

APPLICATION OF MOLECULAR GENETICS IN THE IMPROVEMENT OF CARCASS AND MEAT QUALITY TRAITS IN PIGS

Anna Antonyk¹, Thierry Van De Wetering², Arkadiusz Terman¹

¹West Pomeranian University of Technology in Szczecin, Department of Genetics, Al. Piastów 45, 70-311 Szczecin

²Pomeranian Medical University in Szczecin, Department of Genomics and Forensic Genetics, ul. Powstańców Wielkopolskich 72, 70-111 Szczecin



Anna Antonyk: 0000-0001-8936-2953

Thierry Van De Wetering: 0000-0002-3910-649X

Arkadiusz Terman: 0000-0003-0724-2128

Abstract

Pork is one of the most frequently chosen types of meat among consumers. According to recent data, demand for pork continues to increase, and in Poland its consumption reaches as much as 45 kg per person annually. Contemporary consumers prefer high-quality meat products characterized primarily by health-promoting properties. Pork quality is influenced not only by breeding work, but also by genetic principles associated with planned animal selection and reproductive management aimed at producing offspring with desirable production, health and utility traits, as well as by environmental factors. These include pig production methods, which are among the key factors determining the quality of fresh pork. They encompass both animal housing systems and feeding strategies, which affect the technological, sensory and nutritional properties of meat. Pig housing systems, including intensive and extensive systems, differ significantly in their effects on meat quality. Intensive production ensures high efficiency, but may be associated with a greater risk of stress and deterioration of meat quality. In contrast, extensive systems and the use of local breeds often result in meat with higher intramuscular fat (IMF) content, higher pH and better sensory characteristics. Access to outdoor areas, greater living space and natural environmental conditions affect animal activity, which in turn influences muscle structure and meat quality. At the same time, these effects are not unequivocal and depend on many environmental and genetic factors. Studies also indicate that local pig breeds, despite lower production efficiency, may provide raw material of high technological and sensory quality. Through rigorous selection and appropriate mating of individuals, pork production has increased considerably. Genetic research contributes significantly to improving pork quality, particularly its chemical composition. Identification of genes that may become genetic markers, together with knowledge of the effects of external factors, expands our understanding of muscle growth and development. This supports breeders in meeting current consumer demand for the production of high-quality pork.

Keywords: pork, meat quality, SNP, QTL

Introduction

Pork is one of the principal sources of animal protein in the human diet, characterized by high biological value and a favorable amino acid profile. The protein content of fresh pork averages 25–27 g/100 g of product, as confirmed by USDA nutritional data (USDA, 2023). In terms of minerals, pork provides significant amounts of macro- and microelements. Potassium content is approximately 350–550 mg/100 g, phosphorus 200–240 mg/100 g, magnesium 20–30 mg/100 g and calcium 7–20 mg/100 g, although these values depend on the carcass cut and degree of fatness (USDA, 2023; Lawrie and Ledward, 2006).

Pork is also an important source of thiamine (vitamin B1), with a content of approximately 0.5–0.7 mg/100 g, making it one of the richest sources of this vitamin among red meats (Toldrá, 2022). Thiamine plays a key role in carbohydrate metabolism and nervous system function. Cholesterol content in pork averages 60–90 mg/100 g, depending on the carcass cut and intramuscular fat content (Wood et al., 2008; USDA, 2023). Current studies indicate that moderate consumption of lean pork is not unequivocally associated with adverse effects on the lipid profile of healthy individuals (Wyness, 2016). Pork also provides heme iron, zinc and selenium, which are highly bioavailable compared with plant-derived products (FAO, 2022). These components play important roles in immune processes and the functioning of antioxidant enzymes.

Due to production traits that are important from a breeding perspective, such as high prolificacy and the high meat yield obtained from a single animal, pork constitutes an important component of the global meat supply (Vicente and Pereira, 2024). Global pig production is a major element of the worldwide meat supply chain, encompassing breeding, fattening, slaughter and processing. Pork accounts for approximately 33% of total meat consumption worldwide, although consumption varies regionally. In recent years, consumer interest in meat quality has increased, in association with improved living standards and growing health awareness.

When consumers choose pork, sensory traits such as appearance, taste and aroma are of key importance and determine purchasing decisions. Improving pork quality may increase its market attractiveness and consumption. Consequently, this is an important factor shaping the direction of pig production improvement toward obtaining high-quality raw material (Lebret and Čandek-Potokar, 2022).

