Review Article

Journal of Nutritional Biology

Advances in Genetic Improvement of Meat Quality Traits in Pig

Naskar S^{1*}, Vashi Y², Banik S³ and Mandal PK⁴¹ICAR-Indian Institute of Agricultural Biotechnology, Ranchi, Jharkhand, India²Assam Don Bosco University, Sonapur, Assam, India³ICAR-National Research Centre on Pig, Guwahati, Assam, India⁴Rajiv Gandhi Institute of Veterinary Education & Research, Puducherry, India

***Correspondence:** Soumen Naskar, ICAR-Indian Institute of Agricultural Biotechnology, Ranchi - 834010, Jharkhand, India, Tel: +91 6512261123; E-mail: snrana@gmail.com

Rec date: Mar 20, 2018; Acc date: May 08, 2018; Pub date: May 14, 2018

Abstract

This article reviews the advances in molecular genetics that have led to the genetic improvement in meat quality in pigs. During the past few decades, genes, or markers associated with genes have been identified that affects meat quality. The huge amount of information emerging from genomic studies is opening up new opportunities for the genetic selection of pigs. Several genes that influence meat quality have already been, or are close to being identified. Some of them have already been implemented into breeding programs by marker-assisted selection. Fields like functional genomics and proteomics are helping in better understanding of the function and regulation of genes and how these participate in complex networks controlling the phenotypic characteristics of a trait. An integrated approach of genomics and proteomics with bioinformatics tools will further exploit the available molecular genetics information. This will allow animal breeders to make progress more rapidly to meet the demand for high quality pork.

Keywords: Pig; Meat quality; Candidate gene; Genetic improvement; Marker assisted selection

Introduction

During the last 20 years, the genetics underlying pork quality traits has become subject of increased interest of research due to the processors', packers' and consumers' demands for food with better quality [1]. Meat quality traits are recognized as quantitative traits, which are affected by genetic and environmental factors [2,3]. While some pork quality traits can be divided in either technological (water-holding capacity, firmness, glycogen content) or sensorial (tenderness, juiciness, flavor), there is also some overlap for some traits that belong to both categories (pH, colour, muscle fibre characteristics) [4]. Generally, good pork quality is associated with darker (more red) meat, increased water holding capacity, juiciness, tenderness and better texture.

From the beginning of animal domestication, man have been trying to get progeny from the animals that seemed best fit for the purpose, changing the genetic design of animals without knowledge of the underlying genes. For most of this period selection was empirical and directed by, what Darwin refers to as, unconscious selection.

Selection in pig breeding went through different phases. Initial phase of selection focused on easily measurable parameters such as body weight, growth rate, number of teats, number of piglets born alive, number of piglets weaned, duration of the interval weaning to serving, number of productive cycles per sow, and so on. Later on, internal parameters were included. Using ultrasonic

equipments, back fat thickness and loin eye area were measured on living animals and taken into account in the selection programme. Computer technology was also introduced. Databases were created which were then analysed through BLUP (Best Linear Unbiased Prediction) programmes to give an estimated breeding value for each individual [5].

It was not until the late 18th and 19th century and in particular after the 1950s, the pig breeding increasingly based on scientific genetic theory. The pig breeding programmes have been very successful in effecting genetic improvement of economically important traits, especially daily gain (+100%), backfat thickness (-75%), and feed efficiency during the last decade [6].

Genetic Maps, Gene Discovery and the Molecular Age

In the early 1990s, the PiGMap consortium was formed to better understand the pig genome [7]. Since then, geneticists have come a long way to generate genetic maps of the porcine genome. During initial years, genetic linkage maps consisting of anonymous genetic markers and a limited number of known genes were developed. Development of comparative genome maps also aided in the quest for potentially useful genes in pigs [8].

The development of molecular markers and genome maps facilitated application of molecular genetics approaches, increasing the rate of genetic gain and identifying genes and polymorphisms controlling variation in traits of interest. The hunt for QTL in pigs has been ongoing for more than two decades now, beginning with the first report of QTL for fatness on pig chromosome-4 [9]. Interestingly, it was the first QTL reported in livestock. As of 17th May, 2017 there are 17,955 pig QTL in the database from 576 publications representing 635 pig traits (Table 1).

