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Application of genomic technologies to the improvement of meat quality of farm animals

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Abstract

Meat quality is of economic importance in farm animals. It is controlled by multigenes and the environment. During the past few decades, advances in molecular genetics have led to the identification of genes, or markers associated with genes, that affect meat quality. Work on sequencing farm animal genomes will help us to understand how genes function in various organisms and might be applied in the field to study the molecular control of meat quality. Candidate gene and genome scans are two main strategies to identify loci associated with the trait of meat quality. Several genes that influence meat quality have already been, or are close to being, identified. Some of them have been applied to the breeding of farm animals by marker-assisted selection. This will accelerate cumulative and permanent genetic improvement of herds.

Keywords: Genomic; QTL; Farm animals; Meat; Quality; Marker-assisted selection

1. Introduction

Much progress in farm animal breeding has been made in the last few decades, but achieving greater understanding in the improvement of meat quality was very slow before molecular markers became an accessible technology with wide applications in breeding schemes.

The trait which we will call "meat quality" is one of economic importance in farm animals. From the appearance of the raw material, quality requires analysis and classification of fat content, composition, tenderness, water-holding capacity, color, oxidative stability and uniformity. It is influenced by several factors, such as breed, genotype, feeding, fasting, preslaughter handling, stunning, slaughter methods, chilling and storage conditions (Rosenvold & Andersen, 2003). In brief, all the factors affecting meat quality can be divided into two aspects on the genetic basis and on management systems. For management systems, such as feed, handling details, slaughtering and meat processing, there are so many market specifications existing which have been emphasized for many years (Mullen, Stapleton, Corcoran, Hamill, & White, 2006). For the genetic basis, the correct selection of breeds or lines is very important because the genetic influence on meat quality is very different among breeds as well as among animals in the same breed. Selective breeding has been carried out in large populations for thousands of years. Such strong selection, especially in recent centuries, has resulted in the accumulation of new mutations with favorable phenotypic effects (Andersson, 2001). These new mutations can provide greater options, especially when molecular technology is used in breeding schemes.

In farm animal breeding, selection is effective for most traits, with many achievements through a process that has been slowly accelerating in recent years, particularly in relation to the trait of meat quality. Indeed, the trait of meat quality is difficult to improve by traditional selection because the heritability of meat quality is low and the measure for the quality trait is difficult, expensive, and only possible after slaughter. Moreover, meat quality

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is determined polygenically. There exists little knowledge of genes and their interactions that are involved in meat properties. The understanding of meat quality on a genetic basis is scanty, and needs to be addressed at first. With a better knowledge of meat quality genetics, molecular breeding aspects will be developed. At the present time, the main task of genetics is to identify factors in the molecular or biological components of meat quality that will be useful for marker-assisted selection in breeding, i.e. giving "designer meat" by genetic and molecular methods. The finding of potential genes or chromosome regions responsible for meat quality will benefit the producers. In these years, a lot of work has been carried out in this field to find potential genes or chromosome regions associated with the meat quality trait in different farm animals, such as pig, cattle, sheep and chicken. It will be an exciting period when the molecular breeding method is used to "design the meat" on the base of genomics knowledge and technologies. The aim of this paper is to introduce the developing field of farm animal genomics, to describe the strategies and technologies to map and characterize meat quality trait loci, to review genes and their function that are involved in determining meat quality, and to discuss marker-assisted selection and its use in farm animal breeding.

2. The developing field of farm animal genomics

Genome research in farm animals progressed rapidly in recent years, moving from linkage maps to genome sequence. The work on farm animal genome sequencing began in the early 1990s, and assists in the understanding of how genomics function in various organisms (Fadiel, Anidi, & Eichenbaum, 2005). It will be applied in different fields, such as to study the molecular components of meat quality and ways of improving it.