For many years, scientists have worked to identify quantitative trait loci (QTL) and genetic markers using genome-wide association studies (GWAS). These efforts have made it possible to distinguish the genetic basis of traits such as meat pH and color. Widely used genome-wide association studies detect genotype–phenotype relationships by testing differences in the frequencies of single nucleotide polymorphism (SNP) alleles among studied individuals. Genetic studies play an important role in improving pork quality, particularly its chemical composition. Identification of candidate genes and genetic markers, as well as analysis of environmental effects, enables a better understanding of the mechanisms regulating muscle tissue growth and development. The resulting knowledge provides important support for breeders in adapting production to changing consumer demands worldwide (Zhuang et al., 2022).

Recent findings also indicate that the body responds differently to different dietary protein sources. Consumption of plant proteins, such as soy or wheat, may be associated with weaker stimulation of muscle protein synthesis compared with animal-derived proteins. In this context, pork, as a source of complete protein with high bioavailability, remains an important component of the human diet (Vissamsetti et al., 2023).

Meat quality traits

Indicators of pork quality include color, tenderness, pH, drip loss, flavor, marbling and juiciness. Amino acids are among the essential nutritional and flavor-related components of meat. Consumer preferences for pork are determined primarily by sensory traits such as tenderness, juiciness and flavor, which are indirectly related to its chemical composition, including intramuscular fat (IMF) content and muscle fiber characteristics. Meat with a higher IMF content and a more favorable muscle fiber structure is generally rated as more acceptable in sensory terms. At the same time, increased muscle fiber density may be associated with lower meat color intensity (less redness) and reduced toughness (Chen et al., 2024). One important production trait in pigs is the degree of carcass fatness, which is closely related to meat quality and fattening performance. The literature has shown that lean meat content is negatively correlated with fatness traits, meaning that as muscularity increases, the proportion of fat in the carcass decreases (Ropka-Molik et al., 2020). Excessively low IMF content may impair technological properties and consumer acceptance of meat, whereas an appropriate level is considered beneficial for the quality of the final product (Hussain and Khan, 2017).

Modern pig breeding programs are largely focused on increasing carcass lean meat content, which may lead to changes in the genetic structure of populations, including an increased contribution of particular breeding lines and reduced genetic variability in selected production traits. These phenomena are a consequence of long-term phenotypic and genetic selection, although their extent and impact on genetic diversity depend on the breeding program and its assumptions (Ropka-Molik et al., 2020).

Meat color is one of the basic quality traits evaluated by consumers and is an important factor affecting the acceptance and assessment of fresh pork. Variation in meat color results mainly from biochemical processes occurring after slaughter, including the rate of pH decline, the degree of myoglobin oxidation and storage conditions. Therefore, efforts are made to stabilize color and limit undesirable surface changes, such as discoloration, which may reduce the commercial attractiveness of pork (Nery da Silva et al., 2021; Gagaoua et al., 2023a).

In scientific studies and technological practice, meat color is most commonly assessed using the CIE $L^*a^*b^*$ system, which provides an objective description of color in three-dimensional space. This system comprises three parameters: L^* , a^* and b^* , each describing a different aspect of meat color perception.

The L^* parameter (lightness) indicates the degree of meat lightness and is strongly associated with physicochemical properties, including ultimate pH and water-holding capacity. Higher L^* values indicate lighter meat, whereas lower values indicate darker meat. This parameter is frequently used as an indicator of pork quality deviations (e.g. PSE or DFD) (Gagaoua et al., 2023b).

The a^* parameter describes the red–green component, with higher a^* values corresponding to more intense meat redness. This value is closely related to myoglobin content and its chemical state, including the proportions of oxy- and metmyoglobin, which determine the final meat color (Gagaoua et al., 2023b; Poveda-Arteaga et al., 2023).

The b^* parameter refers to the yellow–blue component and may be modified by the lipid composition of meat, oxidative processes, and storage and processing conditions. An increase in b^* indicates a shift toward yellow, which may be associated with progressive oxidation of lipids and muscle proteins (Gagaoua et al., 2023a, b). Consequently, the $L^*a^*b^*$ system is one of the fundamental tools for objective meat color assessment, enabling color to be linked to biochemical processes occurring in muscle tissue after slaughter.

