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Indications of associations between polymorphism of the selected genes located on the porcine chromosome 4 and carcass quality traits*

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***DGAT1, AGL* and protoncogen *c-myc* genes have been mapped on chromosome 4 and considered as candidate genes for carcass quality traits. The aim of the study was to characterize the polymorphism of these genes in four groups of pigs and to evaluated the relationship between the *DGAT*1, *AGL* and *c-myc* genotype and carcass traits. The animals of cross-breed PLW x PL were used only to characterize these polymorphisms. All animals studied appeared to be polymorphic at these loci. Statistical analysis was carried out for each breed separately using the least square methods of the GLM procedure. The relationship between the polymorphism and several productive traits was identified in each of the study group of pigs. Animals carrying heterozygous genotype at this locus showed most extreme values for some of the traits tested. Our results suggest that these genotypes might be utilized in the selection of valuable pig carcass traits.**

KEY WORDS: *DGAT*1 / *AGL, c-myc* / gene polymorphism / carcass meatiness / pigs

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Muscle deposition of carcass and meat quality are quantitative traits, which means that their final expression is affected by genetic and environmental factors. Muscular or hepatic expression genes have been found to correlate highly with growth or carcass traits in pigs [Pierzchała *et al*. 2012, Xu *et al.* 2020]. Pork quality is primarily by the palatability and nutrition of the meat, which can very depending on the cut of pork [Alfaia *et al*. 2019, Chen *et al*. 2021]. The genetic component is comprised of the expression of many genes, known as quantitative trait loci (QTLs). Currently, there are two methods of identification of QTL in animals. One of this method is mapping genes by linkage analysis. The second method is based on the evaluation of the effect of polymorphisms in candidate genes for the trait of interest.

Last two decads is period when on multiple porcine chromosomes have been identified that carried QTL for carcass traits and the growth rate in pigs [Geldermann *et al*. 2003, Thomsen *et al*. 2004]. In last years with the emergence of high-density SNP arrays, genome-wide association study have identified a list of significant loci for growth and fatness traits in different pig populations [Meng *et al*. 2017; Gong *et al*. 2019]. One of the most important region on porcine genome is chromosome 4, where have been mapped first QTL for carcass traits. It has been made by scientifists from University of Agriculture in Uppsala, Sweden [Andersson *et al*. 1994]. They reported that in the region located between loci *S0001* and *ATP1B1* there are genes which affect the fat content of the carcass and fatback thickness. It was further proven that the tested region of the chromosome 4 bounded by loci *Sw835* and *ATP1B1* contains genes that affect the thickness of subcutaneous fat [Andersson *et al*. 1994]. Therefore, for many years chromosome 4 has been at the center of interest of researchers from many scientific centers. About a lots number of QTL, on multiple chromosomal regions, have been identified candidate genes for carcass and meat quality traits in pigs.

So far, candidate genes for pig carcass traits are: *RYR1*, growth hormone (*GH*), insulin-like growth factors (*IGFI* and *IGFII*), genes of *MyoD* family, leptin and leptin receptor (*LEP* and *LEPR*), pituitary transcription factor 1 (*PIT1*), genes coding calpains (*CAPN*) and their inhibitor-calpastatin (*CAST*), melanocortin-4 receptor (*MC4R*) and several other genes [Dekkers *et al*. 2007]. Researchers are trying to identify genes within this group that have the greatest effect on a particular trait. These genes are known as major genes e.g. ryanodin receptor ($RYR1^T$), involved in pig susceptibility to stress, and rendement napole (RN^-) determining the occurrence of acid in Hampshire-type meat, are among them. Also, on porcine chromosome 4 have been reported the candidate genes for productive traits in pigs, for example: *DGAT1*, *AGL*, *AMPD1*, protooncogen *c-myc*, genes coding cathepsins S and K (*CTSS* and *CTSK*), genes which products shape the content of intramuscular fat (*FABP4* and *FABP5*), gene encoding lamin protein (*LMNA*).

For our analysis were chosen three genes, previously reported as candidate genes on growth and carcass quality traits: *DGAT1*, *AGL*, and *c-myc*.

