009)
BW2W; BW4W; BW6W; BW8W; BW10W; BW12W; G0-4; G4-8	1	389; 399; 94 & 398; 89 & 398; 89 & 392; 111 & 392; 399; 392	0.05[a]	Huiyang Beard Chicken x Commercial Broiler Breed	Sheng *et al.* (2013)
BW13; BW16	2	61.7; 60.9	0.05[a]	Satsumadori x White Plymouth Rock	Tatsuda and Fujinaka (2001)
BW		119		Layer	Siwek *et al.* (2004)
BW2W	2	281	0.01[a]	Huiyang Beard Chicken x Commercial Broiler Breed	Sheng *et al.* (2013)
G0-14; BW14	3	71.7; 71.7	0.05[a]	White Plymouth Rock	Wahlberg *et al.* (2009)
BW21; BW28; BW35		108.9; 106.2; 112.7	0.05[b]	Broiler	Wang *et al.* (2012a)
BMW		225 - 246	0.05[a]	White Leghorn x Broiler	Ikeobi *et al.* (2004)
BW	4	217	0.05[a]	White Leghorn x Rhode Island Red	Sasaki *et al.* (2004)
		215		Cobb-Cobb broilers x Hyline White Leghorn	Schreiweis *et al.* (2005)
CW		201		Oh-Shamo x White Leghorn	Tsudzuki *et al.* (2007)
G42-56; BW56		35.4; 37.8		White Plymouth Rock	Wahlberg *et al.* (2009)
G56-70; BW70		36.6; 36.6			
CW, WW		166 (138-243)		White Leghorn x Broiler	Ikeobi *et al.* (2004)
DW, TW		79 - 82			
BW14; BW21; BW28; BW35; BW42; BW49; BW56; BW63; BW70; BW77; BW84; CW	5	23.1; 17.7; 20.2; 22.6; 23.1; 22.6; 22.1; 22.6; 23.6; 26; 26; 27.5	0.05[b]	Broiler	Wang *et al.* (2012a)
DMW		79 - 83	0.05[a]	White Leghorn x Broiler	Ikeobi *et al.* (2004)
DW		32 - 57			
G42-56; BW56; BW70	7	106; 101.4; 101.4	0.05[a]	White Plymouth Rock	Wahlberg *et al.* (2009)
DW, WW, DMW		98 - 101		White Leghorn x Broiler	Ikeobi *et al.* (2004)

Trait	Chr. No.	Position (cM)*	*P*-Value (Pg[a]/Pc[b])	Chicken Breed/Line	Reference
BW6W; BW9W	8	59; 93	0.05[a]	White Leghorn x Commercial Broiler	Sewalem *et al.* (2002)
BW	11	70	0.05[a]	Red Jungle Fowl x White Leghorn	Kerje *et al.* (2003); Jennen *et al.* (2005)
BW	12	45	0.05[a]	Red Jungle Fowl x White Leghorn	Kerje *et al.* (2003)
		63	0.05[b]	Cobb-Cobb broilers x Hyline White Leghorn	Schreiweis *et al.* (2005)
BW3W; BW6W; BW9W	13	47; 68; 69	0.05[a]	White Leghorn x Commercial Broiler	Sewalem *et al.* (2002)
BW		69		White Plymouth Rock	Jennen *et al.* (2005)
BMW, DMW, DW		32 - 70		White Leghorn x Broiler	Ikeobi *et al.* (2004)
G0-14; BW14	20	49.4 - 61; 50.3 - 62	0.05[b]	White Plymouth Rock	Jacobsson *et al.* (2005); Wahlberg *et al.* (2009)
BW	27	48	0.05[a]	White Leghorn x Commercial Broiler	Sewalem *et al.* (2002)
		20; 37		Red Junglefowl x White Leghorn	Kerje *et al.* (2003)
		60		White Leghorn x Rhode Island Red	Sasaki *et al.* (2004)
TW, WW		47 - 50		White Leghorn x Broiler	Ikeobi *et al.* (2004)
BW6W; BW8W; BW10W; BW12W; G4-8	27	13; 13; 13; 13; 11	0.05[a]	Huiyang Beard Chicken x Commercial Broiler Breed	Sheng *et al.* (2013)
BW	28	47	0.05[b]	White Plymouth Rock	Jacobsson *et al.* (2005)
BW	Z	165	0.05[a]	White Leghorn x Commercial Broiler	Sewalem *et al.* (2002)
		57		Layer	Siwek *et al.* (2004)
		55		Red Junglefowl x White Leghorn	Kerje *et al.* (2003)
		137		White Leghorn x Broiler	Ikeobi *et al.* (2004)