One important meat quality trait is water-holding capacity (WHC). In pork, this parameter refers to the ability of muscle tissue to retain water under technological influences such as

cutting, grinding or thermal processing. WHC is one of the key indicators of meat quality because it affects appearance, juiciness, texture and processing yield, understood as the amount of final product obtained from a given mass of raw material (Kim et al., 1995; de Sousa Reis et al., 2023). A high WHC value is desirable because it limits mass losses associated with water exudation and improves juiciness and sensory acceptance (Kim et al., 1995). Acidity is among the factors affecting water-holding capacity. Higher postmortem pH is positively correlated with WHC, meaning that meat with a higher pH contains more water (Xiao-ling et al., 2009). Low pH may cause protein denaturation and consequently reduce WHC (Joo, 2018). During meat aging, WHC usually decreases immediately after slaughter, but may increase as aging progresses due to degradation of cytoskeletal proteins, which allows water to be reabsorbed into muscle fibers (Kristensen et al., 2001). Changes in muscle structure, particularly degradation of cytoskeletal proteins over time after slaughter, improve WHC because structures that retain water outside muscle fibers break down, facilitating reabsorption (Kristensen et al., 2001). Reduced WHC is associated with pale, soft and exudative (PSE) meat, characterized by low pH, pale color and increased drip loss, resulting in poorer technological and sensory quality. With regard to relationships among meat quality parameters, it has been shown that within a single pork carcass WHC may not vary significantly with meat color. However, comparisons among different carcasses show a tendency toward a negative correlation between WHC and meat lightness (L^*), with lighter meat having lower water-holding capacity (Xiao-ling et al., 2009).

An important determinant of pork quality is intramuscular fat (IMF) content, which influences sensory traits such as tenderness, juiciness, palatability and overall consumer acceptance. IMF also affects technological properties of meat, including water-holding capacity and muscle tissue structure (Lebret and Čandek-Potokar, 2022; Listrat et al., 2020). From the standpoint of pork sensory quality, an IMF range of 2.5–3.5% is most commonly considered optimal; values below 2% may lead to poorer tenderness and increased dryness, whereas levels above 4% may be viewed negatively by some consumers because of excessive fatness (Fernandez et al., 2021; FAO, 2022). IMF levels vary significantly among pig breeds and production types. In modern meat-type breeding lines such as Pietrain or Duroc $\times$ terminal lines, IMF content usually ranges from 1.0 to 2.5%, as a result of intensive selection for high carcass leanness (Wood et al., 2008). Breeds such as Landrace and Large White are characterized by moderate IMF levels (approximately 1.5–3.0%) together with high slaughter performance. In contrast, local and traditional breeds, including pure breeds or autochthonous European populations, may have much higher IMF levels, reaching 3–7% or even more than 8%, which is associated with better sensory properties but lower production efficiency (Čandek-Potokar et al., 2022; Pugliese and Sirtori, 2021). IMF has been shown to be a trait with complex genetic determination, strongly associated with lipid metabolism and genes regulating adipogenesis. At the same time, genetic correlations between fatness traits and fatty acid composition indicate that selection focused solely on increasing leanness may reduce IMF and impair sensory quality (Zhang et al., 2021; Listrat et al., 2020). Therefore, IMF is one of the key parameters included in modern breeding programs, which increasingly seek a compromise between production efficiency and the sensory quality of pork.

Table 1. Relationship between pig type/breed, intramuscular fat (IMF) content and meat quality traits

Pig type/breed	Examples	IMF content (%)	Meat quality characteristics	References
Meat lines – intensive selection	Pietrain, terminal lines*	1.0–2.0	high lean meat content, lower tenderness and juiciness, risk of dry meat	Wood et al., 2008; Lebret and Čandek-Potokar, 2022
Commercial breeds – moderate lean meat content	Landrace, Large White	1.5–3.0	balanced technological and sensory quality	Fernandez et al., 2021

Duroc-type breeds	Duroc	2.5–4.0	higher marbling, improved tenderness and palatability	Listrat et al., 2020; Wood et al., 2008
Local and traditional breeds	Mangalica, Iberian, autochthonous breeds**	3.0–7.0 (>8.0)	high sensory quality, intensive marbling, lower growth and fattening performance	Čandek-Potokar et al., 2022; Pugliese and Siratori, 2021

* Terminal lines – breeding lines used mainly for the production of high-lean fattening pigs.

** Autochthonous breeds – local native pig breeds included in genetic resource conservation programmes.

Modern pig breeding programs rely heavily on commercial crossbreeding aimed at producing fattening pigs with high carcass leanness, rapid growth and favorable meat quality parameters. Terminal lines, used as the paternal component, play a particularly important role in these systems by improving the fattening and slaughter traits of the offspring (Lujka et al., 2021).

