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ASSOCIATION OF SINGLE NUCLEOTIDE POLYMORPHISMS IN CANDIDATE GENES WITH ECONOMICALLY USEFUL TRAITS IN CHICKENS (*Gallus gallus domesticus* L.)

(review)

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Abstract

Economically useful traits of chickens associated with productivity are inherited polygenically. With the discovery of numerous DNA regions characterized by single nucleotide polymorphism (SNP) and the development of modern genomic technologies, a detailed assessment of the results of breeding in poultry farming has become possible to successfully predict the effect of breeding (L. Wang et al., 2011; C.M. Seabury et al., 2017). This review summarizes data on genes and SNP markers used in domestic chicken breeding and describes new polymorphic allelic variants in genes that are associated with integrated productivity indicators in chickens from the world gene pool. In Russia, domestic meat, egg and dual-purpose chicken breeds are currently subjected to thorough genotyping. Polymorphic variants of key genes *LCORL* (*ligand dependent nuclear receptor core-pressor-like*) and *NCAPG* (*non-SMC condensin I complex, subunit G*) that affect egg-laying performance has been found. Differences in SNP between egg and meat and egg and decorative chickens were revealed (T.A. Larkina et al., 2021). For the *NCAPG* gene, a significant association of rs14991030 alleles with shell weight, percentage of shell weight to egg weight, and shell thickness was identified (O.Yu. Barkova et al., 2016). In Russian White chickens, single nucleotide polymorphisms of the dysferlin gene (*DYSF*) were identified and their association with economically valuable traits was studied (O.Yu. Barkova et al., 2021). For safe breeding and selection of chicken populations and breeds, it important to prevent the spreading of genetic diseases and to ensure the maintenance of heterozygosity of the domestic gene pool. In the Smena 8 broiler meat cross line B5, typing SNPs in the *DMA*, *RACK1*, and *CD1B* genes responsible for a higher IgY titer revealed the fixation of an allele of a lower IgY titer at the Gga_rs15788237 locus and the predominance of an unfavorable allele at the Gga_rs15788101 locus and a favorable allele at the Gga17_rs160 locus. Changes in the Gga_rs16057130 and Gga_rs15788101 loci in the B5 broiler line bred at Smena State Breeding Center (Moscow Province) are most likely associated with selection for productivity traits (A.M. Borodin et al., 2020). Poultry genome studies are currently focused on analyzing large datasets across several generations to find associations (GWAS, genome-wide association studies) between SNPs and economically important traits such as growth rate, egg quantity and quality, meat and fat deposition. (A. Wolc, 2014; S.K. Zhu et al., 2014; J.H. Ouyang et al., 2008). Genome-wide genotyping using a high-density SNP array revealed candidate genes *GRB14* and *GALNT1* whose single nucleotide polymorphisms had statistically significant associations with egg production and egg quality parameters, including egg weight, eggshell weight, yolk weight, eggshell thickness and strength, albumen height and Haugh value for hens aged 40-60 weeks (W. Liu et al., 2011). GWAS analysis identified candidate genes *ZAR1*, *STARD13*, *ACER1b*, *ACSBG2*, and *DHRS12* which were associated with the weight of yolk, follicles, and ovaries of hens from the beginning of oviposition to 72 weeks of age. As estimated by SNP analysis, the heritability was moderate for yolk weight (h^2 of 0.25-0.38) and relatively low for follicle weight ($h^2 = 0.16$) and ovary weight ($h^2 = 0.20$) (C. Sun et al., 2015). Two genes, *MSX2* and *DRD1* are associated with embryonic

and ovarian development and contain significant SNPs associated with egg quality, i,e,, height of albumen and Haugh value. Three genes, the *RHOA*, *SDF4*, and *TNFRSF4* have been identified as candidate genes for eggshell coloration (Z. Liu et al., 2018). It has been reported (S.A. Azmal et al., 2019) that in the Chinese chicken breed Jing Hong, SNPs in the *RAPGEF6* gene are associated with the egg laying rate during late oviposition. Several studies support the notion of dopamine involvement in the regulation of egg production in birds. Four SNPs (G+123A, T+198C, G+1065A, C+1107T) in dopamine receptor gene (*DRD1*) were found which significantly affect the age of the first oviposition (it characterizes the rate of puberty of hens), the weight of the first egg and the yield of standard eggs (H. Xu et al., 2010). The *VIP* (receptor for vasoactive intestinal peptide-1) gene polymorphisms are associated with brooding instinct and egg production rate (M. Zhou et al., 2010). X. Li et al., (2019) found five polymorphisms in the promoter region of the *FSHR* (follicle-stimulating hormone receptor) gene and determined their association with the total egg production for 43 weeks of life and with the age of laying the first egg. H. Zhou et al. (2005) found significant associations of single nucleotide polymorphism in the *IGF1* (insulin-like growth factor 1) gene promoter with growth rate, body composition, skeletal condition and physiological parameters of chickens. Meat quality is due to a complex of quantitative traits and is controlled by multiple genes such as *FABP* (fatty acid binding protein) (K.H. Cho et al., 2011), *CAPN1* (micromolar calcium activated neutral protease gene) (J.T. Shu et al., 2015), *PRKAG3* (*protein kinase AMP-activated non-catalytic subunit gamma 3*) (Y. Yang et al., 2016). The identified statistically significant associations of single nucleotide polymorphisms with economically important traits can be used in poultry breeding and selection programs.

