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Molecular diversity of Ukrainian native chicken breeds: a review

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SUMMARY

The current Ukrainian native chicken gene pool is experiencing a decline in the number of breeds and maintained flocks. The major chicken breeds and lines of Ukrainian selection currently involve the Poltava Clay, Birkivska Barvysta, White Plymouth Rock and Rhode Island Red, representing different utility purpose types (i.e. layer and dual purpose). The local germplasm conservation agenda implies, among other measures, exploration of the genetic diversity of Ukrainian native chicken breeds using various types of molecular markers (e.g. indels, PCR-RFLPs and microsatellites). The purpose of this article is to review recent results of the complex genetic studies for assessing the features of population structure and variation in local breeds and lines. In particular, native gene pool stocks were examined for polymorphisms of the following genes: *PRL, PRLR, GH, GHR, IGF1, PIT1, TGF-β1, TGF-β2, TGF-β3* and *Mx*. Based on these results, association of the identified polymorphic loci with productive traits (i.e. egg and meat performance) was investigated. For each of the experimental chicken lines, promising genotypes were established for further implementation in marker-assisted selection programs. Using microsatellites, the main variability parameters were established in the experimental populations, their genetic differentiation was analysed, and genetic distances were calculated between the experimental lines.

KEYWORDS

Ukrainian chicken gene pool; native breeds; populations; genetic diversity; genes; alleles; microsatellites

Introduction

Compared to other sectors of livestock production in Ukraine, the poultry industry is the most developed field with much potential for further development and advancement (Bezhenar and Vasiuta 2015; Mel'nyk et al. 2009; Piroh 2017). Indeed, it is the only branch of animal husbandry that has been demonstrating positive growth dynamics in recent years (Karpenko 2015; Tereshchenko et al. 2010, 2013; Tereshchenko et al. 2011), but with a relatively high percentage of poultry still kept in small private farms and backyards (Ionov et al. 2012; Tereshchenko 2011).

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In recent years, large breeding companies have developed a monopoly of resources in the market, and this subsequently leads to potentially higher financial risks for small local breeding farms (Ryabokon et al. 2006; Sakhatsky, Tereshchenko, and Duyunov 2003; Tereshchenko et al. 2008). In addition to the economic consequences, market monopolisation also poses a threat to the existing native germplasm breeds of different poultry species (Gadyuchko et al. 2003; Romanov et al. 1995). The main reason for this resides in the considerable underperformance of the local breeds in terms of the combination of their breeding abilities and their production traits as compared to the commercial lines (Larkina et al. 2021). Despite the current difference in the economically important traits, however, the chickens of native breeds and pedigreed groups have a unique gene pool formed due to the effect of multiyear breeding and selection (Altukhov et al. 2004). They are characterised by high indices of viability and adaptability to local conditions. Moreover, taking into account the exceptionally complex genotypes inherent in the native chicken breeds and their specific productive and adaptive traits, it is essential to conduct fundamental research on genetic characteristics of the conserved and experimental populations (Romanov 1996). This is also consistent with the general task of preserving the unique genetic resources in various countries of the world by implementing the appropriate strategies and methodologies such as biobanking (Tereshchenko et al. 1996, 1998, 2010; Wongloet et al. 2023). Specific genetic material, unique to individual local chicken populations, requires the study and passportisation of current breeds by the combination of marker genes and evaluating the level of manifestation of economically valuable traits, etc. (Podstreshnyi et al. 2009). It should be noted that intense selection work is the main factor leading to a potential loss of genetic diversity at the DNA level, which, primarily, is a danger to indigenous populations of poultry (Altukhov, Moiseeva, and Volokhovich 1980; Tixier-Boichard et al. 1999).

The preservation and investigation of diverse genetic resources of rare breeds and control, heterogeneous and synthetic chicken populations, as well as reserve lines, are among the most urgent tasks for poultry breeders (Romanov 1995; Romanov et al. 1994; Romanov and Sakhatsky 1995a, 1995b; Tadano et al. 2013). In 1981, the creation of chicken gene pool collections was initiated at the Selection and Genetic Center of the Ukrainian Poultry Research Institute, Birky, Kharkiv Region, Ukraine. By 1995, it comprised 13 rare breeds, 22 reserve lines and synthetic and control populations (Romanov 1995; Romanov and Sakhatsky 1995a, 1995b). Their preservation and annual propagation were conducted by panmixia, with the effective population size of at least 200 birds (on an average, 300 hens and 60 roosters). Currently, the State Poultry Research Station (the successor of the Poultry Research Institute), of the National Academy of Agrarian Sciences of Ukraine, has only a reduced number of chicken breeds of Ukrainian selection presented by several lines. The most typical representatives of this gene pool nucleus are the breeds of different utility purpose (type), including layer and dual propose (i.e. meat-egg and egg-meat types) (Baydevlyatova et al. 2009; Bondarenko et al. 1989; Katerynych et al. 2017; Khvostyk et al. 2017; Larkina et al. 2021; Romanov 1988; Romanov et al. 2021a). Specifically, these are breeds of layer hens (Birkivska Barvysta (Mosiakina et al. 2005)), meat-egg chickens (e.g. White Plymouth Rock (Katerynych et al. 2016), Figures 1(a,b)), and egg-meat chickens (Poltava Clay (Romanov and Bondarenko 1994; Moiseyeva et al. 2006), Figure 1(c), and Rhode Island Red (Romanov 1994), Figure 1(d)). At present, however, the above chicken breeds