In Polish breeding programs, the maternal component is represented mainly by Polish Large White and Polish Landrace, whereas Pietrain and Duroc are most commonly used as terminal breeds. These breeds are characterized by high slaughter performance and good feed efficiency (Radko et al., 2023). Lujka et al. (2021) showed that the use of Duroc and Pietrain boars significantly affected piglet body weight and growth rate already during the early rearing period. The authors emphasized that the paternal component may substantially determine offspring production efficiency. Studies on fattening-pig carcass quality showed that crossbreds sired by Pietrain boars achieved the highest carcass leanness, whereas the use of Duroc improved meat quality traits, particularly intramuscular fat content and sensory parameters (Polovinski-Horvatović et al., 2023).

Genomic selection and genetic marker analysis are also becoming increasingly important in modern pig breeding. Babicz et al. (2022) indicated that growth hormone gene polymorphism (GH/HaeII) may affect muscularity and meat quality traits in crossbreds involving Polish Large White, Polish Landrace, Duroc and Pietrain pigs.

Preserving the genetic variability of native breeds is an important component of modern livestock genetic resources conservation programs. Radko et al. (2023) demonstrated clear genetic distinctiveness of the Puławska breed relative to commercial breeds, which may indicate its importance in maintaining valuable adaptive traits. Current directions in terminal-line improvement include not only increased leanness and growth rate, but also improved animal resistance, reduced susceptibility to stress and improved technological meat quality. Particular importance is attached to eliminating the RYR1 gene variant responsible for PSE meat defects, especially in Pietrain populations (Djurkin Kušec et al., 2021).

Factors affecting pork quality

Initially, pig selection was based mainly on phenotypic evaluation, including assessment of conformation and production traits of individual animals. On the basis of these observations, animals with desirable production and reproductive traits were selected, gradually increasing the frequency of favorable alleles in the population. However, this method was characterized by limited efficiency, primarily because of the low accuracy of breeding value evaluation in young animals and the substantial influence of environmental factors on the expression of quantitative traits (Dekkers, 2012; Goddard and Hayes, 2009). With the development of molecular genetics, phenotypic selection was supplemented and then largely replaced by genomic selection based on information from DNA markers distributed throughout the genome. This made it possible to estimate genomic estimated breeding values (GEBV) using statistical models such as BLUP (best linear unbiased prediction) and its genomic extensions. The introduction of genomic selection significantly increased the accuracy of breeding value estimation, particularly

in young animals, and accelerated genetic progress in pig populations (Meuwissen et al., 2001; Knol et al., 2016).

Modern pig breeding programs use methods based on genomic data, including multi-trait models and multi-population analyses, which increase the accuracy of breeding value prediction and enable more efficient management of genetic variability in breeding herds (Wang et al., 2024; Yin et al., 2024). Genomic selection also allows more precise control of inbreeding and optimization of parental selection in commercial lines (Su et al., 2025). It is particularly important for improving pig terminal lines, where the main emphasis is placed on fattening performance, leanness and carcass quality parameters while maintaining high production efficiency (Sharif-Islam et al., 2024). In recent years, animal welfare has improved considerably, with positive effects on product quality, food safety and consumer health (Casal et al., 2019). A growing body of evidence shows that dietary nutrients and bioactive compounds influence muscle energy metabolism, browning of white adipose tissue, fat distribution and muscle fiber-type composition in humans and rodents. Recent studies have demonstrated that modulation of muscle energy metabolism and lipid accumulation through nutritional approaches can effectively improve meat quality (Yan et al., 2023). By combining radio-frequency identification (RFID) systems with electronic feeding stations (EFS), breeders can monitor the feeding behavior of individual fattening pigs, including daily feed intake (kg) and daily feeding duration (s). This system helps generate variables reflecting daily patterns of feeding behavior, including the proportion of intake consumed at night and circadian rhythm (Bus et al., 2024). Skeletal muscle mass development is among the most economically important traits in pigs because it substantially determines slaughter yield and the amount of pork obtained from the carcass. The intensity of muscle tissue growth and development is a key determinant of live pig production efficiency and thus affects the volume of pork supplied to the market. The literature emphasizes that muscularity traits are strongly genetically determined and constitute a primary selection target for improving the production value of slaughter pigs (Mohammadabadi et al., 2021).

With the development of genetics and the availability of molecular biology techniques, livestock selection has expanded from an approach based solely on phenotypic evaluation to selection incorporating genotypic information. Phenotypic selection was based on assessment of production traits such as muscularity, growth rate and slaughter performance. The current approach includes analysis of DNA markers and genetic variants associated with production traits, allowing more accurate evaluation of animals' breeding potential. Integration of phenotypic and genotypic data forms the basis of modern methods for breeding value estimation and animal selection (Rexroad et al., 2019).