The population structures used for the majority of these studies involved experimental crosses using pig breeds exhibiting extremes for the phenotypes of interest, with the expectation that alleles for QTL controlling these phenotypes would be segregating. The class of genetic markers used for genotyping most populations was microsatellites because there were genome-wide microsatellite marker sets available, providing the ability to detect QTL using linkage analysis methods typically with 100-200 microsatellites [10]. Significant effects of major genes and candidate genes have been reported

[11]. For example, the MC4R (melanocortin 4 receptor) gene was found to significantly affect growth rate by 7 to 9% by influencing feed intake. The MC4R gene maps to chromosome 1 close to a significant QTL. Due to the MC4R effect on feed intake, variation in this gene is also significantly associated with 5 to 8% differences in back fat and relates to one QTL for back fat thickness on chromosome-1 [12]. The work done so far on some candidate genes for their associations with pork quality traits is presented in table 2.

Marker Assisted Selection (MAS)

Marker-assisted selection (MAS) combines the genetic information with the classical performance records and genealogical information to increase selection accuracy. There are two types of MAS: one is the candidate gene approach which uses causative mutations with a major effect on a particular trait, and another uses linkage disequilibrium (LD) between markers with QTL. The breeding value is predicted based on the combined information of polygenic effects and significant markers. MAS can be more useful for traits that are expressed late in the life of the animal, have low heritability, are sex-limited, expensive to measure or controlled by a few genes. However, for most recessive alleles with lethal or semi-lethal effects, natural selection will maintain their frequencies very low making MAS unnecessary.

The impact of MAS in breeding programs has been modest because the QTL that exceeds the chosen significance thresholds usually accounts only for a minor fraction of the trait variance. However, it would be a question of time whether availability of the number of markers was the only limitation for the success of MAS [45].

Potential of Mas

Information at DNA level can assist in the selection of quantitative traits including those that can be selected by traditional means. Molecular information increases the accuracy of selection and therefore the selection response. Importantly, these responses can be sustained if new markers are continually identified. New markers can be added to the selection index as old markers begin to reach fixation.

Many studies on QTL and candidate analyses have yielded interesting results. The QTL scans have identified several chromosomes that are now targets for further confirmation of the chromosomal region, advanced fine mapping of the QTL and positional comparative

candidate gene analysis. MAS can accelerate genetic improvement of the herd by leading to decisions that predict improved performance of the animals [46]. For complex traits controlled by multigenes and the environment, it should be realized that markers for MAS are not exhaustive and many other genes contribute towards the 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 [47]. Implementation of MAS requires careful consideration of issues ranging from sample collection and storage, genotyping and data analysis [48]. Furthermore, MAS should be seen as a tool to assist with, not as a replacement for traditional selection techniques.

Genomic Selection

Recent developments in technology have removed limitations of MAS, by using high-density of markers across the genome to capture a larger percentage of the genetic variance for the trait of interest [49]. Advances in genome sequencing, identification of large numbers of SNPs, and the cost-effective high-throughput genotyping of tens of thousands of such SNPs, combined with the further development of statistical analysis methods has led to a paradigm shift in the strategy of using genetic markers for the prediction of breeding values for genomic selection (GS). GS assumes that each QTL is in LD with at least one closely linked marker and the effects of chromosome segments will be the same within the population. Therefore, the density of markers must be high enough to ensure that all QTL are in LD with at least one marker [50]. The commercially available SNP genotyping panels for the pig is presented in table 3.

A reference population with genotypic and phenotypic records is needed to carry out genomic selection to develop a genomic estimated breeding value (GEBV) prediction equation [52]. This prediction equation is then applied to the candidate population with genotypic records but without phenotypic information to predict GEBV for each individual, and this is used to select the best animals for breeding in the selection population [49,52].

Development of a first commercial SNP panel for high throughput genotyping [53] and sequencing of the pig genome [54] were the starting points for the application of genomic selection in pigs. The first SNP panel commercially available from Illumina contained about 60K SNPs that cover all autosomal and X chromosomes

[53].

Perspectives of Genomic Selection in pigs

Genomic selection in pigs has only recently been implemented and it is still not so common as in dairy cattle. However, field applications of genomic selection are opening new opportunities also in pig breeding. Pig breeding schemes currently have developed a very efficient data recording scheme which easily could include genomic information.

Breeding programmes should be eventually redesigned to fully capitalise the benefits of genomic selection [55]. Selecting animals based on their GEBV or GS would allow selection of animals at an early stage of their life and increase accuracy of prediction. Consequently, this would increase the genetic gain by decreasing generation interval, increasing the selection accuracy and the frequency of favourable alleles [52]. Although GS is revolutionizing, it faces challenges like requirement of large reference population size to predict GEBV accurately. Whereas, it is known that larger reference populations result in higher genomic prediction accuracy, in most of the studies so far small reference populations have been used for genomic prediction [52]. Involvement of multiple breeds in livestock industries poses another major challenge in GS. For divergent breeds, it has been shown that large reference population sizes and more than 300,000 SNPs are needed [56]. Using non-additive genetic effects is another challenge in using genomic selection. It might be beneficial to improve the selection accuracy by including non-additive genetic effects such as dominance and epistatic effects. Methods for genomic prediction like estimation of interactions between high density of markers [57], estimation of both dominance and epistatic effects by using single-marker Bayesian approach [58], and the dominance model [59] allow us to estimate non-additive genetic effects.