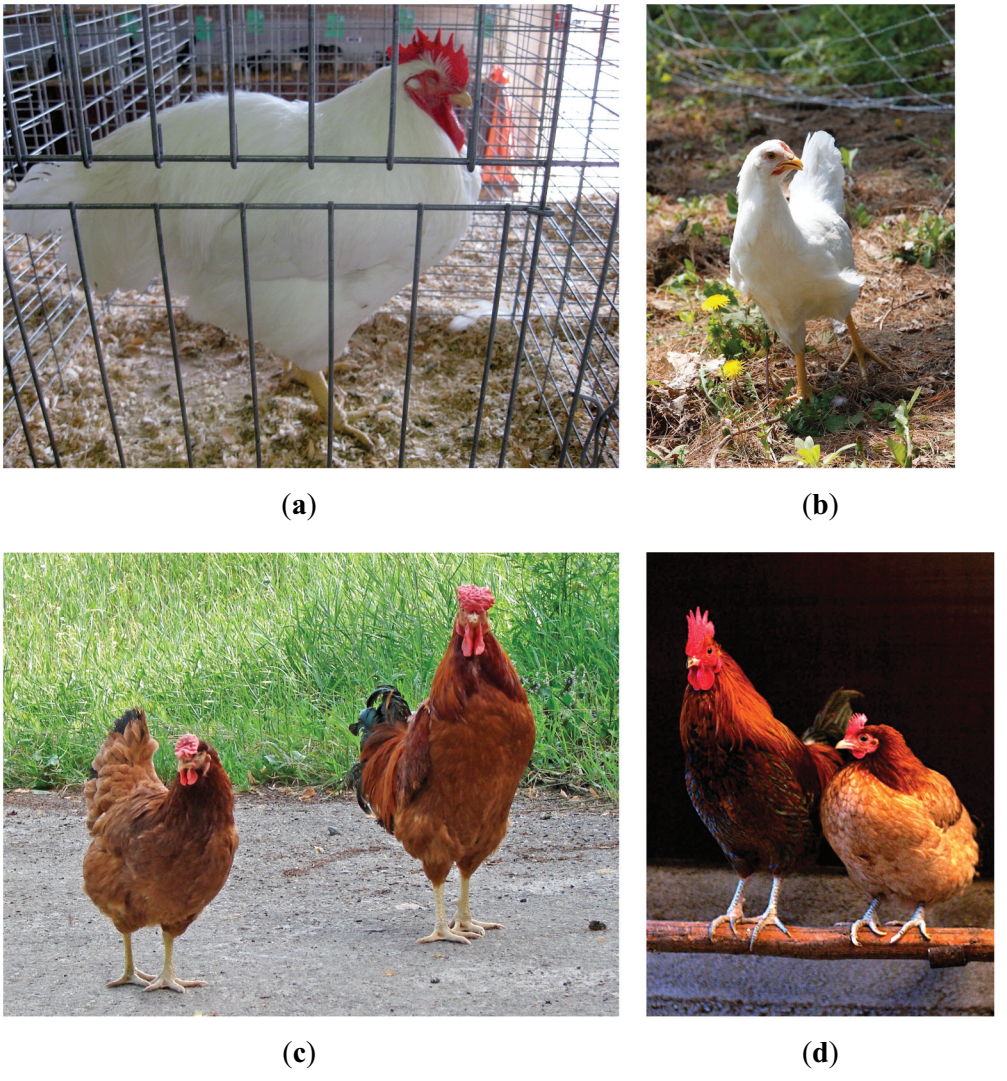

Figure 1. Examples of the Ukrainian chicken gene pool breeds: (a,b) White Plymouth Rock rooster and pullet, respectively; (c) Poltava Clay female and male; and (d) Rhode Island Red male and female. Image sources (a): https://commons.wikimedia.org/wiki/File:White_Plymouth_Rock_rooster.JPG, by Steven Walling, CC-BY-30 (b). https://commons.wikimedia.org/wiki/File:First_Root_Farm_chicken.jpg, by Tim Sackton, CC-BY-SA-20 (c).; https://commons.wikimedia.org/wiki/File:Poltava_chicken_breed_ male_and_female.jpg, by Timophey Tkachik, CC-BY-SA-30 (d).; https://commons.wikimedia.org/wiki/File:Male_and_female_chicken_sitting_together.jpg, by Andrei Niemimäki, CC-BY-SA-2.0.

and lines do not have any direct relevance in the context of industrial poultry production. They are used only for the limited needs of small farms, which is greatly determined by the higher adaptive abilities of the chickens of Ukrainian selection when they are kept locally (Khvostyk et al. 2016). The lack of considerable state support and interest of large poultry producers in Ukraine jeopardises the existence of these gene pool breeds as a whole, which will lead to the irreparable loss of unique genetic material if they vanish.

The monitoring and study of genetically conditioned traits in different local and imported poultry breeds are one of the priority tasks in trying to solve the problem of germplasm conservation (Bondarenko and Podstreshny 1996; Dementieva et al. 2020b; Romanov et al. 2021b; Weigend et al. 2004b; Zakharov-Gesekhus et al. 2007). It is also consistent with global trends and urgent not only for Ukraine but also for other countries (Ben Larbi, M'Hamdi, and Rekik 2018; Zhang et al. 2023). Therefore, along with the problems of preserving the gene pool as a whole, the issue of determining which specific features of the genetic structure of the populations of native Ukrainian chicken breeds to conserve is the primary goal for poultry breeding in that country. At present, the studies of specific loci and allelic diversity of the breeds and lines of local poultry populations by the combination of different types of molecular genetic technologies using a range of markers are carried out in many countries (Romanov et al. 2020; Weigend and Romanov 1999, 2002; Weigend et al. 2004b). Such investigations, however, have practically been not conducted in Ukraine over recent years and the experimental works required to apply the benefits of modern achievements in molecular genetics have been reported only as a result of some rare studies performed mainly among commercial chicken breeds (Romanov and Weigend 2001a, 2001b; Shelov et al. 2009, 2013). The majority of publications on determining the genetic specificities of native breeds and chicken lines of Ukrainian selection usually covers only the issues of biochemical polymorphism, immunogenetics and the variation in the manifestation of productive features. These include the phenotypic manifestation in general, which explains the delay in the application of novel DNA technologies in domestic poultry breeding in Ukraine (Bondarenko 1976; Katerinich, Tkachik, and Bondarenko 2014; Khvostyk and Bondarenko 2017; Moiseeva and Novik 1977; Kutnyuk, Volohovich, and Moiseeva 1986; Romanov et al. 1999a; Tkachyk, Tereshchenko, and Katerynych 2010).

Considering the reduced number, shrinking local distribution and threat of irreplaceable loss of the populations of unique native Ukrainian lines, breeds and breed groups, the necessity to study their genetic makeup takes centre stage. To address this issue, starting in 2010, the Laboratory of Genetic Control and Molecular Diagnostics was established at the Poultry Research Institute (and later at the Livestock Farming Institute, Kharkiv, Ukraine), which served as a basis for investigating the genetic structure features of the chicken populations of Ukrainian selection. They used different types of molecular genetic markers and techniques, including polymerase chain reaction – restriction fragment length polymorphism (PCR–RFLP; e.g. Bal et al. 2020; Dementieva et al. 2022; Sironi et al. 2010).

In this regard, the aim of this paper was to overview the results of the relevant investigations over the last decade (Kulibaba 2015, 2018b; Kulibaba and Podstreshnyi 2012; Kulibaba and Tereshchenko 2015; Kulibaba et al. 2015, 2017, 2020) pertaining to the features of genetic variability among the chicken populations and lines of Ukrainian selection (i.e. gene pool populations of the State Poultry Research Station). These primarily used PCR-RFLP variants of major genes (*PRL, PRLR, GH, GHR, IGF1, PIT1, TGF-β1, TGF-β2, TGF-β3* and *Mx*) related to the manifestation of economically valuable traits, as well as such molecular markers as microsatellites.