Keywords: gene, SNP, single nucleotide polymorphism, allele, chickens, meat productivity, egg productivity, full genome associations, GWAS

Over the past two decades, knowledge about the genomes of farm poultry of different breeds and species has deepened significantly. The development of molecular genetics methods has made it possible to study both genes and entire genomes. The genomes of *Gallus gallus* L., *Taeniopygia guttata* (Vieillot, 1817), *Meleagris gallopavo* L., and another 45 bird species have been sequenced [1]. The principles of using molecular genetic markers to improve the accuracy of predicting the breeding value of an animal have been proposed and largely implemented. Computer technologies have created the prerequisites for the rapid development of complex systems for such forecasting [2, 3]. Significant success in predicting breeding value is associated with DNA marking based on genome-wide genotyping of candidate animals for several thousand single nucleotide polymorphisms (SNP, single nucleotide polymorphism) and analysis of their association with breeding qualities [4].

Single nucleotide polymorphisms (SNPs) are the most common markers of genetic variation (there is approximately one SNP for every 200 nucleotides), followed by short (≤ 100 nucleotides) insertions and deletions (InDels, insertions and deletions). Approximately 20 million SNPs have been identified in chickens. Not only the presence, but also the characteristics of these polymorphisms are important for association with physiological processes in the body.

Single nucleotide polymorphisms cause changes in gene expression, which directly affects the formation of certain traits. With the discovery of numerous DNA sites characterized by single nucleotide polymorphism and the advent of SNP chip technology, it has become possible to evaluate the results of selection in detail at the genomic level for subsequent successful prediction of the selection effect in poultry farming [5, 6].

The purpose of this review is to summarize data on genetic variants of candidate genes and associations of single nucleotide polymorphisms with economically significant traits in chickens, to discuss the practical use of SNPs as an additional criterion in assessing reproductive characteristics and predicting egg productivity in the early stages of puberty of industrial and local breeds of chickens. The search for scientific sources was carried out mainly in the databases eLIBRARY.RU (https://www.elibrary.ru/defaultx.asp) and PubMed® (NCBI, The National Center for Biotechnology Information, https://pubmed.ncbi.nlm. nih.gov/), as well as using lists of citations in the retrieved publications.

Economically useful traits of chickens associated with productivity are

characterized by polygenic inheritance. Preventing the spread of genetic diseases in the domestic poultry gene pool and maintaining the required level of heterozygosity are factors that ensure the safety of Russian populations and breeds during breeding work and in practical poultry farming.

Currently, domestic scientists are actively conducting research on genotyping chicken breeds for meat [7-9], meat-egg [10, 11] and egg [12, 13] productivity areas.

Egg production is an important economic characteristic of poultry and a current subject of breeding and molecular genetic research. Egg production and the quality of hatching eggs are traits that exhibit a polygenic mode of inheritance. Key genes and functional SNPs affecting egg production rates have been studied [14, 15]. On the chicken chromosome GGA4, a region including the *LCORL* (*ligand dependent nuclear receptor corepressor-like*) and *NCAPG* (*non-SMC condensin I complex*, *subunit G*) genes is associated with growth traits. In an area close to this region, single nucleotide polymorphism sites associated with egg production traits have been identified. When studying the genetic variability of the *NCAPG-LCORL* locus in chickens of 49 gene pool breeds and hybrid forms from the Common Use Center Genetic Collection of Rare and Endangered Breeds of Chickens (VNIIGRZh, St. Petersburg; http://www.biores.cytogen.ru/rrifagb_anm) using SNP analysis identified five statistically significant SNPs: GGaluGA265966, GGaluGA265969, rs15619223, rs14491017 and rs14491028 [10]. The resulting characteristics of genetic variations and the genetic structure of populations based on SNPs of key genes for chicken productivity make it possible to determine the characteristics of local populations and can be used in breeding. Among chickens of different productivity directions, the authors identified differences in SNPs located in the locus that covers the NCAPG-LCORL genes. Egg-laying chickens differed significantly from chickens of other productivity types. Thus, significant differences between the egg-meat and egg-decorative groups were identified in the substitution GGaluGA265969. Presumably, putative association of this SNP with chicken body weight may explain such differences [10].