In March 2004, the first draft of the chicken genome was released (Antin & Konieczka, 2005). In May 2006, the Genome Sequencing Center submitted an improved 6.6X draft chicken genome assembly. The chicken genome has a haploid size of 1200 Mb. It is not only a food animal that comprises 41% of the meat produced in the world, but also a model organism for studies of disease and biology (Dequeant & Pourquie, 2005). With the chicken genome sequence, especially the genome-wide screening in three chicken breeds yielding a set of 2.8 million SNP markers (Wong et al., 2004), chicken breeders will have a framework for investigating polymorphisms of informative quantitative traits to continue the directed evolution of these species (Fadiel et al., 2005).

In October 2004, the first draft of the bovine genome sequence was deposited in a free public database. In June 2005, the Bovine Genome Sequencing Project released the second version of the bovine genome, Btau_2.0, which was a 6.2X whole genome shotgun assembly. In August 2006, the Bovine Genome Sequencing Project released the third version of the bovine genome assembly, Btau_3.1, which was a 7.15X mixed assembly that combines whole genome shotgun sequence with BAC sequence (http://www.ncbi.nlm.nih.gov/genome/guide/cow/).

Plans for the porcine genome project are underway. The whole-genome sequencing for pig began in 2005. What is more, the "Sino-Danish Pig Genome Project" has published the pig genome sequence with <1X coverage (Wernersson et al., 2005). In the near future, the sequencing of the porcine genome will allow gene markers for specific traits to be identified, assisting breeders in generating pig stocks selection.

The focal point of interest in sheep is the quest to maximize sheep meat and wool production. The third genetic linkage map of sheep included well over 1000 markers and BAC libraries have been produced (Maddox et al., 2001) and contigs assembled around several regions of interest to individual laboratories (Womack, 2005). The sheep genome sequence will be completed by the Sheep Genome Project.

Besides the genome sequence database, there are several major sources of information on farm animal genomics. The ArkDB (http://www.thearkdb.org) is one of them and it is available through the Roslin Institute (UK) and Texas A&M University (USA) (Hu et al., 2001). The ArkDB provides detailed genomic mapping data on chicken, cow, pig and sheep, including data on PCR primers, genetic linkage map assignments of specific loci and markers, and cytogenetic map assignments (Law & Archibald, 2000). All this genome information, especially the sequence information will permit cross-species comparison of the effects of candidate gene allelic polymorphisms on meat quality. Integration of the linkage map, the RH map, the BAC fingerprinted contig (FPC) map and the genome sequence information will help to identify the candidate genes affecting meat quality.

3. The strategies and technologies to map and characterize the loci of the meat quality trait

Meat quality trait has a multifactorial background and is controlled by an unknown number of quantitative trait loci (QTL). The main goal of genome research in farm animals is to map and characterize trait loci. There are two main strategies to identify trait loci, association tests using candidate genes and genome scans based on linkage mapping DNA markers (Andersson, 2001). The information of the meat quality trait loci can be applied in breeding programs by using marker-assisted selection (MAS).

3.1. Candidate gene approach

The candidate gene approach studies the relationship between the trait of interest and known genes that may be associated with the physiological pathways underlying the trait (Andersson, 2001). If the candidate gene is a true causative gene, this approach can be very powerful and can detect loci having even small effects. The implementation of a candidate gene approach consists of the following steps:

(1) construction or collection of a resource population, (2) phenotyping of the specific components of the trait(s), (3) selection of genes or functional polymorphisms that potentially could affect the traits, (4) genotyping of the resource population for the selected genes or functional polymorphisms, (5) statistical analysis of the phenotypic and genotypic data (Da, 2003). This is an effective way to find the genes associated with the trait. So far, a number of genes have been investigated.

Although great progress has been made by using candidate gene approach, the limitation of this approach is obvious. The candidate gene tests must be interpreted with caution because spurious results can occur due to linkage disequilibria to linked or non-linked "causative" genes, or because the significance thresholds have not been adjusted properly when testing multiple candidate genes (Andersson, 2001). It also requires prior knowledge of the physiology of the specific trait, which is not always available. On the other hand, there are sometimes many candidate genes for the trait; it will take a long time to evaluate all of them. Furthermore, some genes that are not part of the known physiological pathways may contribute to the trait under investigation. Before the genome was sequenced, the selection of candidate genes was based upon cross-species gene comparison. It was difficult to analyse and compare genes from different species. The genome sequence, especially the SNP map, would solve a lot of questions on the selection of candidate genes. For example, the chicken SNP map provides abundant and useful SNP information to find the causative mutations among broiler, layer, silkie and red jungle fowl, which will accelerate the research.