Chicken lines of Ukrainian selection

The current gene pool of the chickens of Ukrainian selection basically includes the breeds, lines and subpopulations of the Birkivska Barvysta, Poltava Clay (the native breeds) plus Rhode Island Red and White Plymouth Rock chickens. The Birkivska Barvysta breed, of synthetic origin, was established around the mid 2000s (Mosiakina et al. 2005), whereas the Poltava Clay breed was developed in the late nineteenth century (Moiseyeva et al. 2006; Romanov and Bondarenko 1994). Rhode Island Red and White Plymouth Rock were breeds imported from abroad over the last century. The layer hens of the Birkivska Barvysta line A (of the Silver Leghorn type) are characterised by a high level of hatchability (88–94%) and hen day egg production (81.3 eggs over 40 weeks of life) (Mosiakina et al. 2005).

The egg-meat chickens are represented by two breeds: Poltava Clay and Rhode Island Red. The Poltava Clay line 14 is notable for its dual-purpose usage, adaptation features resistance to neoplastic diseases, primarily Marek's disease, and the respective high indices of egg and meat performance (Moiseyeva et al. 2007). Its production traits are as follows: hen day egg production, 235–240 eggs per year of lay; egg weight, 59.5–60.5 g; body weight, 2.2–2.3 kg; and viability, 93–95% (Mosiakina et al. 2006). The Rhode Island Red breed is represented by two lines, 02 and 38 (Ryabokon et al. 2005). The performance indices of line 02 are as follows: hen day egg production, 230–240 eggs per year of lay; egg weight, 61.0–62.5 g; body weight, 2.1–2.4 kg; and viability, 94–96%. This line is used as a reserve in the selection and breeding work. Line 38 is well adjusted to different maintenance conditions and is characterised by the following productivity traits: hen day egg production, 240–245 eggs per year of lay; egg weight, 59.0–61.0 g; body weight, 2.0–2.1 kg; and viability, 95–97%.

The meat-egg chickens of the coloured types (coined colloquially as 'Hercules') are represented by five experimental subpopulations that differ in the colour of their plumage and production traits. These chickens include the following subpopulations: H-1, speckled; H-2, white (of the White Plymouth Rock breed (Katerynych et al. 2016)); H-3, golden; H-4, colourful; and S, silver (Podstrieshnyi et al. 2011). All these experimental chicken subpopulations are characterised by the manifested dual-purpose features and good adjustment to the maintenance conditions at the farms and domestic households. Body weight of 48-week chickens from different subpopulations varies from 2.46 to 3.11 kg; egg weight at 40–48 weeks of age from 60.2 g to 62.8 g; hen day egg production over 40 weeks of life from 74.2 eggs to 89.6 eggs; and viability from 79.7% to 92.6% (Khvostik et al. 2013).

Prolactin and prolactin receptor genes

Prolactin (PRL) is one of the best-known and important proteins that has been extensively studied in poultry genetics (e.g. Dementieva et al. 2020a; Violet and Kannan 2024). It is a peptide hormone secreted by the hypophysis and is closely involved in the regulation of more than 300 different physiological functions of the organism (Smiley 2019). The results of numerous investigations demonstrated the associations between different allelic variants of the *PRL* gene and egg productivity traits in chickens (Dementieva et al. 2020a; Nguyen et al. 2024; Rohmah et al. 2022; Tu, Phuong, and

Ngu 2023). In poultry, PRL plays one of the key roles in regulating the process of broodiness that is unique for this class of animals (Chakraborty and Saha 2021; Romanov et al. 1999b). Broodiness in poultry is closely related to the total performance indices of birds (hens inclined to broodiness are characterised by rather low egg productivity), which defines *PRL* as a promising selection marker (Romanov 2001; Sarkar 2022).

Prolactin receptor (PRLR) belongs to the class of transmembrane molecule receptors for hormones, which defines the relevance of its functions (Brooks 2012). The potential changes in the structure of receptor molecules or in their gene expression may lead to rather pronounced consequences that are of considerable relevance in the context of productive traits in poultry. The *PRLR* gene is located on the Z chromosome, which defines its hemizygous state in hens. Taking into consideration the exceptional relevance of PRLR in the regulation of reproductive processes in poultry, research has focused on the analysis of associations between different allelic variants of *PRLR* and egg production indices as well as meat performance parameters (Liang et al. 2019; Wilkanowska et al. 2014; Yadav et al. 2018).

Genetic study of *PRL* polymorphisms has involved the analysis of the presence/absence of the 24-bp insertion in the promoter region of the gene (24-bp indel) and a single nucleotide polymorphism (SNP) for transition of cytosine into thymine in the position −2402 (C-2402 T) using the *Alu*I restriction endonuclease (Cui et al. 2006; Alipanah, Shojaian, and Bandani 2011). The *PRLR* gene variation is analysed using *Bam*HI restriction-based polymorphism in exon 5 (Rashidi et al. 2012).

Both types of the *PRL* locus mutations, i.e. 24-bp indel (alleles I and D) and C-2402 T (alleles C and T), were explored in the chicken experimental populations of Ukrainian selection. The results of this investigation demonstrated the *PRL* gene polymorphism by the presence of the insertion in the promoter area in the chicken populations (Kulibaba and Podstreshnyi 2012). In particular, in such breeds as the White Plymouth Rock and Birkivska Barvysta, there were birds of all three possible genotypes, i.e. II, ID and DD, while the Rhode Island Red chickens had the genotypes ID and DD. However, only chickens of the DD genotype were found in the line 14 of the Poltava Clay breed; the birds of two other genotypes were not found, which highlighted the monomorphic character of this locus in this experimental population.

Furthermore, the frequency for alleles I and D in chicken populations of the meat-egg (line H-2), layer (line A) and egg-meat (lines 14 and 38) types differed significantly ($p < 0.001$). For instance, in line H-2, most chickens bore the deletion allele in the homozygous or heterozygous state (76 and 21 chickens, respectively), while the total number of homozygotes for the insertion allele was only 3. As for line A, the numbers of homozygotes and heterozygotes for the insertion were 50 and 46 chickens, respectively, whereas the number of homozygotes for the deletion was 4. The differences in the frequency of alleles in these lines were highly significant ($p < 0.001$). The chickens homozygous for allele D prevailed in the Rhode Island Red line 38. In line H-2, a lower number of heterozygotes was found as compared to the expected one, and in line A, there was an increased number with no impairment of the genetic equilibrium. At the same time, in the population of the egg-meat chickens of line 14, this locus was found to be monomorphic by the presence of the insertion (the frequency of allele D was 1), which distinguishes the studied population from the others rather vividly (Kulibaba

2015). In turn, the egg-meat chicken population of the Rhode Island Red breed takes the intermediate position between lines H-2 and 14 in terms of the ratio between the genotypes and alleles.