A series of works is devoted to identifying SNP markers for quantitative traits of egg quality and studying the relationship between alleles of markers and traits of laying hen eggs. Associations of the SNP marker rs14991030 in the condensin gene *NCAPG* were studied (the *NCAPG* gene encodes the non-SMC condensing I complex subunit G) with egg production traits in chickens [13, 16]. A significant relationship was found between the rs14991030 allele of the *NCAPG* gene and the shell weight, the percentage of egg to shell weight, and the shell thickness. The studies were carried out on chickens of two lines of the Russian cross UK Kuban 7 with a brown shell, derived from the gene pool of the Rhode Island breed. Also the experiments involved a two-line CD hybrid of the parent form of the Lohmann Brown cross. Analysis of variance based on the SNP marker rs14991030 data (the line UK 72) revealed significant differences between genotypes AG, AA and GG for the shell weight and shell percentage (i.e., the average proportion of shell weight to the weight of the entire egg). In the CD cross, of all the traits, only the eggshell thickness had a significant difference. A significant effect of the rs14991030 polymorphism was described for traits that differed significantly between three genotypes of the UK 72 line. When replacing the G allele with the A allele, an effect was noted in shell weight and shell percentage. In the CD cross, the replacement of the G allele with the A allele led to a change in shell thickness. Chickens with the GG genotype had thicker shells, indicating the additivity of allele replacement. The presence of the A allele was manifested by an increase in shell weight, shell thickness, and shell percentage (as a percentage) of egg weight [13]. Analysis of the expression of a region of chromosome 4 in the immediate environment

of the microsatellite MCW0114 in the tissues of the chicken oviduct (transcript CR523443, the ChEST985k21clone, was detected for this region) made it possible to determine the relationship with shell thickness. Six SNPs were found in the immediate vicinity of the CR523443 sequence, three of which were associated with eggshell thickness. A genetic analysis of the association of single nucleotide substitutions with other economically useful egg traits was carried out [12]. A significant relationship between SNP2_1 alleles and eggshell thickness in chickens of the UK 72 line was established. The statistical significance of the effect of C/T substitution in SNP2_1 was assessed. For this trait, the dominance of the T allele was revealed. Associations of SNP2_1 with shell weight, egg production, and egg weight were shown [17).

In order to identify possible associations with economically valuable characteristics, single-nucleotide polymorphisms of the dysferlin gene were studied in the Russian White chickens from the gene pool population of the Genetic Collection of Rare and Endangered Chicken Breeds (All-Russian Research Institute of Genetics and Breeding of Farm Animals, St. Petersburg-Pushkin) [18]. Genotyping 185 chickens using the Illumina Chicken 60K SNP iSelect BeadChip technology (Illumina, USA) identified the single nucleotide polymorphism rs16455118 for the first time. Four single-nucleotide substitutions found were located in the intron 32 on the chromosome 4. These were rs317801013 (G/A) at position 90672849, rs16455118 (C/A) at position 90672756, rs318045896 (A/G) at position 90672862 and a mononucleotide polymorphism (T/G) at position 90672805. The T/G mononucleotide polymorphism on chromosome 4 at position 90672805 was submitted for registration to the ENSEMBL database (https://www.ensembl.org). The results obtained may be useful for creating a system of molecular genetic markers [18].

The results obtained in studying the diversity of four original lines (B5, B6, B7, B9) of the Smena 8 broiler meat cross allowed us to conclude that they are highly genetically conservative [7].

A quantitative real-time PCR-based test and an algorithm have been developed for identifying the homo- and heterozygous state of the *K* and *k* alleles in 1-day-old chicks. The *K* and *k* alleles are sex-linked and responsible for the growth rate of wing feathers. Using this test, the percentage of genotypes *KK*, *Kk* and *kk* was determined among 145 roosters of the original lines B5, B6, B7 and B9 of the domestic meat cross Smena 8. Further breeding work involves traditional and molecular genetic assessment of the birds in order to exclude roosters of the line B7 with genotypes *KK* and *Kk*, roosters of the line B9 with genotypes *Kk* and *kk* and their descendants as not corresponding to the target breeding parameters [8]. A single nucleotide substitution rs317093289 of the gene *FSHR* (*follicle stimulating hormone receptor*) was analyzed in the original line CM9 of the Smena 9 cross. Among the studied chickens of this line, the TA genotype was most frequent (42%), the TT genotype had a frequency of 24%, the AA genotype 34 %. At 210 days of age, the bird with the TA genotype exceeded the bird with the AA genotype by 2.4% in egg weight, the group with the TT genotype was close to the TA group (the differences between the TT and TA groups are not significant). The studied SNP had a significant effect on egg production. The TA genotype exceeded the TT genotype in the number of eggs laid for 210 and 308 days by 15.0 and 2.8%, respectively [9].