3.2. Genome scans approach

The genome scan approach studies the relationship between a trait and markers selected across the genome to identify chromosomal locations associated with the trait (Andersson, 2001). The genome scan will find out the map location of a trait locus with a major effect. It involves the following steps: (1) design and construction of a resource population, (2) phenotyping traits of the resource population, (3) selection of genetic markers, (4) genotyping of the population for selected markers, (5) construction of linkage maps, (6) statistical analysis of the phenotypic and genotypic data derived from the resource population (Da, 2003).

The design of a resource population is the first step in genome scanning, which will decide whether QTL can be found. A resource population is a population generated for a particular research purpose, with phenotypic information and sufficient DNA supply for genotyping; for example, an intercross between two divergent breeds of farm animal or a population containing particularly interesting phenotypic data. Because the design of the intercross between two divergent populations of farm animals has a more powerful approach for QTL mapping, it is used in most resource populations, e.g. the wild boar and large white pigs (Andersson-Eklund et al., 1998; Andersson-Eklund, Uhlhorn, Lundeheim, Dalin, & Andersson, 2000; Knott et al., 1998; Nii et al., 2005, 2006), Asian and European breeds of pig (Jungerius et al., 2004; Stratil et al., 2006), *Bos taurus* (Angus) and *Bos indicus* (Brahman) cattle (Kim, Farnir, Savell, & Taylor, 2003), the broiler and the silkie (Gao et al., 2006), the jungle fowl and the layer (Wright et al., 2006). In this design, the F_1 animals show a high heterozygosity at marker loci and, in particular, at those loci that account for phenotypic differences between the two populations. If the construction of a resource population is too costly, a population containing particularly interesting phenotypic data can be used, e.g. a half-sib families comprising >1000 progeny from a single male can be collected in a species, such as cattle (Mizoshita et al., 2004). And selective genotyping and DNA pooling are cost-saving strategies that apply to any of the above designs (Carleos, Baro, Canon, & Corral, 2003; Taylor & Phillips, 1996).

Using the genome scan, the large amount of QTLs can be obtained in farm animals. It can provide a useful bridge to link genome information with phenotype. There is a database, Animal quantitative trait loci (QTL) database (AnimalQTLdb), which contains all publicly available QTL data on farm animal species for the past decade (Hu, Fritz, & Reecy, 2007). It comprises QTL location (chromosome, location, location span), flanking markers, peak markers, test statistics, QTL effects and traits. And it is easy to locate and make comparisons within and between species with this database. To date (January 19, 2007), there are 1675 QTL from 110 publications representing 281 different traits for pig, 846 QTL from 55 publications representing 91 different traits for cattle, 657 QTL from 45 publications representing 112 different traits for chicken (http://www.animalgenome.org/QTLdb/). Several groups have worked on the identification of QTL controlling meat quality and most of them are about pork quality. QTL with significant influences on meat quality were located on almost every porcine chromosome. In PigQTLDB (Hu et al., 2005), there are 12 types for meat quality and total 1405 QTL for meat quality, such as 595 QTL for Anatomy, 18 QTL for Chemical, 25 QTL for Conductivity, 1 QTL for Enzyme Activity, 64 QTL for Fat Composition, 439 QTL for Fatness, 26 QTL for Flavor, 79 QTL for Meat Color, 5 QTL for Odor, 66 QTL for PH, 3 QTL for Stiffening and 84 QTL for Texture at present (January 19, 2007) (http://www.animalgenome.org/QTLdb/pig.html). Although, a genome scan can give full genome coverage for that trait, it will fail to detect trait loci with smaller effects if they do not reach the stringent significance of the thresholds.