Quite soon, it is expected that SNP genotyping technologies will be substituted by sequencing-based approaches in genomic selection, as sequencing costs should decrease with the introduction of new sequencing approaches and technologies. However, despite the decrease in costs, sequencing might still be too expensive for implementation on a large number of animals [51].

Genes Affecting Meat Quality Traits in Pigs

Myogenic regulatory factors (MRF) gene family

Myogenesis and postnatal muscle tissue growth are regulated by the myogenic regulatory factors (MRF) gene

family. The *MRF* gene family consists of five structurally related transcription factors: myogenin, MyoD1, MRF-4, MYF-5 and MYF-6. They regulate both skeletal muscle fiber development and postnatal hypertrophic growth. The MyoD and MYF-5 genes regulate proliferation of myoblasts and satellite cells (postnatal type) by having the ability to fuse with existing myofibers, but lacking the ability to form new myofibers. Myogenin is expressed during fusion of cells to form multinucleated myofibers. The role of MYF-6 has been mainly described as maintaining the muscle tissue. The MRF gene family is considered as strong candidate gene for skeleton muscle mass, i.e., meat mass. The candidate gene approach generally comprises of recognizing the gene of a trait on the basis of physiological function, followed by study of genomic variation of that gene to detect the ultimate causal mutation leading to modified protein with a single changed activity or slightly change in the level of expression of an unmodified protein. Finally, a candidate gene for the given trait can be validated by means of an association study. In general, an association study is comprised of investigation of resource families with large population (for example fullsib families) by genotyping of the polymorphic site at candidate gene.

The stress susceptibility gene mutation, RYR1

One of the first discovered gene mutation affecting pig meat quality was ryanodine receptor gene mutation (RYR1), also known as the Halothane gene (HAL) or malignant hyperthermia gene (MH). The ryanodine receptor belongs to the calcium channels. Among several different ligands for this receptor, anaesthetic halothane can activate them causing releasing of Ca^{2+} , especially rapid releasing calcium ion is observed in hypersensitive mutated form. Animals carrying such mutation are characterized by increased muscle mass and reduced fat content. Since effective selection programme for reduced back fat and increased lean yield was introduced, this mutation has widespread influence among commercial pig breeds. This mutation is responsible for the increase of the occurrence of porcine stress syndrome (PSS) and pale soft exudative pork (PSE). Porcine stress syndrome manifests as a loss of consciousness or even death of animals caused by environmental stress, such as transport from farms to slaughterhouses. PSE is described as pale and watery pork, and is associated with rapid drop of pH and strong muscle post-mortem rigor contraction. Halothane sensitivity has also been shown to reduce the value of pork for the production of cooked hams and curried dried hams. Pig breeds differ in occurrence of these pork defects. This mutation is most frequent

in Pietrain breed compared to other pig breeds. Since carriers of this mutation can also produce undesirable PSE pork, a test for detection of this mutation has been in use in pig breeding programs.

The rendement napole (RN) gene

Rendement Napole (RN) mutation is related with higher level of muscle glycogen and causes a paler colour, poor ham quality and high drip loss. RN mutation causes a 70% higher level of glycogen. Studies aimed at localizing and describing the causal gene mutation responsible for this pork defect, revealed a gene of muscle specific monophosphate-activated protein kinase protein (PRKAG3). A single nucleotide mutation (G→A) that inhibits the activity of this enzyme and responsible for breaking down storage of glycogen has been discovered. Use of such mutation has found favor in pig industry. The RN is most frequent in Hampshire breed, but it was estimated that 80% of the high glycogen pork came from commercial white-breed pig population. The high value of glycolytic potential was not due to the presence of the RN-allele (200Q) in the tested commercial pigs [26]. However, their data confirmed the effect of other mutations at the *PRKAG3* locus (T30N and G52S) on meat quality. Moreover, they observed that muscle glycogen content significantly depended on PGAM2 (phosphoglycerate mutase 2) genotype.