It is known that selection of animals for high productivity leads to a weakening of their immunity, fertility, and a decrease in the ability to withstand stress [19, 20]. These negative effects may result from either pleiotropy of genes during breeding for increased productivity, or a combination of unfavorable alleles with alleles subject to selection, or genetic drift. Understanding the nature of the adaptive mechanisms acting on the chicken genome provides insight into the complex relationship, while simultaneously opening up new directions for improving

this commercial species, which is so important for food security [21]. Until recently, poultry selection and breeding methods were aimed at improving production and reproductive traits without taking into account health-related traits due to the lack of appropriate genetic markers that could be integrated into breeding programs. New opportunities have arisen due to significant advances in genomics and related technologies. Currently, the research strategy is aimed at identifying genes, gene structures and regulatory regions that can be used in breeding. In addition, there is growing interest in deciphering the genetic parameters underlying the immune response. More and more data is accumulating on the negative impact of selection for economic traits on the immune system of chickens due to a decrease in the variability of genes encoding elements of the immune system [22, 23]. SNP typing of three genes was carried out, the *DMA* (*major histocompatibility complex, class II, DM alpha*), *RACK1* (*receptor for activated C kinase 1*) and *CD1B* (*CD1b molecule*) responsible for an increased IgY titer in line B5 of broiler meat cross Smena 8. All three SNPs are localized within the corresponding genes. Fixation of the allele that determines a lower IgY titer was detected in the Gga_rs15788237 locus, the unfavorable SNP allele in the Gga_rs15788101 locus, and the predominance of the favorable SNP allele in the Gga_rs16057130 locus. Changes in the Gga_rs16057130 and Gga_rs15788101 loci in chickens of the meat cross Smena B5 line are most likely associated with the selection for productivity traits, which in the future can lead to the fixation of alleles in these loci. Studying the negative impact of selection for economic traits on immunity should help reduce negative consequences and find ways to obtain disease-resistant animals [22].

Technical advances in genotyping (GWAS, genome-wide association studies) allow researchers to analyze large amounts of information obtained over a number of generations in order to search for associations between SNPs and economically significant traits in birds, such as growth rate, quantitative and qualitative indicators of eggs, meat and fat deposition [24-26]. The accuracy of genotyping depends, among other things, on the density of SNPs on the chips [27-30]. Despite the great interest in SNP arrays, the cost of genotyping is still too high for large-scale population studies. Genotyping coverage using the commercial Chicken 600K Affymetrix® Axiom® SNP chip varies among different chicken populations of egg-type. This chip consists of approximately 560 thousand tested SNPs for commercial lines and crosses of egg- and meat-type chickens, of which about 14 thousand SNPs are associated with economically important traits of egg-type chickens [31-33].

Z. Liu et al. [34] used the high-density Affymetrix 600 K chicken SNP chip (Affymetrix, Inc., USA) for GWAS of a population of 1078 chickens from the age of first egg laying to 80 weeks of age to identify genomic variations associated with egg mass. The results showed that a 90 kb genome region (169.42~169.51 Mb) in GGA1 is significantly associated with egg weight in 36-week-old hens and is also potentially associated with egg weight in hens at 28, 56, and 66 weeks of age. The rs13972129 locus on GGA1, most significantly associated with egg weight in hens at 36 weeks of age (EW36), was associated with 3.66% (SE = 0.04) of phenotypic variation. Two candidate genes, *DLEU7* (*deleted in lymphocytic leukemia 7*) and *MIR15A Mir-15* (*microRNA precursor family*), may map to this narrow significant region and pleiotropically influence egg mass. In addition, the *CECR2* (*Histone acetyl-lysine reader*) gene on GGA1 and two genes, *MEIS1* (*Meis homeobox 1*) and *SPRED2* (*Sprouty-related*, *EVH1 domain-containing protein 2*) on GGA3 which are involved in embryogenesis and organogenesis are also classified as candidate genes associated with first egg weight and egg weight in hens at 56 weeks of age. According to the authors, the results may provide a theoretical basis for obtaining eggs of ideal size based on selective breeding based on the studied markers [34].