Candidate genes play an important role in identifying the genetic determinants of meat quality traits because they are directly or indirectly associated with phenotypic expression of production traits. In the direct approach, genes with known biological functions are analyzed on the basis of their involvement in physiological and biochemical processes such as muscle tissue development or lipid metabolism.

The indirect approach, in turn, is based on identifying positional candidate genes located within quantitative trait loci (QTL). Genetic mapping is used to define genome regions associated with particular traits, followed by identification of potential genes responsible for their variation (Wang et al., 2013). The development of high-throughput genome-analysis methods such as next-generation sequencing (NGS) and genome-wide association studies (GWAS) enables more efficient identification of genetic variation underlying phenotypic traits (Ropka-Molik et al., 2020).

Single nucleotide polymorphisms (SNPs) are among the most widely used molecular markers in genome-wide association analyses and candidate gene studies. This is due to their high abundance in the genome and relatively easy, high-throughput genotyping. These studies

use genotype–phenotype association analyses to estimate the effects of allelic variants and identify relationships between specific SNP polymorphisms and production traits such as slaughter performance, growth rate or meat quality. Integrating the candidate-gene approach with high-throughput genotyping techniques makes it possible to identify genetic variants significantly associated with production traits. The use of these methods increases selection accuracy and accelerates genetic progress in livestock breeding (Karisa et al., 2013; Antonyk et al., 2025).

Genetic markers

For many years, one of the most important genetic markers in pig breeding was the recessive allele of the RYR1 gene associated with stress susceptibility. Animals carrying this allele exhibit an abnormal physiological response to stressors, including changes in hormonal regulation and immune responses such as natural killer (NK) cell activity and cytokine production (Fujii et al., 1991; Ciepielewski et al., 2016).

The IGF2 gene polymorphism located in intron 3, which is strongly associated with muscle tissue development, is also important for improving pig production traits. It is used in breeding programs as a selection marker for carcass traits such as lean meat percentage and muscle growth rate (Burgos et al., 2012; Wang et al., 2023). Other genetic polymorphisms important in pig breeding have been identified in the CAST, PRKAG3, LEPR, MC4R and IGF2 genes. These genes have documented effects on traits related to fat content and distribution in pork carcasses and on pork quality (Rohrer et al., 2012; López-Buesa et al., 2014). Expression of genes such as CAST, COL1A1 and ADIPOQ is associated with quality traits including water loss, fat content and texture, while differences among genetic lines affect these parameters (Gomes et al., 2025).

Meat quality traits in pigs are determined by complex interactions among multiple loci involved in lipid metabolism, muscle energy metabolism and proteolytic processes occurring postmortem. The results discussed in this review confirm the polygenic nature of these traits and the predominant contribution of association signals identified in GWAS analyses.

In lipid metabolism, a key role is played by SCD, which encodes the enzyme catalyzing the conversion of saturated fatty acids to monounsaturated fatty acids (MUFA). According to Kim et al. (2024), variation in this gene affects the fatty acid profile of meat by modulating the proportion of monounsaturated fatty acids, which in turn influences the quality properties of muscle lipids.

Traits related to intramuscular fat (IMF) content and carcass fatness are regulated by genomic regions associated with adipogenesis and energy metabolism. GWAS results (Wang et al., 2023; Gomes et al., 2025) indicate that variation in these regions may significantly affect lipid accumulation in muscle tissue, although the observed effects are associative in nature.

Meat tenderness remains a trait strongly dependent on the activity of the proteolytic system. The CAST gene acts as a key inhibitor of calpains, regulating the rate of myofibrillar protein degradation during meat aging (Ciobanu et al., 2004). This directly affects the final tenderness of the product.

Postmortem traits related to meat pH are determined by genes involved in glycogen metabolism and muscle energy regulation. In particular, regions containing PRKAG3 have been associated with changes in the rate of pH decline and susceptibility to meat quality defects (Milan et al., 2000; Verardo et al., 2017).

Meat color is a complex trait determined by interactions among numerous metabolic and structural processes. GWAS analyses indicate the involvement of genomic regions associated with muscle metabolism and the response to oxidative stress (Liu et al., 2024; Wang et al.,

2023). However, the lack of unequivocal functional validation limits the ability to assign direct biological effects to individual variants.

Drip loss is a polygenic trait resulting from disturbances in water–electrolyte homeostasis and structural changes in muscle fibers during the postmortem period (Yu et al., 2025; Kamiński et al., 2024). The identified loci represent association signals and require further functional validation.