Marbling fat HFABP and AFABP genes

Intramuscular fat content has a major influence on meat quality in pigs. Amount of intramuscular fat decides of marbling of the muscle. It was determined that pork loin should have at least 2% fat in the lean meat; otherwise it is too dry after cooking. Fatty acid-binding proteins (FABPs) are members of the superfamily of lipid-binding proteins. There are nine different tissue-specific FABPs that have been identified: L (liver), I (intestinal), H (muscle and heart), A (adipocyte), E (epidermal), II (ileal), B (brain), M (myelin) and T (testis). The primary role of all the FABP family members is regulation of fatty acid uptake and intracellular transport. Because of their physiological properties, some FABP genes were tested in order to identify mutations altering lipid metabolism. Heart fatty acid binding protein (H-FABP) and adipocyte fatty acid binding protein (A-FABP) are involved in transport and metabolism of fatty acids. These two genes were chosen as candidate genes for improvement of muscle marbling content but they did not increase the back fat. In H-FABP, the tested mutation causing improvement of marbling content was placed in promoter region. A-FABP gene was analyzed using microsatellite sequence placed in the

second intron.

The HFABP and AFABP were responsible for an increase of fat content by 1% in Duroc and Meishan pig breed [60-62]. Polymorphisms in the adipocyte and heart fatty acid-binding protein genes, A-FABP and H-FABP, are significantly associated with genetic variation of intramuscular fat content in a Duroc pig population. This was supported by information about the role of H-FABP but not for A-FABP in a Meishan crossbred pig population. In view of that, the effect of closely linked genes could not be excluded.

Calpastatin (CAST) gene

The rate and extent of skeletal muscle growth depends mainly on three factors: rate of muscle protein synthesis, rate of muscle protein degradation, and the number and size of skeletal muscle cells. Studies have shown that calpain activity is required for myoblast fusion [63] and cell proliferation in addition to cell growth [64]. A number of studies have shown that the calpain system is also important in normal skeletal muscle growth. Increased rate of skeletal muscle growth can result from a decreased rate of muscle protein degradation, and this is associated with a decrease in activity of the calpain system, primarily due to a large increase in calpastatin activity [65]. These observations suggest that genes coding for calpains and calpastatin may be considered as candidate genes for lean content of carcass in pigs.

By investigating the impact of CAST *HinfI*, *RsaI* and *MspI* genotypes on carcass traits in different pig breeds, it was shown that CAST/*HinfI* genotype had no impact on carcass traits, whereas, CAST/*RsaI* and CAST/*MspI* affected some of the meat and fat deposition traits in pigs [66]. By analysing meat quality traits influenced by CAST/*MspI* genotype, it was observed that animals with BB genotype at this locus were characterized by the most profitable values of all analysed traits [67].

Growth hormone (GH) and growth hormone releasing hormone (GHRH) gene

The GHRH is an endogenous stimulator of somatotropin secretion. It is released by hypothalamus and stimulates the proliferation of pituitary somatotroph cells during their development regulating production and secretion of GH. GH is a peptide hormone with about 190 residues which regulates growth, development and various metabolic activities. The *AluI* polymorphism in the third exon of *GHRH* gene was found to be significantly associated with fat thickness and meat content of carcass

in different breeds of pigs [68] and with average daily gain and fat thickness [69]. Although most amino acids of the GH protein are conserved, there are still many single nucleotide polymorphisms which are reported in the traits of growth, lean rate and milk production. The *GH Ddel* polymorphisms are associated with fat thickness ($P=0.0326$) and average daily gain ($P=0.0127$) [69]. Different *Ddel*, *NarI* and *BsmNI* polymorphisms have been found in the coding sequence of *GH* in different breeds.

Peroxisome proliferator-activated receptor gamma coactivator-1 (PPARGC1)

Fat deposition and its body distribution in pigs is economically important for production of pigs that are low in back fat but having intramuscular fat, which contributes to the improvement of sensory traits of meat. Recent research has focused on the identification of candidate gene for predicting meat quality and muscle tissue development. The peroxisome proliferator-activated receptor-gamma coactivator-1 (PPARGC1) is a transcriptional coactivator of many nuclear hormone receptors including peroxisome proliferator-activated receptor-gamma, which has been shown to be involved in lipid metabolism and play central regulatory role in adipocyte differentiation [70]. Because of its role in body composition and fat distribution, PPARGC1 is a candidate gene for fatness and leanness.

The complete coding sequence of the porcine PPARGC1 gene including a single nucleotide polymorphism in exon 8 has been determined in recent times. A T/A substitution at nucleotide position 1378 results in an amino acid substitution (Cys→Ser) at position 430 in the amino acid sequence. Differences of T/A allele distribution between Chinese and Western pig breeds were described [71]. T (Cys) allele was present in all 13 analysed pig breeds. However, A (Ser) allele was present only in Western pig breeds, and in one Chinese (Taoyuan) breed.