The fact that in line A, as compared to other lines of chickens, there was a significantly greater number of birds homozygous for allele I was in agreement with the data of other authors about the positive association between this allele and egg production traits (Alipanah, Shojaian, and Bandani 2011; Chakraborty and Saha 2021; Cui et al. 2006; Nguyen et al. 2024; Rashidi et al. 2012; Romanov et al. 1999b; Sarkar 2022; Tu, Phuong, and Ngu 2023; Wilkanowska et al. 2014). A probable mechanism of the association between the 24-bp insertion in the promoter region of the *PRL* gene and the egg performance of poultry is related to possible changes in the interaction with the factors of transcription activation, which led to the corresponding changes in the degree of the manifestation of the phenotypic traits (egg production).

A somewhat different pattern was observed with regard to the SNP C-2402 T at the *PRL* locus in the experimental populations of chickens. In contrast to the 24-bp indel polymorphism of the *PRL* promoter region, the mutation C-2402 T was found to be polymorphic in all the experimental populations of chickens, so that the chickens of all three possible genotypes (i.e. CC, CT and TT) were present in all the chicken lines. The frequency of alleles C and T in the investigated chicken lines of different utility purpose was characterised by certain significant differences. When comparing the chicken lines of the layer and meat-egg types, their genetic makeup assessed by the frequency of C-2402 T substitutions had an insignificant between-line difference relative to the genetic structure in terms of the presence of the 24-bp indel. Compared to H-2, line A had a somewhat higher number of heterozygotes and a lower number of homozygotes, but the genetic equilibrium was not impaired. The differences between the lines in terms of alleles with the same letter symbol were highly significant ($p < 0.001$). Hereby, in line 14, the *PRL* gene was polymorphic for C-2402 T, in contrast to the 24-bp indel. In terms of the frequency of alleles, this population showed an intermediate position between lines H-2 and A. The number of heterozygous birds in line 14 was the greatest (52) among all the populations. This chicken line was in the state of genetic equilibrium. By the ratio between the frequency of alleles and genotypes, the population of Rhode Island Red chickens was maximally close to line H-2 of meat-egg chickens and was characterised by the maximum number of birds homozygous for allele T (Kulibaba 2015; Kulibaba and Podstreshnyi 2012).

The general analysis of the observed and expected distributions of *PRL* genotypes in this gene pool sampling proved the presence of some excess of heterozygotes in the chicken populations of lines 14 and A. At the same time, the values for the observed and expected heterozygosity in the lines H-2 and 38 almost coincided. The highest level of polymorphism was notable for Poltava Clay chickens and the lowest one for line H-2 (Kulibaba 2015; Kulibaba and Podstreshnyi 2012).

The *PRL* polymorphism investigations demonstrated that complete linkage disequilibrium (LD) was observed for the Birkivska Barvysta layer hens and Rhode Island Red chickens of the egg-meat type (in both cases, the values of the standardised disequilibrium measure D' was 1). In the population of the layer hens, there were many more individuals of the IC haplotype (0.82). Herewith, the chickens of the DT haplotype prevailed in the Rhode Island Red population (0.86). In line H-2 of the meat-egg

chickens, the birds of the DT haplotype prevailed too (0.72), with the value of D' in this population being 072 (Kulibaba 2015; Kulibaba and Podstreshnyi 2012).

The association between the abovementioned *PRL* alleles and the productivity parameters was determined for different chicken breeds of Ukrainian selection. As for line A of Birkivska Barvysta, alleles I and C correlated with the number of eggs for 40 weeks of lay. In line 14 of the Poltava Clay breed, the chickens homozygous for allele C were characterised by the greater egg number for 12 and 40 weeks of lay and greater egg weight at 30 weeks of age. In turn, the prevalence in heterozygotes ID and CT over homozygotes DD and TT was found in line 38 of Rhode Island Reds in terms of the egg performance traits (Kulibaba 2015; Kulibaba and Podstreshnyi 2012).

The study of *Bam*HI-based polymorphism in exon 5 of the *PRLR* gene showed the monomorphic character of *PRLR* in all the experimental populations of chickens. All the investigated breeds were remarkable for the presence of chickens only with genotype A/0 (*Bam*HI+/0), which was an immediate indication of the monomorphism at this locus. The monomorphic nature of exon 5 of the *PRLR* gene was confirmed by the results of using the single-strand conformation polymorphism (SSCP) analysis when the absence of alternative variants was determined (Kulibaba 2015).

Growth hormone and growth hormone receptor genes

The growth hormone (*GH*) gene is one of the most promising genes in terms of marker-assisted selection (MAS), since its allelic variants are related to the productive traits of various chicken breeds and different utility purpose GH (also somatotropin, or somatotropic hormone) belongs to the class of peptide hormones and is synthesised by the adenohypophysis (Kansaku et al. 2008). It is characterised by a broad spectrum of physiological functions, including the growth and differentiation of different tissues and organs, and affects the synthesis of this protein, the metabolism of carbons, lipids, etc. (Ranke and Wit 2018). GH is closely related to regulating the activity of other hormones; for instance, it stimulates the synthesis and secretion of the insulin-like growth factor 1 (IGF1) by the hepatic cells, which, in turn, defines the growth functions of somatotropin (Ipsa et al. 2019; Ranke and Wit 2018). The *GH* gene contains five exons and four introns; it is located on chromosome 27 and is characterised by a high level of polymorphism (Kansaku et al. 2008).

The growth hormone receptor (GHR) is a transmembrane polypeptide that plays a relevant role in regulating the proliferation and differentiation of various types of cells and tissues (Waters 2016). Moreover, at the physiological level, the functioning of GH is closely related to GHR, since the functional activity of any hormone is directly dependent on its receptor. The changes in the *GHR* structure and its expression mode are directly related to several performance traits of poultry, including body weight and egg production (in general, most traits mediated by GH). The functioning of GHR is indirectly related to the functions of the system of insulin-like growth factors, i.e. GH/IGF-1 axis (Dehkhoda et al. 2018). The interaction between GH and GHR leads to the activation of the synthesis and secretion of the insulin-like growth factors, which take a direct part in the initiation of proliferation and differentiation of muscle tissues. The *GHR* gene consists of nine exons and eight introns and is located on the Z chromosome that results in the hemizygous state of this gene in the hens. The involvement of *GHR* in the

regulation of different physiological functions makes it an optimal candidate for studying the association between different allelic variants and the productivity traits of poultry (Kulibaba, Liashenko, and Yurko 2017; Ouyang et al. 2008). It appears that GH is crucial for layer lines throughout the development stage prior to the onset of egg production. There was no association between GH and egg production in lines that varied in their egg production during the laying phase (Höhne et al. 2017).