3.3. Fine mapping

The ultimate goal of a genome scan approach is to identify the genes that underlie polygenic traits and gain a better understanding of their physiological and biochemical functions. In fact, a region of QTL often spans 5–30 cM, and it is too large to find the target genes, so fine mapping needs to be done. It is a step towards restricting the region

of interest and the number of potential candidate genes. The goal of fine mapping is mapping a QTL to a narrow chromosome region so that the physical QTL affecting the phenotype can be identified and cloned.

Fine mapping of the QTL of interest began in the relevant region by adding genetic markers and increasing the marker density to the linkage map. As new maps were obtained, new QTL analyses were performed (Grapes, Dekkers, Rothschild, & Fernando, 2004). However, an extremely valuable tool is the full DNA sequence of the region, where specific QTL are located. And high-resolution mapping of QTL can be obtained by backcross experiments using animals that carry recombinant chromosome (Horvat & Medrano, 1995). The development of advanced intercross lines is another useful approach for improving the resolution of the map in intercross experiments (Darvasi & Soller, 1995; Vitarius, Sehayek, & Breslow, 2006).

3.4. Position cloning

Followed by fine mapping to narrow the region, one of meat quality trait loci will be position cloned. Mapping the location of the meat quality trait is an extremely important step, and is an integral part of the investigation that substantially limits the number of candidate genes that may be identified (Flaherty, Herron, & Symula, 2005).

The cloning of QTL is a challenge for several reasons. A major hurdle is the poor precision in the location of QTL, because the relationship between the genotype and the phenotype is more complex than it is for a monogenic trait; therefore one cannot directly identify recombinants between markers and trait loci (Andersson, 2001). However, it is possible to determine the genotype at a QTL indirectly by progeny testing.

Pure positional cloning is rarely used in farm animals. In practice, the candidate gene approach is often combined with the genome scan strategy, which is positional candidate cloning. Position candidate cloning is the work to be progressed as the main strategy for this purpose. In farm animals, it often relies heavily on the exploitation of comparative data and will become even more powerful with the completion of the human map and the generation of informative databases on gene function and gene expression patterns. The positional cloning of PRKAG3 gene is a typical example in the farm animal mapping research. To clone this gene, the linkage mapping, linkage disequilibrium mapping, radiation mapping, construction of a BAC contig, BAC sequencing and bioinformatic analysis were used. Eventually the result was the identification of the causative missense mutation in PRKAG3 genes. This mutation is associated with the "acid meat" phenotype in pigs (Milan et al., 2000).

3.5. Marker-assisted selection in breeding programs

After identification of QTL, the genes and causative mutations, a further step is normally required for practical use of this variation in selection and breeding programs. This information can be applied in breeding programs by using marker-assisted selection (MAS).

Three types of observable polymorphic genetic loci can be distinguished: (1) direct markers – loci that are the functional mutations, which causative for the trait of interest; (2) LD markers – loci that are in linkage disequilibrium across the population with the functional mutation; (3) LE markers – loci that are in linkage equilibrium with the functional mutation in outbred populations (Dekkers, 2004). The three types of marker loci differ not only in methods of detection, but also in their application in selection programs. Selection on these three types of markers is referred to as gene-assisted selection (GAS), LD markers-assisted selection (LD–MAS), and LE marker-assisted selection (LE–MAS).

GAS is currently the most practical and commercially viable system, because GAS gives certainty to the inheritance of the desired trait and so can be used for selection across the population. To LD–MAS, the extent of linkage in the genome and the population history decide its utility (Dekkers, 2004). Because linkage disequilibrium extends far in cattle breeds (Farnir et al., 2000), it is possible to use markers that are in linkage equilibrium with the QTL in the general population (Dekkers, 2004). However, LD markers are difficult to identify and there are only few detected in livestock populations to date (Freking et al., 2002). Although, LE markers are readily identifiable, LE–MAS is too difficult to use in commercial breeding. LE studies are currently most useful in the initial stages of marker identification, such as finding QTLs that segregate between breeds (Mullen et al., 2006).