The *DGAT1* gene has been mapped on porcine chromosome 4, outside the confidence interval for the fatty acid composition QTL. DGAT1 – diacylglycerol

acyltransferase 1, like acyl-coenzyme A: cholesterol acyltransferase enzymes, is part of a large family of membrane-bound O-acyltransferases [Yen *et al*. 2008]. DGAT1 is a multifunctional endoplasmic reticulum membrane protein, with its likely active site on the luminal side of the endoplasmic reticulum membrane [Bhatt-Wessel *et al*. 2018], and is involved in triglyceride (TG) storage in skeletal muscle and white adipose tissue, connecting diacylglycerol and fatty acid through covalent addition [Bhatt-Wessel *et al*. 2018]. The biological function of this gene were determinated on the basis of deficient mice. *DGAT1* gene alters the triglyceride metabolism in tissues as mammary gland, where causes the absence of milk production. The gene is expressed in most tissues, but the highest expression level in is an small intestine and adipose tissue [Chen *et al*. 2002]. The porcine *DGAT1* gene comprises 17 exons. The cDNA, 1935 bp long, codes for a protein of 489 amino acids and it is homologue with 85%, 86% and 92% to mouse, human and bovine proteins, respectively [Nonneman *et al*. 2002]. In this gene were found several single nucleotide polymorphisms using the MARC Swine Reference Population, in introns and coding regions. Silent SNPs were found in amino acids 173, 197, 245, 321 and 344 [Nonneman *et al*. 2002]. Mercadé *et al*. at research from 2005 year reported four single nucleotide polymorphisms in exons 8, 9, 13 and 17. Three of which occurred in the coding region with no amino acid change at nucleotide positions [Mercadé *et al*. 2005]. The interracial differences in allele frequencies were observed only for a *G*/*A* transition, located in exon 9, at nucleotide position 978. Therefore, this mutation was the topic of our studies.

Meat quality and productivity might be associated with glycogen metabolism. The enzyme which is involved in glycogen degradation is the product of *AGL* gene. Together with phosphorylase, AGL functions as a critical enzyme in carbohydrate metabolism and directs the complete degradation of glycogen. It has two independent catalytic activities: 4-α-glucanotransferase and an amylo-1,6 glucosidase [Herszberg *et al*. 2007]. Both activities occur at different sites on the single polypeptide chain. In human, remarkable clinical and enzymatic variability occurs in glycogen debrancher deficiency. To study of the porcine *AGL* gene PCR primers were designed using human genomic DNA sequence. In porcine *AGL* gene were reported two polymorphisms: the insertion/deletion polymorphism (Indel) and second polymorphism, which were recognized by *Ava*II restriction endonuclease [Stratil *et al*. 2003]. The second of these SNPs was the aim of our study.

Protooncogene *c-myc* is gene which codes a nuclear phosphoprotein, and a transcription factor creates of the typical basic/helix-loop-helix (bHLH) leucine zipper domains. This proto-oncogene is involved in a variety of different cellular processes, such as proliferation, differentiation and apoptosis, also adipogenesis and myogenesis. The expression of *c-myc* is regulated by a variety of hormones, cytokines, growth factors, lymphokines, development and differentiation [Kim *et al*. 2014]. The human *c-myc* gene is located on HSA8, which is homologue to *Sus scrofa* chromosome 4. The structure of porcine *c-myc* gene is highly conserved between species, consisting of three exons, with 90-100% sequence identity between all species in the functionally

relevant domains [Musilová *et al*. 2000]. The complete porcine *c-myc* proto-oncogene and flanking regions were sequenced a total of 6.4 kb, and contain three exons, two putative polyadenylation signals in the 3'UTR, three putative promoter start signals and two TATA-boxes. Because *c-myc* is involvement in adipogenesis, therefore this gene could be a candidate gene contributing to variability in fatness in the pig. With regard to *c-myc* gene the topic of these studies was SNP located in 5'UTR region, recognized by *Eco*RV restriction endonuclease [Reiner *et al*. 1999].

The objective purpose of these studies was to evaluate the effect of particular genotypes: *DGAT1*/*Hinf*I, *AGL*/*Ava*II and *c-myc*/*Eco*RV genes on growth rate and carcass traits in pigs.