In this respect, the study of polymorphisms in the intron areas of the *GH* gene, i.e. *Msp*I-based polymorphism in introns 1 and 4 (Feng et al. 1997; Ip, Zhang, and Leung 2001) and *Sac*I-based polymorphism in intron 4 (Feng et al. 1997), was carried out in the chicken populations of different lines and breeds of Ukrainian selection (Kulibaba et al. 2015; Kulibaba 2018b). In addition, the analysis of the *GHR* gene variability was conducted using the restriction assays for *Hind*III-based polymorphism in intron 2 (Feng et al. 1997) and *Nsp*I-assisted polymorphism in intron 5 (Li et al. 2008).

The results of this investigation demonstrated a considerable difference between the experimental chicken populations (Kulibaba and Podstreshnyi 2012). For instance, when studying the distribution of alleles for the *Msp*I-based polymorphism in *GH* intron 1, the highest differences were identified between the chicken populations of the Poltava Clay and Rhode Island Red breeds. Allele C was present in all the investigated populations, although, according to other studies, it is absent in the commercial chicken lines, being remarkable for native breeds first and foremost (Ip, Zhang, and Leung 2001). At the same time, the highest frequency of this allele was noted for line 38 and the lowest one for the Poltava Clay breed (Kulibaba and Podstreshnyi 2012).

The similarity between all the experimental dual-purpose populations was discovered using the *Sac*I-based polymorphism in intron 4 of the *GH* gene (with a notable significant excess in the frequency of allele B). There were no animals homozygous for allele A amongst the investigated lines. Hereby, there were almost equal values for the frequency of alleles A and B in the population of layer hens (Kulibaba and Podstreshnyi 2012).

The restriction analysis technique followed by the subsequent sequencing was used to examine the *Msp*I-based polymorphism in intron 4 of the *GH* gene in the experimental chicken populations (Kulibaba et al. 2015). This study revealed an error in the hypothesis by Shahnaz et al. (2008) with respect to the presence of the *GH* gene duplication in chickens, as suggested based on the analysis of the additional *Msp*I restriction pattern of intron 4 of this gene. In particular Kulibaba and Tereshchenko (2015) determined that the presence of the additional genotype (restriction pattern) was not related to the duplication of the *GH* gene. As found due to the amplification of the samples of heterozygotes BC at the CCGG site, there was a possible formation of a heteroduplex DNA of two different types. This led to the formation of the additional DNA fragment that does not contain the CCGG site in its composition, which, in its turn, is a factor for the formation of an additional restriction pattern (Kulibaba et al. 2015). The determination of the nucleotide sequence of the respective DNA fragments isolated from the gel allowed for the substantiation and accuracy confirmation of the assumption of the nature of additional genotypes, based on which the genetic structure of the experimental chicken populations was defined. A significant difference in the distribution of allelic frequency was found in the distribution of allelic frequency within the Poltava Clay breed. Line 14 was notable for a clear predominance in the frequency of allele C due to the presence of a considerable number of birds of the CC genotype, whereas this tendency was not

observed in other populations. In turn, the layer hens of line A were remarkable for the prevalence of the frequency of allele A (Kulibaba et al. 2015).

While analysing the nucleotide sequence data of intron 4 of the *GH* gene, a new, previously not described, mutation was determined at the *Alu*I restriction site and defined as a transition C→T in position Chr27:1788455. In that study Kulibaba, Liashenko, and Yurko (2017) designed the appropriate oligonucleotide PCR primers flanking the 460-bp fragment of *GH* intron 4 that contains the polymorphic *Alu*I restriction site, which, in turn, allowed for developing the efficient PCR-RFLP method to identify this polymorphism. The investigation (Kulibaba, Liashenko, and Yurko 2017) demonstrated that this *GH* gene mutation was polymorphic in all the experimental chicken populations of Ukrainian selection. The frequency of allele C (no restriction site) in the experimental chicken populations differed within the range from 4% (Poltava Clay) to 30% (Rhode Island Red). The presence of C→T transition was notable for the prevailing number of chickens. In terms of the distribution of the allele frequencies, the Rhode Island Red population differed from other lines, the largest difference being compared to the Poltava Clay chickens (Kulibaba, Liashenko, and Yurko 2017).

When evaluating the egg performance traits in line A, the chickens homozygous for alleles B (*Msp*I-assisted polymorphism in intron 1) and C (*Sac*I-based polymorphism in intron 4) demonstrated the largest egg number for 40 weeks of lay. Herewith, the over-representation of higher productive indices in heterozygotes AB compared to BB in terms of *Sac*I-based polymorphism was detected in the Poltava Clay chickens. No associations with the egg productivity traits were found for other mutations. The same was true for line 38 of Rhode Island Reds. On the other hand, the relationship with the meat performance parameters was different. The superiority of the values for heterozygotes AB over BB in terms of *Sac*I-based polymorphism and CT over TT in terms of *Alu*I-based polymorphism was observed in line 14. The population of Rhode Island Red chickens was noted for a significant superiority in the values of meat productivity traits for homozygotes AA (*Msp*I, intron 1) CC (*Msp*I, intron 4), and TT (*Alu*I, intron 4) as compared to the chickens of other genotypes. No significant differences between the values of the production traits were found between chickens of different genotypes in terms of *Sac*I-based polymorphism (Kulibaba 2015; Kulibaba and Podstreshnyi 2012; Kulibaba et al. 2015; Kulibaba, Liashenko, and Yurko 2017).

In terms of *Hind*III-based polymorphism of the *GHR* gene in intron 2, different allelic variants were revealed only in line 14 of the Poltava Clay chickens. Other experimental populations were monomorphic if assessed using the *Hind*III-based polymorphism of *GHR*. A similar pattern of the distribution of allelic frequencies was also shown in other studies for different chicken breeds (Li et al. 2008; Seyyedbabayi et al. 2014). A significant difference between different genotypes (*Hind*III-based polymorphism of *GHR*) in the chicken population of line 14 was found for the indices of egg weight and thigh muscle weight. However, the pattern of the *Nsp*I-based polymorphism in exon 5 was completely different (Kulibaba 2015). In all the investigated chicken populations, the *GHR* gene was polymorphic and, accordingly, there were chickens of two possible genotypes, A0 and B0. The chicken populations of various utility purpose differed considerably by the frequencies of alleles A and B ($p < 0.001$). For instance, the greatest frequency of allele A was observed in the chicken population of White Plymouth Rocks (0.72), and the lowest one in the population of Rhode Island Red chickens (0.20). Line A took an intermediate

position, being notable for close values of the frequencies of alleles A and B (0.46 and 0.54, respectively). No associations between different allelic variants of *GHR* and the performance parameters of chickens were found using this polymorphism assay (Kulibaba 2015).