MAS can lead to decisions that predict improved performance in farm animals, and will accelerate cumulative and permanent genetic improvement of the herd. Because the meat quality trait is a complex trait controlled by multigenes and the environment, it is important to realize that markers for MAS are only one or few of many genes that contribute towards that trait. The presence or absence of the numerous other "unmarked" genes and the production environment will determine whether an animal actually displays the desired phenotype (Alison, 2006). Implementation of MAS requires careful consideration of issues ranging from sample collection and storage, genotyping and data analysis (Dekkers, 2004). Furthermore, MAS should be seen as a tool to assist with, not as a replacement for traditional selection techniques.

4. Important genes affecting meat quality traits in farm animals

4.1. Important genes affecting pork meat quality trait

Pork is the major red meat source worldwide. Selection based on body composition, in particular the relative proportion of muscle to fat tissue, is very important in meat-producing animals. During the past 50 years, there has

been an intensive selection for lean growth in several breeds. Several genes that influence body composition have already been identified or are close to being identified. The Halothane gene, the RN gene and the IGF2 gene have been reported to have a direct influence on pork quality. Gene tests to remove their negative effects have been carried out by breeding companies.

4.1.1. The Halothane gene

The "Halothane" gene, referred to as the PSS (Porcine Stress Syndrome) gene, was one of the first trait loci to be characterized at the molecular level in pigs. It causes malignant hyperthermia, which can be triggered by stress or exposure to the anaesthetic gas, halothane. Since the 1960s, the halothane gene has been observed to be closely associated with the development of PSE (Pale, Soft and Exudative) meat (Briskey, 1964), which was first described as "muscle degeneration". PSE meat is caused by an extensive protein denaturation due to the low pH values early post-mortem in combination with the simultaneously high temperatures (Briskey, 1964). Christian (1972) suggested that there was a monogenic variation in stress-susceptibility. The homozygous pigs for the halothane gene reacted to halothane gas, which led to the gene being named accordingly. After a few years, the gene was mapped to chromosome 6 (Davies, Harbitz, Fries, Stranzinger, & Hauge, 1988), and the PSS phenotype is caused by an R614C missense mutation in RYR1 gene (ryanodine receptor 1, an ion channel that regulates the release of Ca^{2+} in skeletal muscle; see Fujii et al., 1991). A recessive mutation of this gene causes susceptibility to malignant hyperthermia, which can be triggered by stress or exposure to the anesthetic gas, halothane.

A number of studies have focused on the effect of the halothane gene on pork meat quality (Apple et al., 2005; Hamilton, Ellis, Miller, McKeith, & Parrett, 2000; Kerth et al., 2001). Pigs homozygous and heterozygous for the halothane gene have higher carcass yield and lean percentage (Herfort Pedersen et al., 2001; Klont, Lambooy, & van Logtestijn, 1994; Leach, Ellis, Sutton, McKeith, & Wilson, 1996; McPhee & Trout, 1995). Although, the positive effect of halothane is prominent, the negative effect on WHC (water-holding capacity) and color is obvious, especially in porcine stress syndrome. The carriers of the halothane gene are highly susceptible to stress. Even during careful handling, the stress accompanying preslaughter treatment is sufficient to trigger a higher rate of post-mortem glycolysis in pigs that are both homozygous and heterozygous for the halothane gene, being most severe in the homozygous pigs (Lundstrom, Essen-Gustavsson, Rundgren, Edfors-Lilja, & Malmfors, 1989).

4.1.2. The RN gene

The Rendment Napole (RN) gene has been discussed over the last few decades as well as the effects of the halothane gene. In 1986, Naveau suggested the existence of a single major gene affecting the meat quality trait, the Napole technological yield or in French, *Rendement Napole* (Rosenvold & Andersen, 2003). Further studies supported the hypothesis of a major gene with two alleles for RN trait, a dominant mutant allele RN^- and a recessive normal RN^+ allele. The RN gene identified in the Hampshire breed is associated with reduced Napole yield and leaner carcasses. Meat from carriers is associated with poor processing quality when producing ham, and low pH in the meat because of post-mortem degradation of glycogen, referred to as "acid meat".