Material and methods

Animals

The analysis was conducted on 707 gilts of two pure breeds: Polish Large White – PLW (n=185) and Polish Landrace – PL (n=216); synthetic line L990 (n=216) and one cross-breed: Polish Large White x Polish Landrace – PLW x PL (n=90). All the pigs were maintained in Poland. The animals of PLW, PL and L990 were kept at the Pig Progeny Testing Station Pawłowice of the National Research Institute of Animal Production, Cracow. The gilts between 25 and 100 kg of body weight (BW) were fed *ad libitum* with a commercial mixed feed, and then slaughtered at 100 kg body weight. Right sides of carcasses were divided into cuts and dissected into meat, fat and bone according to the procedure used in Polish Pig Progeny Testing Station, described previously by Różycki [1996].

The pigs of cross-breed PLW x PL were kept in Pruszcz farm (Kujawy, region Poland). These animals were used only to characterize of selected polymorphisms. Because is small number of this group (only 90 animals) relations between the polymorphism in tested loci and productive traits did not analysed.

For the analyses, the average daily gain, as well as the following nine carcass traits were taken into consideration: weight of right carcass side, weight of ham, weight of loin, weight of sirloin, width of loin eye, height of loin eye and loin eye area, meat content of valuable cuts and meat content in carcass. The synthetic line L990 is the final effect crossbreeding of six breeds: Polish Large White, Belgian Landrace, Welsh Landrace, German Landrace, Duroc and Hampshire and long term (about 30 years) selection. This line is recommended as a male component of crosses with sows of maternal breeds (Polish Landrace and Polish Large White).

Molecular analysis

Genomic DNA was isolated from leukocytes according to Kawasaki [1990]. The *RYR1* genotypes were established using sequence of primers given by Kamiński *et al*. [2002]. Genotypes *DGAT1*, *AGL* and *c-myc* were determined by PCR-RFLP method with following primers sequences as showed in Table 1.

Table 1. Primer sequences, thermal conditions, restriction endonuclease in PCR-RFLP analysis and references

Gene	Primer sequence	Thermal conditions	Restr. enzyme	References
*DGAT*1	5'F:CTTCTGCAGGTAAGAAGGCCAAC 5'R: AGGAACAGCTGGATAAGGAAGC	I. 95°C-2:00 II. *by 33 cycles* 94°C-0:45 57°C-0:30 72°C-0:45 III. 72°C-10:00	*Hinf*I	Mercadé *et al*. [2005]
AGL	5'F: GCTGGGGAAGGGATACTTTTA 5'R: CATCCCGACAATTGTATCTGG	I. 95°C-2:00 II. *by 37 cycles* 94°C-0:45 54°C-0:40 72°C-0:45 III. 72°C-10:00	*Ava*II	Stratil *et al*. [2003]
c-myc	5'F: CCAGTGGAATCTCAAATGCAC 5: R: CATTCCTGTTGTGGCTCAGTG	I. 95°C-2:00 II. *by 35 cycles* 94°C-0:45 55°C-0:30 72°C-1:00 III. 72°C-10:00	*Eco*RV	Reiner *et al*. [1999]

Each PCR reaction was performed in a total volume 10 µl containing 5 µl of RedTaq™ ReadyMix™ PCR Reaction Mix (SIGMA), 0.2 µl of each primer (0.2 µM), 3.6 µl of water (SIGMA) and 1 µl of DNA (20 mg/µl). Thermal conditions for each analysed mutation were presented in Table 1. For RFLP analysis, 5 µl of the PCR reaction mixture was added to 5 µl of a reaction mix containing 5U of restriction endonuclease. Digestion was carried out overnight at 37°C and then DNA fragments were analysed in a 2% agarose gel (0.6 g. agarose Sigma Aldrich, Steinheim, Germany) with ethidium bromide in 1x TBE at a constant current of 50 mA. The appropriate restriction endonucleases for each gene were presented in Table 1.

Statistical analysis

Association analysis were performed for each breed and each gene separately using the least squares method of the GLM procedure [SAS Institute Inc. 2001] according to the following model:

$$Y_{ijkl} = \mu + G_i + \mathrm{RYR1}_j + O_k + \beta(x_{ijkl} - x) + e_{ijkl}$$

where:

Y_{ijkl} – trait measured on *ijkl*-th animal;

μ – overall mean;

$G_{i\text{-th}}$ – effect of genotype;

$RYR1_{j\text{-th}}$ – fixed effect of *RYR1* genotype;

$O_{k\text{-th}}$ – sire effect;

$\beta(x_{ijkl\text{-th}} - x)$ – linear regression for weight of right carcass side (for carcass traits) and age at slaughter (for growth rate traits);

e_{ijkl} – random error.