Pituitary-specific positive transcription factor 1 and insulin-like growth factor 1 genes

The pituitary-specific positive transcription factor 1 (PIT1, also known as POU1F1) is a tissue-specific protein expressed in the front part of the hypophysis; it takes a direct part in regulating the expression of *GH, PRL* and other genes (Manjula et al. 2018). Along with the involvement in regulating the expression of the genes of the abovementioned hormones, PIT1 participates in the processes of proliferation and differentiation of the hormone-secreting cells of the hypophysis (Mukherjee and Porter 2012). The functions of PIT1 are directly related to the functioning of the controlled genes (*GH* and *PRL*) and indirectly related to the traits it may influence, which makes PIT1 a promising target to investigate the interrelations between different allelic variants and the productive traits of animals (Van As et al. 2006). In chickens, the *PIT1* gene consists of six exons and five introns, is located on chromosome 1, and encodes a protein of 327 amino acid residues. The associations have been reported between different allelic variants of *PIT1* and the productivity traits in various chicken breeds from different world regions (Agaviezor, Ajayi, and Udoudo 2020; Bello et al. 2020).

IGF1 belongs to the family of insulin-like growth factors and fulfils several physiological functions related to the growth and differentiation of different types of tissues, which makes it an auspicious candidate for the needs of practical poultry genetics and breeding (Fujita et al. 2019). The *IGF1* gene contains 4 exons and 3 introns and is localised on chromosome 1, encoding a protein of ~153 amino acid residues. The polymorphism of the *IGF1* locus in chicken populations of different breeds and utility purpose has been studied rather well (Bhattacharya et al. 2015; El-Attrouny et al. 2021). The associations were found between different allelic variants of *IGF1* and the meat and egg production traits in different chicken breeds (Kim, Seo, and Ko 2004; Hosnedlova et al. 2020).

The investigations of the genetic structure of chicken populations of Ukrainian selection were conducted (Kulibaba 2018b) by examining the presence of the 57-bp insertion in intron 2 of the *PIT1* gene following Nie et al. (2008). This study revealed the similarity in the values of the allele frequencies for all the investigated populations. However, in terms of the distribution of genotypes, the chickens of the egg-meat type differed from other lines by their higher values of the frequency of homozygotes II compared to DD. At the same time, lines A and H-2 were almost similar relative to the frequencies of homozygous genotypes. The analysis of associations with performance traits resulted in the connection between the DD genotype and meat productivity of Poltava Clay chickens: the chickens of this genotype were characterised by higher values of thigh weight as compared to the chickens of the II genotype. The association analysis did not demonstrate any other associations between allelic variants of *PIT1* (I or D) and productive parameters of the experimental chicken lines (Kulibaba 2018b; Kulibaba and Tereshchenko 2015).

The analysis of the *IGF1* gene variations in the chicken lines of Ukrainian selection was carried out (Kulibaba and Tereshchenko 2015; Kulibaba et al. 2020) using the *Pst*I-based polymorphism in 5' UTR (Li, Li, and Li 2009) and *Hinf*I-assisted polymorphism in the promoter region of this gene (Khadem, Hafezian, and Rahimi-Mianji 2010). The domination of the frequency of allele C_2 over C_1 in 5' UTR was established in all the experimental chicken populations of Ukrainian selection, which reached its maximum value in line H-2 of the meat-egg chickens. Hereby, based on the *Hinf*I-polymorphism in the promoter area of *IGF1*, the preponderance of allele A frequency over allele C was noted only for line H-2; higher values of allele C frequency were observed in all the other investigated lines. The association between genotypes and egg production traits (i.e. egg number for both 12 and 40 weeks of lay) was found only in the Rhode Island Red breed for the over-representation of heterozygotes C_1C_2 when using the *Pst*I-assisted polymorphism. Also, the predominance of the CC genotype by egg number for 40 weeks of lay was determined in the Poltava Clay line 14 using the *Hinf*I-based polymorphism. This line was also noted for the associations between *Hinf*I-assisted polymorphic genotypes and meat performance traits, when the chickens of the CC genotype had higher indices of body weight and drumstick muscle weight (Kulibaba and Tereshchenko 2015; Kulibaba et al. 2020).

Transforming growth factor-β family genes

The family of transforming growth factors-beta (TGF-β) belongs to one of the most relevant groups of proteins that participate in the regulation of the main physiological functions of the organism (Halper, Burt, and Romanov 2004; Poniatowski et al. 2015; YiKim, Kim, and Kim 2005). The members of the TGF-β family belong to multifunctional signalling proteins that play an important role in supporting tissue homoeostasis, growth, differentiation of different cell types and the intercellular matrix formation; they are apoptosis inductors and take part in regulating the immune system (Rosairo et al. 2008). Each member of the TGF-β family is encoded by a separate gene (Halper, Burt, and Romanov 2004). For instance, the *TGF-β1* gene is located on chromosome 13 in chickens and consists of nine exons and eight introns, encoding 393 amino acid residues. *TGF-β2* is located on chromosome 3 and contains seven exons and six introns needed for synthesising a protein of 412 amino acid residues. It is also the largest representative of the TGF-β family. The *TGF-β3* gene is located on chromosome 5, consists of seven exons and six introns, and encodes a protein of 412 amino acid residues. Due to a broad spectrum of physiological functions, the *TGF-β* family members are among the priority genes for investigating the association between their allelic variants and the productive traits of poultry. This makes the *TGF-β* genes promising targets for the application in the MAS programs. The polymorphic variants of each component of the family have been described in various investigations (Chen et al. 2013; Jin et al. 2013; Tang et al. 2010).

The study of the polymorphism of the *TGF-β* family members in the chicken populations of Ukrainian selection was performed (Kulibaba 2018b; Kulibaba and Tereshchenko 2015) using the methods described by Li et al. (2003). These involved the identification of the transversion of cytosine into adenine in position 632 (C632A) for *TGF-β1*; the transition of thymine into cytosine in position −640 (*T*-640C) for *TGF-β2*; and the transversion of cytosine into adenine in position 2833 (C2833A) in intron 4 for

TGF-β3. As a result, various allelic variants were revealed using the said polymorphisms of the *TGF-β* gene family members in each experimental chicken population of Ukrainian selection. As for the polymorphism of the *TGF-β1* gene, it was found that line A had almost equal values of the frequencies of alleles B and F, while the other lines were notable for the prevalence of the allele F frequency values. The association between allele F and the egg and meat production parameters of poultry was determined in all the experimental populations except for the Rhode Island Red (Kulibaba and Tereshchenko 2015).