Most of the loci analyzed represent association signals that may reflect linkage with functional variants of true biological significance. Interpretation of the results should take into account the limitations of GWAS methods and the need for further experimental studies.

Table 2. Influence of individual genetic markers on pork meat characteristics

Gene/marker	Type	Function	Impact on meat characteristics	References
<i>AACS</i>	gene	lipid and ketone body metabolism	↓ WHC	Kamiński et al., 2024; McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
<i>ABCA4</i>	gene	membrane lipid transport	↓ WHC	Kamiński et al., 2024; McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
<i>ABCG1</i>	gene	cholesterol and lipid transport	↑ IMF	Gomes et al., 2025; Wang et al., 2023
<i>ADIPOQ</i>	gene	adipogenesis and lipid metabolism regulation	↑ IMF, ↑ marbling	Gomes et al., 2025; Malagwi et al., 2022; Dall’Olio et al., 2009; Wang et al., 2023
<i>AGPAT5</i>	gene	phospholipid biosynthesis	↑ IMF	Molinero et al., 2025
<i>ALDH5A1</i>	gene	aldehyde and amino acid metabolism	meat color changes, ↑ meat tenderness	Liu et al., 2024; Kamiński et al., 2024; Wang et al., 2023
<i>ANKRD6</i>	gene	cell signaling regulation	meat color variation	Liu et al., 2024; Kamiński et al., 2024; Wang et al., 2023
<i>CAPN1</i>	gene	muscle protein proteolysis	↑ meat tenderness	Chaosap et al., 2025
<i>CAPN10</i>	gene	muscle protein turnover	↑ meat tenderness, ↓ WHC	Liu et al., 2024; Kamiński et al., 2024; Gomes et al., 2025; Wang et al., 2023
<i>CAST</i>	gene	calpain inhibition	↑ meat tenderness, regulation of postmortem aging, ↑ WHC, ↑ IMF	Chen et al., 2025; Ciobanu et al., 2004; Ropka-Molik et al., 2014; Djurkin Kušec et al., 2015; Wang et al., 2023
<i>CBR4</i>	gene	lipid metabolism	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
<i>CHL1</i>	gene	cell adhesion	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
<i>CLCN3</i>	gene	chloride ion transport	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
<i>COL1A1</i>	gene	type I collagen biosynthesis	↑ meat tenderness, ↓ WHC, ↑ IMF	Li et al., 2022; Li et al., 2023; Cho et al., 2020; Wang et al., 2023
<i>DGAT2</i>	gene	triacylglycerol biosynthesis	↑ marbling	Molinero et al., 2025
<i>FABP4</i>	gene	fatty acid transport	↑ IMF	Li et al., 2023
<i>FARP2</i>	gene	cytoskeleton organization	↓ WHC	Kamiński et al., 2024; McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
<i>GALNT15</i>	gene	protein glycosylation	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
<i>GIN1</i>	gene	cellular process regulation	meat color variation	Liu et al., 2024; Kamiński et al., 2024; Wang et al., 2023
<i>HDLBP</i>	gene	lipoprotein binding	↓ WHC	Kamiński et al., 2024; McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023

HPF1	gene	DNA repair regulation	↓ WHC	Kamiński et al., 2024; McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
IGF2	gene	muscle growth regulation	↑ muscle weight, ↑ lean meat yield, ↓ carcass fatness	Clark et al., 2014; Clark et al., 2015; Fontanesi et al., 2010
LEPR	SNP	leptin signaling	↑ IMF, ↑ backfat thickness	Wang et al., 2023; Balatsky et al., 2016; Suárez-Mesa et al., 2024
MACROD2	gene	epigenetic regulation	↑ IMF	Gomes et al., 2025; Wang et al., 2023
MC4R	SNP	appetite and energy homeostasis regulation	↑ carcass fatness, ↑ growth rate	Zhang et al., 2020; Houston et al., 2004; Piórkowska et al., 2010
MTERF4	gene	mitochondrial transcription regulation	↓ WHC	Kamiński et al., 2024; McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
MYH7B	gene	muscle fiber organization	↑ meat tenderness	Liu et al., 2024
NCOA2	gene	transcription regulation	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
OXSM	gene	fatty acid biosynthesis	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
PASK	gene	glucose metabolism regulation	↓ WHC, meat technological quality traits	Kamiński et al., 2024
PDE4B	gene	cAMP signaling pathway	↑ meat tenderness	Liu et al., 2024
PIP4K2A	gene	phosphatidylinositol metabolism	↑ meat tenderness	Kamiński et al., 2024; Gomes et al., 2025; Wang et al., 2023
PPARGC1A	gene	energy metabolism regulation	↓ WHC, ↑ IMF	Kamiński et al., 2024; McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
PPIP5K2	gene	cell signaling regulation	meat color variation	Liu et al., 2024; Kamiński et al., 2024; Wang et al., 2023
PRKAG3	SNP	muscle glycogen metabolism	↑ pH, ↑ WHC, ↓ PSE	Kamiński et al., 2024; Milan et al., 2000; Liu et al., 2019; Molinero et al., 2024
PRKAR2A	gene	protein kinase A regulation	↑ meat tenderness, ↑ IMF	Gomes et al., 2025; Wang et al., 2023
RYR1	SNP	calcium homeostasis	PSE susceptibility, ↓ pH	Scerra et al., 2024
SCD	gene	fatty acid desaturation	↑ MUFA in fatty acid profile	Kim et al., 2024
SLC1A2	gene	amino acid transport	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
TBC1D1	gene	glucose transport regulation	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023
ZAG	gene	lipid mobilization	↓ WHC	McBryan et al., 2010; Yu et al., 2025; Wang et al., 2023