The model included the effect of the genotype of each gene (*DGAT1*, *AGL* and *c-myc*), a fixed effect of the *RYR1* genotype and the effect of the sire. Age at slaughter and weight of right carcass side were included as covariates.

Results and discussion

Polymorphism in the *DGAT1*, *AGL*, and *c-myc* genes

We investigated point mutations (single nucleotide polymorphism – SNP) in each of the tested group of pigs in the *DGAT1, AGL* and *c-myc* genes. All three possible genotypes were observed at each studied group of pigs. The frequency of genotypes and alleles at the *DGAT*1/*Hinf*I, *AGL*/*Ava*II and *c-myc*/*Eco*RV loci as well as *RYR1* genotypes in PLW, PL breeds, line L990 and cross-breed (PLW x PL) is shown in Table 2.

The frequency of *GG* homozygotes in all tested breeds of pigs at the locus *DGAT1*/*Hinf*I was higher when compared to both other genotypes (from 55 in L990 to 72% in PLW). In turn, the frequency of *AA* homozygotes at this locus was the lowest (from about 7% in Polish Large White to about 20% in cross-breed PLW x PL).

Table 2. Frequency of genotypes and alleles at loci *DGAT1/Hinf*I, *AGL/Ava*II, *c-myc/Eco*RV and *RYR1/HinP1*I in studied animals

Breed/Line	Gene/mutation	Genotype frequency			Allele frequency	
	DGAT1/HinfI	*GG*	*GA*	*AA*	*G*	*A*
PLW		0.719	0.211	0.070	0.824	0.176
PL		0.611	0.296	0.093	0.759	0.241
L990		0.560	0.250	0.190	0.685	0.315
PLW x PL		0.567	0.222	0.211	0.678	0.322
	AGL/AvaII	*AA*	*AB*	*BB*	*A*	*B*
PLW		0.351	0.492	0.157	0.597	0.403
PL		0.347	0.482	0.171	0.588	0.412
L990		0.357	0.435	0.208	0.574	0.426
PLW x PL		0.300	0.456	0.244	0.528	0.472
	c-myc/EcoRV	*AA*	*AB*	*BB*	*A*	*B*
PLW		0.762	0.195	0.043	0.859	0.141
PL		0.709	0.245	0.046	0.831	0.169
L990		0.704	0.259	0.037	0.833	0.167
PLW x PL		0.756	0.189	0.055	0.850	0.150
	RYR1/HinP1I	*CC*	*CT*	*TT*	*C*	*T*
PLW		0.913	0.076	0.011	0.951	0.049
PL		0.732	0.259	0.009	0.861	0.139
L990		0.310	0.611	0.079	0.616	0.384
PLW x PL		0.967	0.033	0.000	0.983	0.017

PLW – Polish Large White; PL – Polish Landrace; L990 – Line 990; PLW x PL - Polish Large White x Polish Landrace.

The similar distribution of genotypes was observed at the locus *c-myc*/*Eco*RV. On all tested breeds more than 70% animals were *AA* homozygotes, and only less than 6% animals were *BB* homozygotes (Tab. 2). The frequency of *AB* heterozygotes was about 20-26% in each of groups.

With regard to *AGL*/*Ava*II locus our analysis revealed the similar distribution of selfsame genotype in each group of pigs. For example, the frequency of *AA* genotype comprised between 30% in cross-breed (PLW x PL) to about 35-36% in PLW and Line L990. The highest frequency was reported for *AB* heterozygotes (between 43.7 to about 49%), and the lowest for *BB* homozygotes (16 to 24%) – Table 2.

We have also tested the frequency of *C*1843*T* transition of the *RYR1* gene. In both breeds studied (PLW and PL) very low frequency of *TT* homozygotes was observed (about 1.0 and 0.9% respectively – Table 2). Approximately 8% of pigs demonstrated the *TT* genotype in L990 line. The cross-breed Polish Large White x Polish Landrace animals was free of $RYR1^T$ allele. 97% of tested animals were *CC* homozygote. Only about 3% of animals were *CT* heterozygote (Tab. 2).

The relationship between the *DGAT1*, *AGL* and *c-myc* genotypes and carcass traits

In our studies were found the significant relations between the *DGAT1*, *AGL* and *c-myc* genotypes and several production traits. These results are presented in Tables 3 and 4. The transition *G*→*A* in exon 9 of *DGAT1* gene appeared to be significant only for weight of sirloin in Polish Landrace. *GA* heterozygotes showed a significantly greatest weight of sirloin (Tab. 3). The differences between heterozygotes and *AA* homozygotes ammounted 0.3 kg.