Close values of allele B and L frequencies were observed using the *Rsa*I-assisted polymorphism in *TGF-β2* promoter in line H-2, whereas other populations were notable for the predominance in the allele B frequency. A positive association between the LL and BL genotypes and the egg performance indices was identified in the chicken populations of the Birkivska Barvysta and Rhode Island Red breeds. Line 38 was also characterised by greater values of stomach muscle weight in the chickens of the BB genotype (Kulibaba and Tereshchenko 2015; Kulibaba 2018b). The association between the chickens homozygous for allele L and higher values of the egg production parameters was demonstrated in the study by Li et al. (2003) using commercial chicken lines.

At the *TGF-β3* locus, the prevalence of the allele L frequency value over that for allele B was found in all the experimental populations except for line 14 where close values of allele frequencies were noted. The positive association between allele L and the egg productivity indices was identified in all the experimental populations, which was consistent with the data obtained by Li et al. (2003). Greater values of liver weight were found in the chickens of genotype LL in line 38, whereas higher values of heart weight were notable in the chickens of genotype BB (Kulibaba et al. 2015; Kulibaba 2018b).

Myxovirus resistance gene

Mx protein is one of the key components participating in the inhibition of the replication of RNA-retaining viruses; it belongs to interferon-induced proteins (Haller, Frese, and Kochs 1998). Mx protein acts specifically against RNA-retaining viruses, the most well-known representatives of which are influenza viruses, making Mx of special importance for poultry breeding (Alam et al. 2022; Majeed et al. 2023). There are polymorphic variants of Mx protein, some of which are of priority relevance. For example, the presence of serine (S) in position 631 of Mx protein (Ser631) leads to the inhibition of antiviral activity, while the presence of asparagine (N, Asn631) correlates with the manifested antiviral activity. It was discovered that the above mutation S631N is the direct consequence of the transition of guanine into adenine in position 2032 (G2032A) of the *Mx* gene (Sasaki et al. 2013). It was also shown that the mentioned transition is located at the *Rsa*I restriction site, which allowed for designing a rather simple and convenient method of its determination as described by Sironi et al. (2010). The *Mx* gene contains 14 exons and 13 introns in its structure and is located on chromosome 1. Due to the high priority of the studies in the field of genetic resistance to viral diseases, first of all, the influenza viruses, there have been investigations carried out in various countries and aimed at monitoring the S631N mutation in different chicken breeds, from commercial highly productive lines to native populations (Hassanane et al. 2018; Okafor et al. 2023).

High variability of this *Mx* gene mutation was observed in the chicken populations of several breeds of different utility purpose (Li et al. 2018).

In a study of chicken populations and lines of Ukrainian selection (Kulibaba et al. 2020), analysis of the incidence of S631N mutation in the *Mx* gene using the determination of the *Rsa*I-based polymorphism in exon 13 was performed (De Qin et al. 2010). The investigation by Kulibaba et al. (2020) showed that *Mx* gene was polymorphic in all the chicken populations of different utility purpose. The highest level of polymorphism (by the value of the effective number of alleles) was reported in line A. The highest frequency of the resistant allele A was detected in the population of layer hens of the Birkivska Barvysta breed, and the lowest one in the egg-meat chicken populations of the Rhode Island Red and Poltava Clay breeds. By the distribution of the frequencies of alleles and genotypes, lines 14 and 38 demonstrated a stable population and genetic structure for several generations. Analysis of the association between the genetic variations and economically important traits suggested that allelic variants of the *Mx* gene correlated with the egg production traits of Birkivska Barvysta chickens. Herewith, the chickens of the GG genotype were remarkable for a greater value of egg number for 40 weeks of lay as compared to chickens of genotypes AA and AG. While comparing the values of productivity parameters between the Rhode Island Red chickens of genotype GG and heterozygotes AG, significant differences were found in the indices of egg weight and liver weight. No significant differences were found for other traits. The results of this investigation were concordant with the data reported by De Qin et al. (2010) that suggested a positive association between allele G and the production traits of different local chicken breeds.

Microsatellite diversity

Study of the conventional genetic and population parameters in the chicken lines of different utility purpose and Ukrainian selection was conducted using the combination of microsatellite markers (Kulibaba 2018a; Kulibaba and Liashenko 2018a). These were both selectively neutral (*LEI0094, LEI0166, LEI0192, ADL268, ADL278, MCW034, MCW081, MCW104, MCW123* and *MCW330*) and related to the manifestation of resistance to neoplastic diseases (*MCW0245, MCW0257, MCW0282* and *MCW0288*) (Heifetz et al. 2009; McElroy et al. 2005). According to the results of the studies by Kulibaba and Liashenko (2018a), there was a total of 66 alleles over all the loci and in all the experimental populations. The highest number of alleles (64) was defined in line H-2, and the lowest one (50) in the Birkivska Barvysta and Rhode Island Red breeds. As for the value of the average number of alleles per locus, its lowest value across all the experimental chicken populations was noted for locus *MCW0257* (2), and the highest one for *LEI0192* (6.75).

Only three of all loci were remarkable for the excess of heterozygotes; the others were notable for rather a pronounced excess of homozygous chickens (judging from positive values of the Wright's (1949, 1950) F_{IS} statistics). This reflected the specificities of the selection work carried out within these gene pool populations (including inbreeding (Khvostik and Bondarenko 2016)). The average values of the F_{IT} statistics were 27.5%, with the maximum values being noted for loci *MCW0245* and *MCW0257*. Among all the investigated lines, the highest value of the excess of homozygous chickens (the average

values by all the loci) was identified in the Birkivska Barvysta breed, and the lowest value in the Rhode Island Red. The results of the F_{ST} statistics (fixation index) calculation demonstrated that the experimental populations were characterised by a considerable divergence: 19.5% of the total genetic variability was distributed among breeds, whereas 80.5% was related to the intrabreed component (Kulibaba and Liashenko 2018a).