A genome-wide scan with a high-density SNP chip containing 57636 markers

allowed the authors [35] to discover new loci associated with egg production and quality in White Leghorns and Brown Dwarf chickens. Eight SNPs were identified that correlated with egg production and egg quality parameters, including egg, eggshell and yolk weight, eggshell thickness and strength, albumen height and number of Haugh units determined at 40 and 60 weeks of age for laying hens. Some significant SNPs are located in known genes, including *GRB14* (*growth factor receptor bound protein 14*) and *GALNT1* (polypeptide N-acetylgalactosaminyl transferase 1), which may influence ovarian development and function, but a larger number are located in genes with unclear functions. Further study is required to confirm the functional significance of these newly identified SNPs [35].

GWAS analysis identified loci and genes associated with egg yolk, follicle and ovary weight in chicks (n = 1534) from laying onset to 72 weeks of age [36]. For all ages studied (11 age points), moderate SNP-based heritability estimates for yolk mass were shown (h^2 = 0.25-0.38), while estimates for follicle mass (h^2 = 0.16) and ovary mass (h^2 = 0.20) were relatively low. Independent univariate genome-wide screens for each character studied identified 12, 3, and 31 new significant substitutions associated with yolk, follicle, and ovary weight, respectively. The candidate genes *ZAR1* (*Zygote arrest 1*), *STARD13* (*StAR related lipid transfer domain containing 13*), *ACER1b* (*alkaline ceramidase 1*), *ACSBG2* (*acyl-CoA synthetase bubblegum family member 2*) and *DHRS12* (*dehydrogenase/reductase 12*) were identified as having a probable function in yolk and follicle development [36].

With an increase in the duration of laying period in chickens, the problem of a decrease in the quality of eggs at the end of the laying period has emerged. Thus, external characteristics consist of the color of the eggshell, the egg shape index, the thickness and strength of the eggshell, while internal characteristics include the height of the albumen, the color of the egg yolk, and Haugh units. Basically, these are all quantitative characteristics [37].

With the development of molecular genetics, many studies have been carried out to identify the genetic encoding of egg quality [38-40]. GWAS analysis discovered genomic associations with egg quality at later stages of laying, which have important theoretical and practical significance. A population of 1078 chickens aged 72 and 80 weeks was subjected to GWAS analysis with the high-density Affymetrix 600 K chicken SNP chip. The analysis showed that the genome region at positions 8.95 to 9.31 Mb (~ 0.36 Mb) on GGA13 was significantly associated with egg albumen height and Hau units, and the two most significant SNPs accounted for 3.12 5.75% of the phenotypic variance. Two important genes, *MSX2* (*msh homeobox 2*) and *DRD1* (*dopamine receptor D1*), which are associated with embryonic and ovarian development, have also been found to influence egg quality. Three genesб the *RHOA* (*ras homolog family member A*), *SDF4* (*stromal cell derived factor 4*), and *TNFRSF4* (*TNF receptor superfamily member 4*) have been identified as candidate eggshell color genes [41].

Maintaining high egg production of chickens throughout the entire laying period is of decisive importance for ensuring optimal production performance in industrial poultry farming. Extension of the laying cycle and, therefore, a decrease in egg production rates is one of the problems of modern poultry farming [37, 42, 43]. SNPs in the *RAPGEF6* (*Rap guanine nucleotide exchange factor 6*) gene associated with the intensity of egg laying in the Chinese Jing Hong chicken were studied [44]. The authors assessed the intensity of egg laying in hens of the parent flock at the age of 61-69 weeks both by phenotype and genotype, using a high-density SNP chip (600K Affymetrix Axiom HD SNP-array, Aviagen Ltd., UK). The results of GWAS analysis showed that the egg production trait is significantly associated with five SNPs (AX-75745366, AX-75745380, AX-75745340, AX-75745388 and AX-75745341) located in the *RAPGEF6* gene on chromosome 13. A total of 1676 Jing

Hong laying hens were genotyped, including 858 hens of the 1st generation and 818 hens of the 2nd generation. Three of the five polymorphisms (AX-75745366, AX-75745340 and AX-75745341), which significantly affected egg production at a later stage of laying, are proposed as molecular genetic markers in breeding chickens [44].