As in the previous description, the work to identify the RN gene was typically positional cloning studies in farm animals. The RN gene was mapped to chromosome 15 by Milan et al. (1996b). They mapped the RN gene on SSC 15q2.4–2.5 between the flank markers SW2053 and SW936 (Milan et al., 1996a). The RN gene was located exactly at SSC 15q2.5 by RH mapping (Milan et al., 1998). In 2000, Milan et al. (2000) reported that the RN^- phenotype was caused by an R225Q mutation in the PRKAG3 gene, which encodes a muscle-specific isoform of the regulatory γ-subunit of adenosine monophosphate activated protein kinase (AMPK). The distinct phenotype of the RN-mutation indicates that PRKAG3 plays a key role in the regulation of energy metabolism in skeletal muscle. The other mutations were found in the PRKAG3 gene associated with meat quality of pork loin (Lindahl et al., 2004a, 2004b). Recently, a comparative proteome study of the RN gene effect showed that the expression profiles of several enzymes of the glycogen storage pathways were differentially regulated in a pattern, and the integrated data from this proteome study indicates that regulation of glucose transport was severely affected in mutant animals (Hedegaard et al., 2004). Further studies of these mutations were of great interest in order to explain molecular mechanisms that influence "drip loss" in porcine meat (Otto et al., 2007).

The RN^- phenotype is associated with elevated glycogen content in the sarcoplasma, as well as in the lysosomal compartment, of glycolytic muscle cells. The RN gene has no effect on early post-mortem pH values, but results in a lower pH_{24h} value, which again is associated with a higher reflectance (lighter meat) and inferior WHC (Le Roy, Naveau, Elsen, & Sellier, 1990). In other words, the positive effect of the RN gene cannot be ignored. The RN^- allele is another example of a mutation that has probably increased in frequency because of selection for meat content in pigs. It occurs at a high frequency only in the Hampshire breed and increases glycogen content in muscle by ~70% (Milan et al., 2000).

4.1.3. The IGF2 gene

IGF2, insulin-like growth factor 2, is implicated in myogenesis and lean meat content. A mutation, a single base (A for G substitution) of IGF2 (position 3072 in intron 3), was described as quantitative trait nucleotide (QTN), which was the cause of a major QTL effect on muscle growth and fat deposition in pigs (Van Laere et al., 2003). This

QTL affecting muscle growth and fat deposition was first located on chromosome 2. It explained 15–30% of the phenotypic variation in muscle mass and 10–20% of the variation in back-fat thickness (Jeon et al., 1999; Nezer et al., 1999). Haplotype sharing refined the location with major effect on muscle mass to a 250 kb chromosome segment containing the porcine IGF2 gene (Nezer et al., 2003). The genotyping of pig populations for IGF2 could be an important part of breeding programs in the future because mutation in IGF2 may have potential influence on meat quality and quantity. The A/G mutation has been accidentally selected for in- breeding schemes based on production performance and/or lean meat deposition. Carrodeguas et al. (2005) evaluated a rapid assay based on real time PCR (RT-PCR) to detection this mutation.

4.1.4. Other genes

Besides the above mentioned major genes, genes in the leptin pathway are proving profitable in association studies with growth and backfat, e.g. the MC4R gene (Kim, Larsen, Short, Plastow, & Rothschild, 2000; Meidtner et al., 2006; Park, Carlborg, Marklund, & Andersson, 2002). It was clearly associated with reduced feed intake, faster growth and less backfat. A particular haplotype in the calpastatin (CAST) gene in pork was associated with sensory tenderness and other meat quality traits (Ciobanu et al., 2004; Kocwin-Podsiadla, Kuryl, Krzecio, Zybert, & Przybylski, 2003).