Conclusion

Demand for high-value animal protein is expected to increase fuelled by increase in global human population, urbanization and socio-economic mobility that will require efficient livestock production without compromise on food quality. This shall be harnessed by application of new technologies to accelerate genetic gain. Gene expression profiling approach has helped understand the biology of porcine muscle growth and development better, and important genes and signalling pathways are being identified that may affect meat quality [72]. Emergence of “-omics” will open up new vistas that has

already uncovered associations capable of generating new biological hypotheses. Nutrigenomic approach may also help in identifying nutrition-responsive major genes for meat quality trait formation [73]. Although rapid genetic improvement for both existing and new traits will be a challenging task, integration of new and emerging technologies with conventional breeding is expected to help achieve progress more rapidly than was possible in the past to ensure that the demand for quality pork is satisfied.

Competing Interest

The authors have declared that no competing interest exists.

References

- Dransfield E, Ngapo TM, Nielsen NA, Bredahl L, Sjöden PO, Magnusson M, et al. Consumer choice and suggested price for pork as influenced by its appearance, taste and information concerning country of origin and organic pig production. *Meat Sci.* 2005 Jan;69(1):61–70.
- Schäfer A, Rosenvold K, Purslow PP, Andersen HJ, Henckel P. Physiological and structural events post mortem of importance for drip loss in pork. *Meat Sci.* 2002 Aug;61(4):355–66.
- Rosenvold K, Andersen HJ. Factors of significance for pork quality-a review. *Meat Sci.* 2003 Jul;64(3):219–37.
- Ramos AMCA (2006) Molecular dissection of genomic regions influencing important economic traits in the pig. PhD Thesis, Iowa State University.
- Buys N. RECENT TECHNOLOGICAL ADVANCES IN PIG GENETIC IMPROVEMENT. 2000;3.
- Merks JWM. One century of genetic changes in pigs and the future needs. :12.
- Archibald AL, Haley CS, Brown JF, Couperwhite S, McQueen HA, Nicholson D, et al. The PiGMap consortium linkage map of the pig (*Sus scrofa*). *Mamm Genome.* 1995 Mar;6(3):157–75.
- Rothschild MF. Advances in pig molecular genetics, gene mapping and genomics. :15.
- Andersson L, Haley CS, Ellegren H, Knott SA, Johansson M, Andersson K, et al. Genetic mapping of quantitative trait loci for growth and fatness in pigs. *Science.* 1994 Mar 25;263(5154):1771–4.
- Ernst CW, Steibel JP. Molecular advances in QTL discovery and application in pig breeding. *Trends Genet.* 2013 Apr;29(4):215–24.
- Bidanel JP and Rothschild MF (2002) Current status of quantitative trait locus mapping in pigs. *Pig News Info* 23(2): 39N-53N.
- Kim KS, Larsen N, Short T, Plastow G and Rothschild MF (2000a) A missense variant of the porcine melanocortin-4 receptor (MC4R) gene is associated with fatness, growth, and feed intake traits. *Mamm Genome* 11: 131-135.
- Muñoz G, Alves E, Fernández A, Ovilo C, Barragán C, Estellé J, et al. QTL detection on porcine chromosome 12 for fatty-acid composition and association analyses of the fatty acid synthase, gastric inhibitory polypeptide and acetyl-coenzyme A carboxylase alpha genes. *Anim Genet.* 2007 Dec;38(6):639–46.
- Jiang ZH, Gibson JP. Genetic polymorphisms in the leptin gene and their association with fatness in four pig breeds. *Mamm Genome.* 1999 Feb;10(2):191–3.
- Kim TH, Choi BH, Beever JE. Polymorphism in the porcine agouti signalling protein (ASIP) gene. *Anim Genet.* 2004 Oct;35(5):418–20.
- Ciobanu DC, Bastiaansen JWM, Lonergan SM, Thomsen H, Dekkers JCM, Plastow GS, et al. New alleles in calpastatin gene are associated with meat quality traits in pigs1. *Journal of Animal Science.* 2004 Oct 1;82(10):2829–39.
- Russo V, Fontanesi L, Davoli R, Nanni Costa L, Cagnazzo M, Buttazzoni L, et al. Investigation of candidate genes for meat quality in dry-cured ham production: the porcine cathepsin B (CTSB) and cystatin B (CSTB) genes. *Anim Genet.* 2002 Apr;33(2):123–31.
- Knoll A, Cepica S, Stratil A, Nebola M, Dvorrák J. Numerous PCR-RFLPs within the porcine CYP21 (steroid 21-hydroxylase) gene. *Anim Genet.* 1998 Oct;29(5):402–3.
- Skinner TM, Doran E, McGivan JD, Haley CS, Archibald AL. Cloning and mapping of the porcine cytochrome-p450 2E1 gene and its association with skatole levels in the domestic pig. *Animal Genetics.* 2005 Oct 1;36(5):417–22.
- Clop A, Cercos A, A Tomas A, Perez-Enciso AM, Varona L, Noguera JL and Sánchez AAM (2002) Assignment of the 2,4-dienoyl-CoA reductase (DECR) gene to porcine chromosome 4. *Animal Genetics*, 33: 164-165.
- Kim J-J, Rothschild MF, Beever J, Rodriguez-Zas S, Dekkers JCM. Joint analysis of two breed cross populations in pigs to improve detection and characterization of quantitative trait loci1. *Journal of Animal Science.* 2005 Jun 1;83(6):1229–40.