A several significant relations were found between analysed mutation in *AGL* gene and values of some carcass traits in tested animals. This polymorphism affected on weight of loin, height of loin eye and weight of final body in Polish Landrace. The *BB* homozygotes showed higher value for two traits of loin: weight of loin and height of loin eye than *AA* homozygotes and *AB* heterozygotes. Homozygotes for the *A* allele presented less profitable value of two traits of the loin: (weight of loin and height of loin eye) than heterozygotes and *BB* homozygotes. In turn, *AB* heterozygotes showed higher weight of final body than *AA* and *BB* homozygotes (by 0.11g and about 0.4 g respectively). In Polish Large White, the *AGL*/*Ava*II genotype appeared to be significantly associated with weight of final body and width of loin eye (Tab. 3). The *BB* homozygotes showed a significantly higher weight of final body than *AA* homozygotes and heterozygotes. In Polish Landrace pigs was observed the reverse tendency with regard to this trait: *BB* homozygotes showed the lowest weight of final body. In regard to width of loin eye the most profitable value was observed for *AB* heterozygotes. This difference ammounted to 0.05 cm and about 0.3 cm compared to *AA* and *BB* homozygotes, respectively.

A significant relations were also observed in gilts between production traits and the genotype at the *c-myc* locus (Tab. 3 and 4). In L990 this mutation to be significant for width of loin eye and loin eye area. With reference to both traits *TT* homozygotes showed a significantly higher value than *CC* homozygotes and heterozygotes. The

Table 3. Relations between the porcine genotypes *DGAT1*\/*Hin*fI and *AGL*/*Ava*II and carcass traits of Polish Large White and Polish Landrace pigs (least square means ±standard error – LSM±SE)

Gene	Genotype	Breed							
		Polish Large White			Polish Landrace				
		WFB (kg)	LW (cm)	WFB (kg)	WL (kg)	LH (cm)	WSL (kg)	MCC (%)	MCVC (%)
AGL	*AA*	102.6^{Aa}±0.18	10.39^{a}±0.16	102.4^{A}±0.19	6.60^{A}±0.14	7.23^{a}±0.15	ns	ns	ns
	AB	102.84^{B}±0.17	10.44^{A}±0.16	102.51^{A}±0.17	6.82^{B}±0.13	7.41^{b}±0.14	ns	ns	ns
	BB	102.87^{b}±0.17	10.12^{Bb}±0.16	102.13^{Aa}±0.21	6.91^{B}±0.16	7.43±0.17	ns	ns	ns
DGAT1	*GG*	ns	ns	ns	ns	ns	0.36±0014	ns	
	GA	ns	ns	ns	ns	ns	0.38^{A}±0.016	ns	
	AA	ns	ns	ns	ns	ns	0.35^{B}±0.017	ns	
c-myc	*AA*	ns	ns	ns	ns	ns	ns	945.83^{A}±26.77	
	AB	ns	ns	ns	ns	ns	ns	990.33^{B}±29.11	
	BB	ns	ns	ns	ns	ns	ns	954.05±43.32	

$^{aA...}$Within columns, means followed by different letters differ significantly at: small letters – P≤0.05; capitals – P≤0.01; ns-no significantly.
WFB – weight of final body; LW –width of loin eye; WL – weight of loin; LH – height of loin eye; WSL – weight of sirloin; ADG – average daily gain.

Table 4. Relations between the porcine genotypes *c-myc*/*Eco*RV and *RYR1*/*HinP1*I and carcass traits of line L990 pigs (least square means±standard error – LSM±SE)

Gene	Genotype	LW (cm)	LA (cm^2)	WSL (kg)	WH (kg)	MCC (%)	MCVC (%)
c-myc	*AA*	10.008^{A}±0.08	54.29^{A}±0.77	ns	ns	ns	ns
	AB	10.082^{A}±0.09	54.43^{A}±0.92	ns	ns	ns	ns
	BB	10.65^{B}±0.22	60.72^{B}±2.14	ns	ns	ns	ns
RYR1	*CC*	ns	ns	0.33^{a}±0.01	8.44^{A}±0.1	57.1^{A}±0.4	64.9^{A}±0.4
	CT	ns	ns	0.33^{a}±0.001	8.54^{A}±0.01	57.7^{A}±0.3	65.4^{A}±0.3
	TT	ns	ns	0.36^{b}±0.01	9.06^{B}±0.01	60.3^{B}±0.8	68.0^{B}±0.8