The study of polymorphism of prolactin genes and its dopamine receptor may be of practical importance for chicken breeding. It is known that the hormone prolactin in birds takes part in the regulation of the reproductive cycle. Thus, an increase in the blood prolactin levels leads to a decrease or cessation of egg production [45]. Dopamine actively influences the secretion of prolactin [46-48]. Five dopamine receptor subtypes have been identified and are divided into two classes called D1-like (DRD1, DRD5) and D2-like (DRD2, DRD3, DRD4). In birds, dopamine is involved in both stimulation and inhibition of prolactin secretion [49]. Activation of DRD1 stimulates prolactin secretion, and through DRD2, secretion is inhibited [50]. These and other studies confirm the regulatory role of dopamine in egg production in birds. The authors assessed the relationship of the *DRD1* gene with egg production and hatchability in 644 chickens [51]. In the *DRD1* gene, 29 single nucleotide polymorphisms were identified. Of these, 7 SNPs were selected to analyze their association with egg production traits in chickens. A significant effect was shown of four SNPs (G+123A, T+198C, G+1065A, C+1107T) on the age of laying the first egg (it characterizes the rate of sexual maturation), the weight of the first egg, and the yield of conditioned eggs [51].

Vasoactive intestinal peptide (VIP), a releasing factor of the hormone prolactin in birds, stimulates the secretion of prolactin and is involved in the regulation of the activity of the prolactin gene. Associations have been found between the polymorphism of the chicken *VIP* gene, brooding instinct and egg production [52]. Sequencing revealed 69 single nucleotide substitutions in a 9305 bp region of chicken *VIP* gene. Five polymorphisms, the C 3134T, "AGG" indel from –2648 to –2650, C+338T, G+780T and A+4691G were used to evaluate their effect on egg production and brooding traits in 644 Ningdu Sanhuang chickens. Analysis of the association of the marker showed that "AGG" indel is associated with the total number of eggs and the number of quality eggs in hens aged from 90 to 300 days. The C+338T polymorphism was found to be associated with egg hatchability [52].

Follicle stimulating hormone (FSH) and its receptor (FSHR) play an important physiological role in animal reproductive function [53, 54]. FSH is a glycoprotein synthesized and secreted by the cells of the anterior pituitary gland. When it enters the bloodstream and binds to a specific transmembrane receptor (FSHR) located on target cells, this hormone and receptor play a vital role in gonadal function and fertility [55]. The nucleotide sequence of the chicken *FSHR* gene was determined in 2005. A number of studies have been carried out on the regulation of *FSHR* transcription in mammals, but its mechanism in chicken is not fully understood [56]. Differences in the *FSHR* gene expression among different chicken breeds may lead to variations in egg production parameters, including age at first egg (AFE), total number of eggs, and egg weight. In addition, polymorphisms in the *FSHR* gene promoter may affect *FSHR* transcription and egg production. A study was conducted [57] on two breeds, a local Chinese breed Dongxiang with black plumage and skin, laying blue-shelled eggs [58] and reduced growth rate and egg production [59]; a Chinese breed Suken with yellow plumage, beak and claws [60] and laying cycle of approximately 268 days with a peak within 40 days. The PCR-RFLP method detected five nucleotide polymorphisms in the *FSHR* gene promoter, including 200 bp indel at –869, C 1684T, C 1608T, G 368A and T 238A associated with egg production traits in both the Dongxiang and Suken breeds. The age at which the first egg was laid in Suken chickens differed significantly ($p < 0.01$) depending on the genotype for indel –869. In poultry farming, the number of eggs laid

during 43 weeks of life is usually an effective indicator of overall egg production [61]. For SNP C 1684T, in Dongxiang chickens with the CC genotype, the number of eggs laid at the age of 43 weeks was greater than in individuals with the TC genotype ($p < 0.05$), while in Suken chickens, on the contrary, for the TC genotype, the AFE indicator was higher than for the CC genotype ($p < 0.05$). For AFE in Suken breed, the CC genotype for SNP C 1608T was superior to the TC genotype ($p < 0.05$), and the AG genotype for SNP G 368A was superior to the GG genotype ($p < 0.05$). In total, this study [57] identified five polymorphisms in the *FSHR* promoter region and rebealed their association with egg production at the age of 43 weeks and of the first egg laying.

Growth and reproduction, which are controlled by multiple genes, are the two most economically important traits for poultry production. The integration of emerging technologies, the identification of related genes, and the unraveling of the molecular mechanisms governing their activity provides the opportunity for more effective selection of chicks for growth rate and reproductive performance [62-64]. QTL (quantitative trait loci) associated with chick growth and reproductive performance (body weight and age at first egg laying) have been investigated in recent decades [65, 66]. The identification and use of potential candidate genes and QTLs that have significant effects on economically important traits are becoming increasingly important in poultry breeding programs [67-71].