22. Gerbens F. Genetic control of intramuscular fat accretion in pigs. :174.
23. Zuo B, Xiong YZ, Deng CY, Su YH, Wang J, Lei MG, et al. cDNA cloning, genomic structure and polymorphism of the porcine FHL3 gene. *Anim Genet.* 2004 Jun;35(3):230–3.
24. Glenn KL, Ramos AM, Rothschild MF. Analysis of FMO genes and off flavour in pork. *Journal of Animal Breeding and Genetics.* 2007 Feb 1;124(1):35–8.
25. Fontanesi L, Scotti E, Buttazzoni L, Davoli R, Russo V. The porcine fat mass and obesity associated (FTO) gene is associated with fat deposition in Italian Duroc pigs. *Animal Genetics.* 2009 Feb 1;40(1):90–3.
26. Fontanesi L, Davoli R, Nanni Costa L, Scotti E, Russo V. Study of candidate genes for glycolytic potential of porcine skeletal muscle: identification and analysis of mutations, linkage and physical mapping and association with meat quality traits in pigs. *Cytogenet Genome Res.* 2003;102(1–4):145–51.
27. Pas MFWT, Leenhouders JI, Knol EF, Booij M, Priem J, Lende TVD. Marker polymorphisms in the porcine genes for muscle glycogen synthase (GYS1) and muscle glycogen phosphorylase (PYGM). *Animal Genetics.* 2003 Apr 1;34(2):157–8.
28. Otieno CJ, Bastiaansen J, Ramos AM, Rothschild MF. Mapping and association studies of diabetes related genes in the pig. *Anim Genet.* 2005 Feb;36(1):36–42.
29. Van Laere A-S, Nguyen M, Braunschweig M, Nezer C, Collette C, Moreau L, et al. A regulatory mutation in IGF2 causes a major QTL effect on muscle growth in the pig. *Nature.* 2003 Oct 23;425(6960):832–6.
30. Lei MG, Xiong YZ, Deng CY, Wu ZF, Harbitz I, Zuo B, et al. Sequence variation in the porcine lipoprotein lipase gene. *Anim Genet.* 2004 Oct;35(5):422–3.
31. Kim KS, Marklund S, Rothschild MF. The porcine melanocortin-5 receptor (MC5R) gene: polymorphisms, linkage and physical mapping. *Anim Genet.* 2000 Jun;31(3):230–1.
32. Larsen NJ, Marklund S, Kelly KA, Malek M, Tuggle CK, Yerle M, et al. New insights into porcine-human synteny conservation. *Mamm Genome.* 1999 May;10(5):488–91.
33. Wyszynska-Koko J, Pierzchala M, Flisikowski K, Kamyczek M, Rózycki M, Kuryl J. Polymorphisms in coding and regulatory regions of the porcine MYF6 and MYOG genes and expression of the MYF6 gene in *m. longissimus dorsi* versus productive traits in pigs. *J Appl Genet.* 2006 Jun 1;47(2):131–8.
34. Davoli R, Fontanesi L, Cagnazzo M, Scotti E, Buttazzoni L, Yerle M, et al. Identification of SNPs, mapping and analysis of allele frequencies in two candidate genes for meat production traits: the porcine myosin heavy chain 2B (MYH4) and the skeletal muscle myosin regulatory light chain 2 (HUMMLC2B). *Animal Genetics.* 2003 Jun 1;34(3):221–5.
35. Urbanski P, Kuryl J. Two new SNPs within exon 1 of the porcine MYOD1 (MYF3) gene and their frequencies in chosen pig breeds and lines. *Journal of Animal Breeding and Genetics.* 2004 Jun 1;121(3):204–8.
36. Grindflek E, Hoen N, Sundvold H, Rothschild MF, Plastow G, Lien S. Investigation of a peroxisome proliferator-activated receptor gamma haplotype effect on meat quality and carcass traits in pigs. *Anim Genet.* 2004 Jun;35(3):238–41.
37. Milan D, Jeon JT, Looft C, Amarger V, Robic A, Thelander M, et al. A mutation in PRKAG3 associated with excess glycogen content in pig skeletal muscle. *Science.* 2000 May 19;288(5469):1248–51.
38. Ciobanu D, Bastiaansen J, Malek M, Helm J, Woollard J, Plastow G, et al. Evidence for new alleles in the protein kinase adenosine monophosphate-activated gamma(3)-subunit gene associated with low glycogen content in pig skeletal muscle and improved meat quality. *Genetics.* 2001 Nov;159(3):1151–62.
39. Fujii J, Otsu K, Zorzato F, de Leon S, Khanna VK, Weiler JE, et al. Identification of a mutation in porcine ryanodine receptor associated with malignant hyperthermia. *Science.* 1991 Jul 26;253(5018):448–51.
40. Guimaraes SEF, Rothschild MF, Ciobanu D, Stahl CH, Lonergan SM. SNP discovery, expression and association analysis for the SDHD gene in pigs. *Journal of Animal Breeding and Genetics.* 2007 Aug 1;124(4):246–53.
41. Kopečný M, Stratil A, Poucke MV, Bartenschlager H, Geldermann H, Peelman LJ. PCR-RFLPs, linkage and RH mapping of the porcine TGFB1 and TGFB1 genes. *Animal Genetics.* 2004 Jun 1;35(3):253–5.
42. Davoli R, Braglia S, Lama B, Fontanesi L, Buttazzoni L, Baiocco C, et al. Mapping, identification of polymorphisms and analysis of allele frequencies in the porcine skeletal muscle myopalladin and titin genes. *Cytogenet Genome Res.* 2003;102(1–4):152–6.
43. Okumura N, Hayashi T, Sekikawa H, Matsumoto T, Mikawa A, Hamasima N, et al. Sequences and mapping of genes encoding porcine tyrosinase (TYR) and tyrosinase-related proteins (TYRP1 and TYRP2).