↑ = increases, ↓ = decreases

Epigenetics

An important aspect of current research on pork quality is understanding the relationships between genetic factors and epigenetics, which concerns changes in gene expression that do not result from alterations in the DNA sequence but from modifications in how genes are read by the cell (Jain and Epstein, 2024). Epigenetics comprises mechanisms that regulate gene expression without changing the DNA sequence, acting mainly through chromatin modifications, DNA methylation and histone modifications. These processes influence gene activity and may lead to phenotypic changes in response to environmental factors (Jain and Epstein, 2024; Radford, 2018). Epigenetics involves several fundamental molecular mechanisms, including DNA methylation. This is based on the addition of small chemical (methyl) groups to DNA bases,

which usually suppresses gene activity (Jain and Epstein, 2024). Another well-known mechanism is histone modification, in which chemical changes to histones can facilitate access to genes through activation or restrict it through silencing. Epigenetic mechanisms also explain why cells containing the same DNA behave differently. They determine cell specification and differentiation during embryonic development, maintenance of cellular identity in the mature organism, and changes in sensitivity to environmental signals (Radford, 2018). Authors of scientific publications emphasize that epigenetic changes are dynamic and partly reversible, which is one of the key differences from permanent changes in the DNA sequence. Cells can also modify epigenetic marks in response to environmental stimuli such as stress, environmental conditions or exposure to toxins (Handel et al., 2010).

The genome contains a large group of non-coding regulatory DNA and RNA elements, among which enhancers play an important role. These are non-coding DNA sequences located mainly in intergenic and intronic regions that regulate gene expression by increasing the transcriptional activity of target genes (Wang et al., 2023). With the development of genomic research and access to increasingly large datasets, it has been shown that the number of enhancers in the genome is considerably greater than the number of protein-coding genes.

A transcriptional enhancer is a short non-coding DNA sequence with a regulatory role in the control of gene expression. These elements may be located a considerable distance from the promoters of target genes, either upstream or downstream of the transcriptional orientation, and often occur in intergenic or intronic regions. Enhancer activity is regulated by tissue-specific transcription factors and cofactors that enable spatial contacts with target gene promoters. As a result, enhancers permit precise control of gene expression in a manner dependent on cell type and developmental stage (Blayney et al., 2023; Yang et al., 2025). Disease-relevant enhancers generally show cell-type-specific activity, which complicates simple assignment of SNPs (as well as *de novo* mutations) identified in potential enhancers (Friedman et al., 2024). Non-coding genetic variants may alter normal developmental processes by disrupting enhancer function. Vashisht et al. (2025) reported that the number of disease-associated variants affecting enhancer function greatly exceeds the number affecting protein-coding genes. Scientific reports contain an increasing amount of information on enhancers in the pig genome. Several tissue-specific enhancers have been identified, including in the heart, liver and skeletal muscle. They control expression of genes associated primarily with muscle growth, metabolism and immunity (Bai et al., 2023; Wang et al., 2024; Zhao et al., 2021).