$^{aA...}$Within columns, means followed by different letters differ significantly at: small letters – P≤0.05; capitals – P≤0.01; ns-no significantly.
LW – width of loin eye; LA – loin eye area; WSL – weight of sirloin; WH – weight of ham; MCC – meat content of carcass; MCVC – meat content of valuable cuts.

lowest value of these two traits of loin showed the *CC* homozygotes (Tab. 4). In Polish Landrace, the *c-myc*/*Eco*RV genotype appeared to be significantly associated with average daily gain. The *CT* heterozygotes showed higher average daily gain than *CC* and *TT* homozygotes (by 45 and 36 g, respectively).

The effect of *RYR1* genotype on productive traits was included into the statistical model in the present study. Although, this effect appeared to be negligible in PLW and

PL gilts. The association between the *RYR1* genotype and the value of one carcass trait analysed was found to be significant in L990 line (weight of sirloin).

The *DGAT*1, *AGL* and *c-myc* genes belong to the groups located on porcine chromosome 4. From twenty or more years this is very important region of porcine genome which harbours many quantitative trait loci (QTL) affecting growth, meat quality, fatness and carcass composition [Čepica *et al*. 2003].

One of the aims of our study was to determine the presence of the polymorphisms in regard analysed SNPs located in the *DGAT1*, *AGL* and *c-myc* genes. Our analysis included two breeds, synthetic line and one cross-breed reared in Poland. In regard to *DGAT1*/*Hinf*I locus were reported the higher frequency of *GG* homozygote than *AA* homozygote and heterozygotes. The similar results showed the studies conducted by Spanish researchers [Mercadé *et al*. 2005]. They analysed this polymorphism on five European breeds: Iberian, Landrace, Large White, Meishan and Piétrain, and they did not reveal polymorphism in Iberian and Landrace pigs. All animals from of these both groups were *GG* homozygotes. Whereas reported this locus as polymorphic in remaining three breeds: Large White, Meishan, Pietrain. In each of three group the frequency of "*G*" allele was much higher than "*A*" allele (from 65 to 95%) [Mercadé *et al*. 2005]. On the other hand we must remember that Spanish analyses were conducted on small group in compare to our studies. The studies of Weisz *et al*. [2011] were showed the opposite results. Czech researchers analysed the *DGAT1*/*Hinf*I polymorphism on population of 101 pigs of Czech Large White sows. They reported the highest frequency of *GA* heterozygotes (47.5%, 48 animals). The frequency of *AA* homozygotes (42.5%), were similar to frequency of heterozygotes, and the lowest frequency were characteristic for *GG* homozygotes (9.9%) [Weisz *et al*. 2011]. The similar tendency in the frequency of genotypes at this locus was observed by other Czech team from Mendel University in Brno. Their observations comprised of 100 pigs in Black Pied Přeštice sows. Also this breed had the lowest frequency of homozygotes of *G* allele – only 1%. The frequency of opposite *AA* homozygotes was the highest – 74%, and *GA* heterozygotes was 25% [Civáňová *et al*. 2007].

In porcine *AGL* gene we reported the similar frequency of each genotypes of each groups. On the contrary, Stratil with co-workers reported the different frequency of individual breeds. They analysed the pigs from 8 of different European breeds (Large White, Landrace, Pietrain, Black Pied Prestice, Czech Meat Pig, Hamsphire, Duroc and Meishan). The frequency of "*A*" allele ranged from 0.32% (in Large White) to 83% (in Meishan). In turn, the frequency of "*B*" allele was the lowest in Meishan pigs (only 17%), and the higher in Large White pigs (68%). But the studies of Czech researchers were conducted on very small number of animals, therefore we can considered these results as preliminary [Stratil *et al*. 2003].

Locus *c-myc*/*Eco*RV characterized the highest frequency of *AA* homozygote compared to other two genotypes (*AB* and *BB*). The lowest frequency we reported for *BB* homozygote – only 8-10 animals in each of tested groups. In the other laboratories, the similar results were not conducted.