44. Rohrer GA, Nonneman DJ, Miller RK, Zerby H, Moeller SJ. Association of single nucleotide polymorphism (SNP) markers in candidate genes and QTL regions with pork quality traits in commercial pigs. *Meat Sci.* 2012 Dec;92(4):511-8.
45. Blasco, A. and M.A. Toro, 2014. A short critical history of the application of genomics to animal breeding. *Livestock Science*, 166: 4-9. DOI: 10.1016/j.livsci.2014.03.015
46. Gao Y, Zhang R, Hu X, Li N. Application of genomic technologies to the improvement of meat quality of farm animals. *Meat Sci.* 2007 Sep;77(1):36-45.
47. Alison, V. E. (2006) DNA-Based Technologies. *Beef Sire Selection Manual*, National Beef Cattle Evaluation Consortium, 66-73.
48. Dekkers JCM. Commercial application of marker- and gene-assisted selection in livestock: strategies and lessons. *J Anim Sci.* 2004;82 E-Suppl:E313-328.
49. Meuwissen TH, Hayes BJ, Goddard ME. Prediction of total genetic value using genome-wide dense marker maps. *Genetics.* 2001 Apr;157(4):1819-29.
50. Miar Y, Plastow G, Wang Z. Genomic Selection, a New Era for Pork Quality Improvement. *Springer Science Reviews.* 2015 Apr 11;3:27-37.
51. Samorè AB, Fontanesi L. Genomic selection in pigs: state of the art and perspectives. *Italian Journal of Animal Science.* 2016 Apr 2;15(2):211-32.
52. Goddard ME, Hayes BJ. Mapping genes for complex traits in domestic animals and their use in breeding programmes. *Nat Rev Genet.* 2009 Jun;10(6):381-91.
53. Ramos AM, RP Crooijmas, NA Affara, AJ Amaral, AL Archibald, et al.(2009) Design of high density SNP genotyping assay in the pig using SNPs identified and characterized by next generation sequencing technology. *PLoS One*, 4:e6524.
54. Groenen MAM, Archibald AL, Uenishi H, Tuggle CK, Takeuchi Y, Rothschild MF, et al. Analyses of pig genomes provide insight into porcine demography and evolution. *Nature.* 2012 Nov 15;491(7424):393-8.
55. Dekkers JCM. Application of Genomics Tools to Animal Breeding. *Curr Genomics.* 2012 May;13(3):207-12.
56. de Roos APW, Hayes BJ, Spelman RJ, Goddard ME. Linkage Disequilibrium and Persistence of Phase in Holstein-Friesian, Jersey and Angus Cattle. *Genetics.* 2008 Jul;179(3):1503-12.
57. Gianola D, Fernando RL, Stella A. Genomic-Assisted Prediction of Genetic Value With Semiparametric Procedures. *Genetics.* 2006 Jul;173(3):1761-76.
58. Xu S, Jia Z. Genomewide Analysis of Epistatic Effects for Quantitative Traits in Barley. *Genetics.* 2007 Apr;175(4):1955-63.
59. Zeng J, Toosi A, Fernando RL, Dekkers JCM, Garrick DJ. Genomic selection of purebred animals for crossbred performance in the presence of dominant gene action. *Genet Sel Evol.* 2013 Apr 26;45:11.
60. Gerbens F, van Erp AJ, Harders FL, Verburg FJ, Meuwissen TH, Veerkamp JH, et al. Effect of genetic variants of the heart fatty acid-binding protein gene on intramuscular fat and performance traits in pigs. *J Anim Sci.* 1999 Apr;77(4):846-52.
61. Gerbens F, de Koning DJ, Harders FL, Meuwissen TH, Janss LL, Groenen MA, et al. The effect of adipocyte and heart fatty acid-binding protein genes on intramuscular fat and backfat content in Meishan crossbred pigs. *Journal of Animal Science.* 2000;78(3):552.
62. Gerbens F, Verburg FJ, Van Moerkerk HT, Engel B, Buist W, Veerkamp JH, et al. Associations of heart and adipocyte fatty acid-binding protein gene expression with intramuscular fat content in pigs. *J Anim Sci.* 2001 Feb;79(2):347-54.
63. Barnoy S, Glaser T, Kosower NS. Calpain and calpastatin in myoblast differentiation and fusion: effects of inhibitors. *Biochim Biophys Acta.* 1997 Sep 11;1358(2):181-8.
64. Mellgren RL. Evidence for participation of a calpain-like cysteine protease in cell cycle progression through late G1 phase. *Biochem Biophys Res Commun.* 1997 Jul;236(3):555-8.
65. Goll DE, Thompson VF, Taylor RG, Ouali A. The calpain system and skeletal muscle growth. *Canadian Journal of Animal Science.* 1998 Dec;78(4):503-12.
66. Kurył J, W Kapelański, M Pierzchała, S Grajewska and M Bocian (2003) Preliminary observations on the effect of calpastatin gene (CAST) polymorphism on carcass traits in pigs. *Anim Sci Pap Rep* 21: 87-95.
67. Krzeczio E, Kurył J, Kocwin-Podsiadła M, Monin G. Association of calpastatin (CAST/Mspl) polymorphism with meat quality parameters of fatteners and its interaction with RYR1 genotypes. *Journal of Animal Breeding and Genetics.* 2005 Aug 1;122(4):251-8.
68. Pierzchała, M, T Blicharski and J Kurył (2003) Growth rate and carcass quality in pigs as related to genotype at loci POU1F1/RsaI (Pit1/RsaI) and GHRH/AluI. *Anim.*