Selection has led to increased growth rates and breast muscle yield in broilers. However, physiological disturbances arose, leading to increased fat deposition and deterioration of the bird's skeleton [72]. To simultaneously improve performance and physiological traits, molecular markers associated with one or both sets of traits may be useful. Insulin like growth factors (IGFs) are a family of polypeptide hormones that are structurally similar to insulin and have multiple metabolic and anabolic functions [73]. IGF-I and IGF-II stimulate the proliferation, differentiation, and metabolism of myogenic cell lineages in different species [74, 75]. IGF genes have been reported to influence growth rate and regulate muscle tissue growth in chickens [76-78].

Further, data [79-82] indicate that IGF1 is a candidate positional gene involved in the control of growth and fat deposition in chickens. A study of 392 egg cross chickens and 321 meat cross chickens revealed statistically significant associations of single-nucleotide polymorphism in the *IGF1* gene promoter with the majority of the studied traits (growth rate, body composition, skeletal condition and physiological properties) [83].

Boning condition is becoming increasingly important for both broilers and layers. Genotype has been shown to play a key role in bone integrity, but little is known yet about the architecture of the genetic basis of this trait [84]. S. Jansen et al. [85] based on a study of genes associated with bone tensile strength and mineralization in laying hens, selected 16 candidate genes and assessed the effects of 490,745 SNP markers [85]. The identified genes and SNPs were associated with bone strength. The authors also identified genes that are critical for bone integrity. The mechanisms of participation of these genes in the formation of the skeletal system require further study with a view to using them to reduce bone disorders in laying hens [85].

Meat quality indicators are economically significant. In meat and poultry products, a high content of nutrients is combined with a relatively low calorie content, but the consumer properties of the resulting products depend on the conditions at all stages of poultry farming, from the fertilized egg to processing of raw materials [86-88].

Basic meat quality characteristics that are of interest and quantifiable (e.g., pH, water-holding capacity, meat color) have collectively become selection criteria

in chicken selection and breeding programs [89). However, improving these quality parameters using traditional breeding methods is difficult because the measurements are time-consuming and require slaughter of the bird, which significantly increases the intergenerational interval and slows overall genetic progress [90]. However, estimates of the heritability of meat quality traits (h^2 ranging from 0.35 to 0.81) indicate that genetic selection is the most effective tool for improving broiler meat quality [91]. Therefore, it is important to understand the genetic background of traits associated with poultry meat quality. They are considered complex quantitative traits and are controlled by many genes. Research has shown that the fatty acid binding protein *FABP* gene plays an important role in improving overall meat quality [92]. The *CAPN1* (*micromolar calcium-activated neutral protease*) gene was found to be significantly associated with tenderness and other quality traits of meat [93], and SNP V315M in the *PRKAG3* (*protein kinase AMP-activated non-catalytic subunit gamma 3*) gene was significantly associated with the water-holding capacity of meat (94). In several studies for different animals, including poultry, it has been shown that *PHKG1* (*phosphorylase kinase catalytic subunit gamma 1*) is a candidate gene influencing meat quality characteristics [95-97]. In local Chinese Ningdu yellow chickens, the effect of single nucleotide polymorphisms in the *PHKG1* gene on traits associated with meat quality was studied, and the associations between polymorphisms of the *PHKG1* gene, meat quality and carcass parameters were analyzed. Significant associations of the SNP marker rs15845448 with 17 studied traits were identified, and this marker can be used in breeding programs for the Chinese Ningdu yellow breed [98].

The Table summarizes the information about candidate genes, single nucleotide polymorphisms in which are statistically significantly associated with economically valuable traits in chickens.

Candidate genes and SNPs associated with economically valuable traits in chickens

Gene	Function	Economically valuable traits associated with SNP in candidate genes
NCAPG (Non-SMC condensin I complex, subunit G)	Condensins are subunit protein complexes that play a fundamental role in the structural and functional organization of chromosomes; condensins I and II are involved in the regulation of gene expression, recombination and repair	Egg productivity [17], egg shell weight and thickness [12, 13, 16, 17]
LCORL Ligand dependent nuclear receptor corepressor-like	One of the key genes that determines the characteristics of body weight in vertebrates	Live weight of chickens [10]
GRB14 growth receptor binding 14	A gene that encodes a protein that binds the growth factor receptor. In humans and mammals, *GRB14* mRNA is expressed at high levels in the ovaries, liver, kidneys, skeletal muscles, etc.	Development and function of the ovaries [35]
GALNT1 UDP-N-acetyl-alpha-D-galactosamine: a polypeptide of N-acetylgalactosaminyltransferase 1	Ensures normal ovarian functions. The characteristics of this gene in chickens are still unclear, and the mentioned study is the first report that its polymorphism is associated with the quality characteristics of eggs	Development and function of the ovaries, quality characteristics of eggs [35]
MSX2 msh homeobox 2, a member of the msh homeobox family	Expressed in many embryonic tissues. In the chicken, it is expressed in the apical ectodermal ridge and ectoderm of the genital tubercle, plays a decisive role in the growth and formation of limb mesoderm	Embryonic development, ovarian development, egg quality [41]
RHOA Small GTPase of the ras homologue (Rho) family	Molecular switches that control a wide range of cellular functions — cytoskeletal reorganization, cell motility and gene expression. The *RHOA* signaling system plays a role in the modulation of actin stress fibers and chondrogenesis	Body growth, eggshell color, egg quality at later stages of laying [41]