Abbreviation: BMW: breast muscle weight; BW: body weight, BW21, BW28, BW35, BW42, BW56, BW63, BW70, BW77 and BW84: body weight at 21 to 84 days; BW2W to BW12W: body weight at 2 to 12 weeks; CW: carcass weight; DMW: Drumstick muscle weight; DW: drumstick weight, G0-14: growth at 0 to 14 days; G42-56: growth at 42 to 56 days; G49-56: growth at 42 to 56 days; G56-70: growth at 56 to 70 days; and G70-77: growth at 70 77 days; LW: liver weight; TMW: thigh muscle weight; TW: thigh weight; WW: wings weight.

*The data was collected from the National Animal Genome Research Programme (NAGRP) website (http://www.animalgenome.org/cgi-bin/QTLdb)

[a]Pg: genome-wide *P*-value

[b]Pc: chromosome-wide *P*-value

Table 2 Candidate genes affecting body weight, carcass and meat quality traits in chicken.

Gene name/ Chromosome	GenBank Acc. No.	SNP name	Significant trait	Significant genotype	Reference
THRSP/GGA1	AY568628 and AY568629	A197835978G	BBW, BW4	GG	
		G197836086A	HW, BW4, BW, LW,	GG AA	D'Andre Hirwa *et al.* (2010)
		9-bp (indel)	AFW	AA	
PIT1/GGA1	AF029892	Rs13687127 (C>T)	BW12, SL12	TT	Nie *et al.* (2008)
		Rs13687128 (C>T)	BW3, BW4, BW5 ADG0-4	CC	
HMGA2/GGA1	-	Rs15231472 (A>C)	BW2, BW6, BW9, BW10, BW12	AA	Song *et al.* (2011)
		Rs13849381 (G>T)	BBW, BW1, BW2, BW3, BW5, BW6, BW10	TT	
ODC/GGA3	NM_001167766 NC_006090.2	g.-638A>G g.-465C>T g.-353C>T) 4-bp indel (g.-633_-632ins)	BW3, BW6, BW9, CW, ADG, BMW, TMW	Haplotype W (A_CC)	Uemoto *et al.* (2011)
POMC/GGA3	AB019555	c.C495T	BW	CT	Bai *et al.* (2012)
FTO/GGA11	HM050377 HM050378 HM050379	G4938404T (M1)	BW6, BW9, BW10, HNW ADG4-8, BW3, BW4, BW6, SL6, SD6	TT	Jia *et al.* (2012)
	HQ874647	C4938374T (M3)	ADG0-4 DW, LMW, SEW, EW, WW, BW4, BW5, BW6,	TT	
		G4677213A (M16)	BW7, BW8, BW9, ADG0-4,	AG	
		A4675075G (M17)	ADG4-8	GG	

Gene name/ Chromosome	GenBank Acc. No.	SNP name	Significant trait	Significant genotype	Reference
AGRP/GGA11	ENSGAL00000002244	c.C9T	BW, DL, EW, ChW	TT	Bai *et al.* (2012)
ACACA/GGA19	NM_205505	c.2292G>A	AFW and %AFW	GG	Tian *et al.* (2010)
PRDM16/GGA21	NC_006108.2 NW_001471565	c. 1161C>T c. 1233C>T c. 1433G>A	LW BBW BBW, BW2 to 12, CW	TT CC GG	Han *et al.* (2012)

Abbreviation: ADG0-4 and ADG4-8: average daily gain from 0 to 4 weeks and 4 to 8 weeks of age; BMW: breast muscle weight; BW: live body weight; BBW: birth body weight, BW1, BW2, BW3, BW4, BW5, BW6, BW7, BW8, BW9, BW10 and BW12: body weight at 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12 weeks of age; CW: carcass weight; DL: drip loss; DW: dressed weight; EW: eviscerated weight; HNW: head and neck weight; LMW: leg muscle weight; LW: liver weight; SEW: semi-eviscerated weight; TMW: thigh muscle weight; WW: wing weight.