Sci. Papers Rep., 21: 159-166.

69. Franco MM, Antunes RC, Silva HD, Goulart LR. Association of PIT1, GH and GHRH polymorphisms with performance and carcass traits in Landrace pigs. *J Appl Genet.* 2005;46(2):195-200.
70. Rosen ED, Spiegelman BM. Molecular regulation of adipogenesis. *Annu Rev Cell Dev Biol.* 2000;16:145-71.
71. Kunej T, Wu X-L, Berlic TM, Michal JJ, Jiang Z, Dovc P. Frequency distribution of a Cys430Ser polymorphism in peroxisome proliferator-activated receptor-gamma coactivator-1 (PPARGC1) gene sequence in Chinese and Western pig breeds. *Journal of Animal Breeding and Genetics.* 2005 Feb 1;122(1):7-11.
72. Wan X, Wang D, Xiong Q, Xiang H, Li H, Wang H, et al. Elucidating a molecular mechanism that the deterioration of porcine meat quality responds to increased cortisol based on transcriptome sequencing. *Sci Rep.* 2016 11;6:36589.
73. Yin J and D Li (2009) Nutrigenomics approach-a strategy for identification of nutrition responsive genes influencing meat edible quality traits in swine. *Asian-Aust J Anim Sci* 22: 605-610.

Copyright: © **Naskar et al.** This is an Open Access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.