4.2. Important genes affecting beef meat quality trait

Important aspects for beef meat quality maybe include meat pH, marbling and tenderness. They have been studied for many years and some SNPs have been found in different genes. Several markers for tenderness have been developed for the inhibitor of calpain gene, the calpastatin and the calpain I genes (Casas et al., 2006; Lonergan, Ernst, Bishop, Calkins, & Koohmaraie, 1995; Page et al., 2004; White et al., 2005). Furthermore, the leptin gene, the thyroglobulin gene, the DGAT1 gene and the growth hormone gene were associated with the marbling trait, and the myogenic regulatory factors gene family was another group of important candidate genes for muscle growth (Mullen et al., 2006).

4.3. Important genes affecting sheep meat quality trait

The requirements in sheep meat quality trait are fewer than for pork or beef, and the focuses are muscularity and fat deposition. A QTL with major effects on muscularity was located on chromosome 2 in sheep (Laville et al., 2004), and accounted for 5–25% of variance. A higher density map was constructed to refine the map position of this QTL because the confidence interval of the QTL spanned 10 cM in previous reports. Finally, it was fine-mapped to a chromosome interval encompassing the myostain (GDF8) gene. There was a G–A transition in the 3'UTR that created a target site for mir1 and mir206 in the GDF8 allele of Texel sheep, which caused translational inhibition of GDF8 gene and contributed to the muscular hypertrophy of Texel sheep. A new class of regulatory mutations was identified that might make an important contribution to the heritability of quantitative traits (Clop et al., 2006).

The callipyge phenotype has also been studied for many years, being mapped to ovine chromosome 18 using a battery of bovine chromosome 21 markers (Cockett et al., 1994). The effect of the callipyge phenotype on traits affected the muscle growth and meat tenderness (Freking et al., 1999; Koohmaraie, Shackelford, Wheeler, Lonergan, & Doumit, 1995). A single base change causes the callipyge muscle hypertrophy phenotype, being the only known example of polar overdominance in mammals (Freking et al., 2002). Although, it causes hypertrophy in sheep buttocks, it yields less tender and palatable meat as a consequence. Because of the high similarity of genomes between sheep and cattle, many of the markers developed in cattle may also be useful in sheep, and this will accelerate the sheep breeding program.

4.4. Important genes affecting chicken meat quality trait

In chicken, more investigations focus on fat deposition, such as the percentage of hypodermal fat, abdominal fat, and intramuscular fat in breast and legs. The intramuscular fat (IMF) was in positive correlation with meat flavor and succulency, especially tenderness of meat (Le Bihan-Duval, Millet, & Remignon, 1999). Increasing IMF and controlling fatty deposition is an increased interest in improving meat quality. QTL for fatness, being found in various crosses between different breeds of chickens. The gene for extracted extracellular fatty acid binding protein (EXFABP) was considered as a candidate locus or linked to a major gene that significantly affected abdominal fat traits in chicken. The DNA marker discovered by Wang et al. (2001) can be used as a molecular marker for assisted selection on chicken fat trait.

5. Applying MAS for improvement of meat quality

In the past, genetic change has been slow due to selection technique methodology with low accuracy. In today's farm animal breeding systems, directional and actual change can come more quickly because of the improved DNA-based technology and genetic markers for selection. Table 1 shows candidate genes associated with meat quality in farm animals.

MAS allows for the accurate selection of specific DNA variations that have been associated with a measurable difference or effect on meat quality trait. Marker information can be used to increase the frequency of the marker that is positively associated with the trait of interest by selecting for animals carrying two copies of that marker, and against those carrying no copies of it (Alison, 2006).