The second aim of our study was analysis the association between the polymorphism and growth rate and carcass traits in pigs. The significant relations were found between the genotypes *DGAT1*, *AGL* and *c-myc* loci and several carcass traits. We observed that the *DGAT1*/*Hinf*I genotype affected only the weight of sirloin in Polish Landrace pigs. Weisz *et al*. [2011] studied a total of 101 Czech Large White sows, and they reported that this mutation affected only lean meat content. The highest value of this trait was characteristic for heterozygotes. No significant associations found between *locus DGAT1*/*Hinf*I and other analysed traits such as: backfat thickness, average daily gain from birth, daily gain in test, breeding value for average daily gain and breeding value for lean meat content.

In other studies, Civáňová *et al*. [2007] did not find out any significant differences among animals of the examined population in regard to this polymorphism. One of the cause is probably the low frequency of homozygous *GG* genotype in the Black Pied Přeštice breed (only 1 animal was *GG* homozygote).

Two years ago Zhao with your co-workers observed the effect of functional SNP *C*379*T* on level of expression *DGAT1* and consequently affect IMF deposition in pork. Intramuscular fat (IMF) is one of the most important indexes of pork taste quality. In their study the IMF content of *CT* genotype individuals was higher than that of *CC* genotype. The *DGAT1* expression levels revealed a significant positive correlation with IMF content. The results may suggest that this polymorphism provides a promising selection marker for improving pork IMG content while not increasing fat deposition in other tissues [Zhao *et al*. 2023].

The present study demonstrated a significant relationship between several carcass traits and the genotype *AGL*/*Ava*II locus in breeds tested (PLW and PL). Table 3 list all significant associations between the *AGL* genotype and carcass traits. A few years ago the researchers from Korea reported the association between SINE indel polymorphism of *AGL* gene with growth and carcass traits. Their studies were conducted in Landrace x Jeju black pigs F_2 population. Three genotypes representing this polymorphism were present among this group of animals. A significant relations was found between the genotype *AGL* locus and several carcass and growth traits such as: weight at birth, 3rd week and 10th week, average daily gain in early duration (from 3 to 10 weeks) and average daily gain in late duration (from 10 to 20 weeks) and backfat thickness [Sang *et al*. 2010]. Also, the studies associations between *AGL*/*Ava*II locus and productive traits have not been reported in the literature.

In present study, we also reported associations between *c-myc*/*EcoR*V locus and carcass and growth traits. Because is the first report of this type published in the literature, the comparison of our results to other results is impossible.

Our previous studies as well as those carried out by other authors showed that the *RYR1* genotype significantly affected carcass traits and could modify the effect of other genes [Rybarczyk *et al*. 2010]. Therefore, in the present study the effect of the *RYR1* genotype was included into the statistical model applied. Although, the effect of

this genotype on productive traits was not significant in PLW and PL. This genotype showed association with one trait (weight of sirloin) in L990 line (Tab. 4).

In the present study, heterozygotes in terms of a mutation of the all studied loci demonstrated the highest value for four interesting traits: (width of loin eye, weight of final body, weight of sirloin and average daily gain) when compared with both homozygous genotypes. In the first time this phenomenon has been observed for certain human genes and is termed negative – or positive heterosis [Comings and MacMurray 2000]. These authors suggested that if the regulation of the gene is dose dependent, the presence of a regulatory sequence in a heterozygous state could modify the gene function. We have made similar observations in our earlier studies [Urbański *et al*. 2013, 2015]. Also in later, the negative -or-positive heterosis widely described in later reports on other animal species and on human genetics [van Huelten *et al*. 2018, Mai *et al*. 2021, Akoth *et al*. 2023, Cedano-Castro *et al*. 2023, Khattab *et al*. 2025].

The biological activity of these analysed genes is one of the reasons that these genes are important in breeding of pigs. *DGAT1* plays very important role in the metabolism of lipids. The product of *AGL* gene is enzyme involved in glycogen degradation. With glycogen metabolism is associated meat quality and productivity, and the level of glycogen is one of the most important determinants of meat quality. It is very important because pork is the most preferred type of meat in Poland and annually consumption is about 40 kg of pork *per capita*, which constitutes about 60% of the total meat consumption. Because of the centuries-old culinary traditions and culture of our region, it is almost certain that pork will remain an important part of our daily diet for many years to come. The third of analysed by our team gene is protooncogen *c-myc*. The protooncogenes plays very important role in other biological processes, for example proliferation, differentiation and apoptosis. So far, have been identified about 100 protooncogenes in eukaryotic organisms. The product of *c-myc* gene is a phosphoprotein which plays an important role in myogenesis, among others, which can shape the expression of *MyoD* family genes [Maltin *et al*. 2001]. The genes of *MyoD* family are at the center of interest of researchers as potential candidate genes associated with meat and carcass quality. Also, this family genes has been analysed by our team [Urbański *et al*. 2006, Wyszyńska-Koko *et al*. 2006, Pierzchała *et al*. 2011].