The Nei's (1972) genetic distance computation suggested that the populations of meat-egg chickens (line H-2) and Rhode Island Reds were characterised by the greatest genetic differences (65.9%), whereas line H-2 and the Poltava Clay breed had the lowest ones (32.3%). Also, 35.9% differences were found between two egg-meat breeds, Poltava Clay and Rhode Island Red. The layer hens of the Birkivska Barvysta breed were most different from Rhode Island Reds (58.8%). The plotting of a phylogenetic tree based on the neighbour-joining (NJ) model demonstrated that the general tree topology conformed to the utility purpose of poultry. The chicken populations of the egg-meat type of Poltava Clay and Rhode Island Red breeds formed a separate cluster. The chicken populations of White Plymouth Rock (meat-egg type) and Birkivska Barvysta (layer chickens) formed separate filiations (Kulibaba and Liashenko 2018a).

The examination of microsatellite variability in chicken populations of different utility purpose (Kulibaba and Liashenko 2018b) was performed along with the analysis of the genetic differentiation among five subpopulations of Ukrainian meat-egg chickens (H-1, H-2, H-3, H-4 and S) based on eleven ISAG-FAO-recommended (Weigend, Romanov, and Rath 2004a) microsatellite markers (*MCW081, MCW034, LEI0192, MCW104, MCW020, ADL268, LEI0166, ADL278, LEI0094, MCW330* and *MCW123*). Accordingly, the total allele pool of all the investigated subpopulations at the selected loci encompassed 38 separate alleles. The lowest number of alleles for all the loci was found in the subpopulation H-4 (30), and the greatest one in the subpopulation H-2 (35). Across all the experimental chicken subpopulations, the minimum genetic diversity estimated by the number of alleles per locus was reported for marker *ADL278* (three alleles per locus), and the highest one for *MCW104* (6.4 alleles per locus). The results of these investigations showed two private alleles determined in the subpopulation H-2 at the *LEI094* locus and in the subpopulation H-1 at the *MCW123* locus (Kulibaba and Liashenko 2018b).

Each investigated subpopulation had a deficit of heterozygous chickens, which was manifested the most in the subpopulation S (15.6%). Subpopulations H-2 and H-3 took an intermediate position and actually coincided in the value of this index (7.5%), while H-1 was notable for its minimum value (5.3%), which, as a whole, suggested a gradual rise in inbreeding among the experimental poultry groups due to the use and effect of the inbreeding method (Moiseeva 1970) in their selection process. The results of applying the F_{ST} fixation indices for the estimation of genetic differentiation showed that a larger part of the determined genetic variability was attributed to the intrapopulation component. This was seen in the calculated F_{ST} values, according to which 9.2% of genetic diversity was distributed between subpopulations and 91.8% within subpopulations. The output of the estimations of Nei's genetic distances pointed out that the most genetically distant subpopulations were H-1 and H-4 (28.8% difference), while the closest ones were subpopulations H-2 and H-3 (13.3% difference). The obtained data were confirmed by the general structure of the phylogenetic tree built using the unweighted pair-group method with arithmetic mean (UPGMA) (Kulibaba and Liashenko 2018b).

Similar investigations (Kulibaba 2018a) were also conducted on the experimental lines 02 and 38 of the Rhode Island Red breed using eight microsatellite loci recommended by ISAG-FAO (Weigend, Romanov, and Rath 2004a). Lines 02 and 38 were found to be rather similar as followed from these investigations. Using the combination of markers, 29 alleles were observed in line 02 and 28 alleles in line 38. The minimum number of alleles per locus in both lines was determined for *LEI094* (2) and *MCW081* (2), and the maximum number for *MCW104* (six for line 02 and seven for line 38). In line 02, the fixation index value was negative at loci *LEI094* (−0.05), *LEI166* (−0.05) and *MCW034* (−0.07). Herewith, the excess of homozygotes was detected for loci *MCW0081, MCW0104* and *MCW0123* (0.25, 0.09 and 0.15, respectively). Insignificant deviations from the genetic equilibrium state were identified for all the other markers. The Nei's genetic distance value between lines 02 and 38 was 0.079, whereas the value of genetic similarity was 0.924. It was found by the F_{ST} value that only 2.7% of the total genetic variability across all the loci was distributed between the populations. The obtained F_{ST} value was thus indicative of poor divergence between lines 02 and 38 of the Rhode Island Red Breed (Kulibaba 2018a).

Conclusions

In view of the declining of a number of Ukrainian native chicken breeds, lines and flocks, one of the paramount and high-priority gene pool conservation measures is to evaluate the main parameters of their current genetic variability. Over the last decade, there have been a few relevant molecular genetics studies to identify the polymorphism of the major genes presumably related to important quantitative trait loci and analyse the features of the distribution of the respective allele and genotype frequencies. Based on the results of the conducted studies in native lines of different utility purpose that we have reviewed here, it has been shown that such genes as *PRL* (24-bp indel and C-2402 T), *PRLR* (*Bam*HI-assisted polymorphism in exon 5) *GH* (*Msp*I polymorphism in introns 1 and 4, and *Sac*I and *Alu*I polymorphism in intron 4), *GHR* (*Hind*III and *Nsp*I polymorphisms in introns 2 and 5, respectively), *IGF1* (*Pst*I and *Hinf*I polymorphisms in 5' UTR and promoter, respectively), *PIT1* (57-bp indel), *TGF-β1* (C632A), *TGF-β2* (*T*-640C), *TGF-β3* (C2833A) and *Mx* (G2032A) were polymorphic in the experimental populations studied. The *PRLR* gene (*Bam*HI polymorphism in exon 5) was monomorphic in all groups. In the Poltava Clay population, the *PRL* gene was represented by a single variant (allele D) based on the presence of the 24-bp insertion in the promoter region. At the same time, according to *Hind*III polymorphism in intron 2, various allelic variants of the *GHR* gene were identified only in the Poltava Clay chickens. For most of the studied loci related to quantitative (phenotypic) traits, the populations were in a state of genetic equilibrium, which suggested the absence of pronounced microevolutionary processes at the current stage of selection work in these breeds and lines.

Notably, a new polymorphism in intron 4 of the *GH* gene (transition C→T at position Chr27:1788455) was described. Based on the results of these studies, all possible genotype variants (CC, CT and TT) were identified in each of the experimental chicken populations. The presence of transition C→T was characteristic of the predominant number of individuals.

The indices of meat and egg productivity were also analysed in individuals with different genotypes at the identified polymorphic loci. Promising genotypes for each of the studied chicken lines were described for use in further MAS programs.

Using a complex of microsatellite loci, the main parameters of microsatellite variability were established, the genetic diversity patterns among Ukrainian native chicken breeds were revealed and the genetic distances between experimental lines were calculated. Collectively, the reviewed research results provide the necessary information on the gene pool features of Ukraine's native genetic resources that can be implemented both in breeding programs (using MAS) and in gene pool conservation strategies.

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