Table 1
Candidate genes associated with meat quality in farm animals

Animal	Candidate genes	Traits	References
Pig	HAL	Meat quality/stress	Fujii et al., 1991
	MC4R	Growth and fatness	Kim et al., 2000
	RN, PRKAG3	Meat quality	Milan et al., 2000
	AFABP/FABP4	Intramuscular fat	Gerbens et al., 1998
	HFABP/FABP3	Intramuscular fat	Gerbens et al., 1999
	CAST	Tenderness	Ciobanu et al., 2004
	IGF2	Growth and fatness	Van Laere et al., 2003
Cattle	CAST	Meat tenderness	Lonergan et al., 1995
	Leptin/Thyroglobulin	Marbling	Mullen et al., 2006
	Myostation	Growth and composition	Grobet et al., 1998
	DGAT1	Intramuscular fat/marbling	Thaller et al., 2003
Sheep	Callipyge	Muscular hypertrophy	Freking et al., 2002
	GDF8	Muscular hypertrophy	Clop et al., 2006
Chicken	EX-FABP	Fatness	Wang et al., 2001
	L-FABP	Fatness	Wang et al., 2006

With pork, MAS has been most successful in the elimination of undesirable traits, ensuring more consistent meat quality from the population. Since, 1991 when PIC first started using a DNA marker test to detect presence of the halothane gene, PIC has pioneered the use of DNA markers in pig breeding. PICmarq^{TM} is used to make more accurate selection decisions in different traits, such as growth, lean, efficiency, meat quality (http://www.pic.com/). From 1990, some of the biggest international breeding companies decided to remove the halothane gene from their selection lines, and some countries eliminated the presence of the halothane gene from their selection lines several years ago, e.g. Denmark, The Netherlands, Sweden and Switzerland (Rosenvold & Andersen, 2003).

With beef, DNA markers associated with marbling and tenderness have become commercially available, such as GeneStar^{TM} Tenderness, which test for favourable SNP's at major genes known to be involved in meat tenderness (Alison, 2006). GeneStar^{TM} Tenderness was the first multi-marker single trait test commercially available to the beef industry. It combines three markers, T1, T2 and T3, for two important genes, Calpastatin and Calpain. The combined effects of these three markers account for ~2.5 pounds of WBSF (Warner–Bratzler shear force). The GeneSTAR® Quality Grade is another DNA genetic marker panel test offered by Bovigen LLC. The marker in this panel is T5, which identifies the presence of the thyroglobulin gene associated with meat quality grade and marbling. And it is the only quality grade or marbling test to have passed by the NBCEC (National Beef Cattle Evaluation Consortium). The Igenity®Carcass Composition is another panel test for beef, which includes information on quality grade, tenderness, marbling and so on. The DNA test panel of the Geneseek Company includes two SNP in the CAPN1 gene that have been linked to meat tenderness. In the United States, the commercially available markers for carcass quality traits have been validated by the NBCEC (http://www.nbcec.org/nbcec/index.html). Table 2 lists companies that provide markers for breeding selection programs for cattle, pig, sheep and so on. Although, there are some commercially available markers for pork meat and beef meat, there are few for sheep meat. For sheep breeding, the markers focus on Spider Lamb Syndrome and Scrapie Resistance Tests. The commercially marker for chicken meat quality is the same state as sheep.

Table 2
List of companies offering commercially available markers for meat quality

Company	Animal	Traits
Biogenetic services (http://www.biogeneticservices.com/)	Cattle Pig	Meat quality Porcine stress syndrome
Bovigen (http://www.bovigen.com/)	Cattle	Tenderness Quality grade Marbling
Genmark (http://www.genmarkag.com/)	Cattle Pig	Double-muscling phenotype Porcine stress syndrome
GeneSeek (http://www.geneseek.com)	Cattle Pig	Tenderness RN gene Porcine stress syndrome
Genetic Visions (http://www.geneticvisions.net/)	Cattle	Tenderness
Igenity (http://www.igenity.com/)	Cattle	Quality grade Marbling
PIC (http://www.pic.com/)	Pig	Porcine stress syndrome/ RN/...

6. Conclusions

To date, advances in molecular genetics have led to the identification of genes or markers associated with genes that affect the meat quality trait. The molecular basis of meat quality is being revealed by functional genomics approaches. These will help us to gain further insight into the biological components and the development of meat quality. It gives greater opportunities to enhance genetic improvement program in farm animal through marker-assisted selection.

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