The localization of *DGAT1*, *AGL* and *c-myc* genes is the second of the main reasons why these genes can affect both tenderness and carcass traits. These porcine genes have been mapped on chromosome 4. It was the first porcine chromosome where have been mapped QTL for carcass traits. First QTLs on chromosome 4 were located in 1994 by the researchers from the University of Agriculture in Uppsala [Andersson *et al*. 1994]. In recent years quite a few studies characterizing the QTL located on pig chromosome 4 were published. They involved also such traits as growth rate, meat and carcass quality [Čepica *et al*. 2003, Geldermann *et al*, 2003, Sławińska *et al*. 2009, Silva *et al*. 2011]. Subsequently, QTLs on SSC4 have been described for reproduction traits: ovulation rate [Rathje *et al*. 1997], number of stillborn piglets [Knott *et al*. 2002].

Also other important genes have been mapped on this porcine chromosome. The example of such genes are genes belonging to the FABP family: the *FABP4* (also known as *A-FABP* gene) and *FABP5*. Both of them are located on chromosome 4, near the QTLs responsible, the content of intramuscular fat [Chmurzyńska *et al*. 2006]. This trait is one of the issues that has been of interest to geneticists for years, because is strongly associated with other sensory properties of meat, such as tenderness, juiciness and flavor. The optimum content of intramuscular fat ranges between 2-3% [Nechtelberger *et al*. 2001]. Attempts to reduce the intramuscular fat content to the level ranging between 0.5-1.5% a trend that has been observed in recent years, and especially in developed countries, affect the quality of pork in negative way. After thermal treatment, meat is dry and leathery.

Ballester *et al*. [2016] analysed other porcine gene located on chromosome 4. APOA2 is a important protein implicated in triglyceride, fatty acid and glucose metabolism, located on SSC4 in a QTL region affecting fatty acid composition, fatness and growth traits. They results suggests that complex regulatory mechanisms, beyond a single polymorphism may be regulating *APOA2* gene expression [Ballester *et al*. 2016]. In last years the "nutrigenomics effect" of fatty acid as a dietary components affecting on animal and human health was studied by researchers from Institute of Genetics and Animal Biotechnology [Szostak *et al*. 2016, Ogłuszka *et al*. 2017, Liput *et al*. 2021,Yeung *et al*. 2025].

Also in last years, the porcine chromosome 4 in the center of interest of the researchers. The team of Xu from China identified 23 siginificant SNPs for four related to growth and fatness in Chinese Sujiang pigs. Six genes were identified as candidate genes for backfat thickness [Xu *et al*. 2020].

The meat and carcass traits (for example such as: carcass backfat thickness, carcass lean percentage and carcass fat percentage) are important to the commercial pig industry. Therefore these traits, also at the present times are at the area of interesting more laboratories. Not only chromosome 4, also other porcine chromosomes, are all the time analyzed from this angle [Wang *et al*. 2022, 2024, Xu *et al*. 2022, Qiu *et al*. 2023, Zhenyu *et al*. 2025].

In our opinion, these analysed polymorphisms *DGAT1*/*Hinf*I, *AGL*/*Ava*II and *c-myc*/*EcoR*V may have a practical application in pig breeding, but studies must be continue. Traditional methods of selection were based only on the data and the results of usability pedigree. The assessment of the value of animal breeding was very cost prohibitive and time consuming. Therefore, traditional methods have been replaced by genomic studies. In recent years, the sequencing of DNA has allowed the identification of a very large number of SNPs. The assessment of the value of animal breeding by SNPs is quicker and more exact than by traditional methods.

In summary, the results of the current study demonstrated that the polymorphisms of the porcine *DGAT1*, *AGL* and *c-myc* genes could be important in terms of certain carcass quality traits in the pig breeds studied.

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