Summary

Genomic selection represents a major advance in pig breeding, enabling more precise and rapid estimation of breeding values and selection of animals for production and reproductive traits. It focuses primarily on improving traits such as growth rate, slaughter performance, meat quality and feed efficiency. In parallel, the development of high-throughput techniques such as STARR-seq, ChIP-Seq (H3K27ac and H3K4me1 markers) and ATAC-Seq enables identification of enhancers and other regulatory genomic elements (Salavati et al., 2022; Wu et al., 2022). Integration of genomic and epigenomic data enables breeders and researchers to make more precise selection decisions aimed at improving production efficiency, meat quality, animal welfare and the sustainability of pig production (Sharif-Islam et al., 2024; Li et al., 2024). Zhuang et al. (2022) mapped quantitative trait loci (QTL) for meat quality traits in a crossbred pig population, confirming the polygenic nature of their genetic determination. An approach based solely on QTL analysis and SNP associations does not always allow unambiguous determination of causal relationships between genetic variants and phenotypic traits. In this context, the development of epigenomic resources such as the Pig-eRNAdb database provides an important complement to genomic analyses by enabling identification of more than 100,000 enhancers in

the pig genome, some of which overlap previously described QTL regions and show tissue-specific activity, including in muscle tissue (Wang et al., 2024). Integrating epigenomic data with QTL results and SNP analyses may facilitate the identification of functional variants, potentially increasing the efficiency of genomic selection and moving beyond simple marker–trait associations. At the same time, it should be emphasized that epigenomic data for *Sus scrofa* remain limited and mainly cover selected tissues such as muscle, liver and adipose tissue. Comprehensive DNA methylation maps and enhancer atlases for key production-relevant tissues, particularly muscle tissue (e.g. longissimus dorsi), are still not fully available. The absence of epigenomic profiles for Polish heritage breeds such as Puławska and Żłotnicka White limits the possibility of fully understanding adaptive mechanisms at the epigenetic level under domestic breeding and housing conditions. This is especially relevant to populations maintained under different environmental conditions and production systems in Poland, despite the availability of phenotypic and genetic data (Antonyk et al., 2025). Identified enhancers and QTL require functional validation through gene editing (CRISPR/Cas9), which is still lacking in pig studies compared with mouse models, limiting the transition from statistical correlations to practical breeding markers. Enhancers often overlap QTL regions associated with production traits, which may help identify functional regulatory mutations (Wu et al., 2022). Many enhancers act in a tissue-dependent manner and therefore show unique activity and relationships with gene expression regulation (Zhang et al., 2023). In recent years, the ENCODE, FANTOM5 and Roadmap Epigenomics projects have been conducted to identify regulatory genomic elements, including enhancers, in humans and animals (Wang et al., 2024). Integrating epigenomic knowledge with appropriate breeding-system management, including nutrition, housing conditions and selection strategies, together with environmental factors such as stress, feed quality and microclimatic conditions, enables production to be better adapted to changing consumer requirements (Zhuang et al., 2022).

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APPLICATION OF MOLECULAR GENETICS IN THE IMPROVEMENT OF CARCASS AND MEAT QUALITY TRAITS IN PIGS

Anna Antonyk, Thierry Van De Wetering, Arkadiusz Terman

SUMMARY

Pork is one of the most frequently chosen types of meat among consumers. According to recent data, the demand for pork continues to increase, with per capita consumption in Poland reaching approximately 45 kg per year. Contemporary consumers increasingly prefer high-quality meat products characterized primarily by their health-promoting properties. The quality of pork is influenced both by breeding factors and genetic aspects related to the planned selection of animals and reproductive management aimed at producing offspring with desirable production, health, and utility traits. Environmental factors also play an important role, including pig production systems, which represent a key determinant of fresh pork quality. These encompass housing systems as well as feeding strategies that affect the technological, sensory, and nutritional properties of meat. Pig production systems, including intensive and extensive systems, differ significantly in their impact on meat quality. Intensive production ensures high efficiency but may be associated with increased stress levels in animals and a deterioration of certain meat quality traits. In contrast, extensive systems and the use of local breeds often result in meat with higher intramuscular fat (IMF) content, higher pH values, and improved sensory characteristics. Access to outdoor areas, increased space allowance, and more natural environmental conditions affect animal activity, which in turn influences muscle structure and meat quality. At the same time, it is emphasized that these effects are complex and depend on the interaction of multiple genetic and environmental factors. Studies also indicate that local pig breeds, despite lower production efficiency, may provide raw material of high technological and sensory quality. Through the application of rigorous selection and appropriate mating strategies, pork production has increased significantly. Genetic research makes a substantial contribution to improving pork quality, particularly its chemical composition. The identification of candidate genes with potential as genetic markers, together with the analysis of environmental influences, has expanded knowledge on muscle growth and development, supporting breeders in meeting current consumer demands for high-quality pork.

Keywords: pork, meat quality, SNP, QTL