Continued Table

SDF4 Stromal cell derived factor 4	Its human ortholog is known as *Cab45*. Regulates cell migration through various molecular mechanisms	Eggshell color [41]
TNFRSF4 Tumor Necrosis Factor Receptor Superfamily, Member 4	*TNFRSF4* can be used to specifically modulate the expression of other genes that directly stimulate effector T cell activity	Eggshell color [41]
RAPGEF6 Rap guanine nucleotide exchange factor 6	Plays a fundamental role in spermatogenesis, indicating that RAPGEF6 is required for reproductive development	Egg production at late stage of laying [44]
PRL Prolactin	One of the hormones of acidophilic cells of the anterior pituitary gland. Almost all known functions are related to reproduction	Regulation of oviposition. Plays a decisive role in the emergence and maintenance of the brooding instinct [41, 45]
DRD1 Dopamine D1 receptor gene Dopamine D5 receptor gene	In birds, dopamine is involved in both stimulation and inhibition of prolactin secretion	Egg production, egg hatchability [49-51]
VIPR1 Vasoactive intestinal peptide receptor-1	Vasoactive intestinal peptide (VIP)-releasing factor of the hormone prolactin in birds	Brooding instinct, egg hatchability, egg production [52]
FSH Follicle-stimulating hormone gene *FSHR* Follicle-stimulating hormone receptor gene	Gonadal and fertility functions	Egg production of chickens, age of laying the first egg [55, 57]
IGF1, IGF2 Insulin-like growth factors I and II	Proliferation, differentiation, metabolism of myogenic cell lines	Growth of muscle tissue in chickens [76-78], growth and fat deposition in chickens [79-82], height, body composition, skeletal condition [83]
FABP Fatty acid binding protein gene	Participation in lipid metabolism, transport of fatty acids at intermediate stages of adipogenesis and fat deposition	Meat quality [92]
CAPN1 Micromolar calcium-activated neutral protease gene	Calpains (intracellular Ca2+-dependent cysteine proteases) (EC 3.4.22.17) are involved in muscle growth and development. CAPN1 degrades myofibrillar proteins and appears to be the main enzyme in the process of postmortem softening	Qualitative characteristics of meat, mainly tenderness [93]
PRKAG3 5'-AMP-Activated Protein Kinase Gamma 3 Subunit gene	Controlling the energy balance of the cell, the AMPK 3-gamma subunit can bind 3 AMP molecules, one of them is constantly bound to the protein, regardless of the energy status of the cell. Has an affinity for the nucleus	Qualitative characteristics of meat, its moisture-holding capacity [94]
PHKG1 Phosphorylase Kinase Catalytic Subunit Gamma 1 gene	A member of the Ser/Thr protein kinase gene family, it encodes a protein with one protein kinase domain and two calmodulin-binding domains. The protein is a catalytic element of a 16-subunit protein kinase complex, consisting of four types of subunits in equimolar ratios	Meat quality, meat color [98]

Thus, genomic approaches in the selection of commercial and local breeds of chickens can significantly accelerate breeding progress both in the breeding of heavy crosses focused on the yield of meat products, and in maintaining high levels of egg productivity in parent flocks. Sequencing chicken genome has meant enormous advances in poultry genetics and breeding research [99, 100], but a more complete and in-depth research are necessary to understand the mechanisms that control desirable traits.

So, due to the improvement of genomic methods, researchers can analyze poultry genomes to directly confirm bird's genetic potential and reveal its effect on economically significant traits. It is necessary to protect the domestic gene pool of chickens from the spread of genetic diseases and maintain the level of individual and group heterozygosity during breeding and selection of Russian populations and breeds. Currently, genotyping of chicken breeds for meat, egg and combined productivity is being actively carried out. A significant amount of information has been accumulated on single nucleotide polymorphisms (SNPs) associated with productivity in chickens of local and some commercial breeds at different periods

of the productive cycle. According to available data, single nucleotide polymorphism affects economically significant traits of chickens, and SNP markers can be used in the development of breeding and genetic programs in poultry farming.

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