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Research Article
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Large-scale genome-wide SNP analysis reveals the rugged (and ragged) landscape of global ancestry, phylogeny, and demographic history in chicken breeds

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Abstract: The worldwide chicken gene pool encompasses a remarkable, but shrinking, number of divergently selected breeds of diverse origin. This study was a large-scale genome-wide analysis of the landscape of the complex molecular architecture, genetic variability, and detailed structure among 49 populations. These populations represent a significant sample of the world's chicken breeds from Europe (Russia, Czech Republic, France, Spain, UK, etc.), Asia (China), North America (USA), and Oceania (Australia). Based on the results of breed genotyping using the Illumina 60K single nucleotide polymorphism (SNP) chip, a bioinformatic analysis was carried out. This included the calculation of heterozygosity/homozygosity statistics, inbreeding coefficients, and effective population size. It also included assessment of linkage disequilibrium and construction of phylogenetic trees. Using multidimensional scaling, principal component analysis, and ADMIXTURE-assisted global ancestry analysis, we explored the genetic structure of populations and subpopulations in each breed. An overall 49-population phylogeny analysis was also performed, and a refined evolutionary model of chicken breed formation was proposed, which included egg, meat, dual-purpose types, and ambiguous breeds. Such a large-scale survey of genetic resources in poultry farming using modern genomic methods is of great interest both from the viewpoint of a general understanding of the genetics of the domestic chicken and for the further development of genomic technologies and approaches in poultry breeding. In general, whole genome SNP genotyping of promising chicken breeds from the worldwide gene pool will promote the further development of modern genomic science as applied to poultry.

Key words: Chicken genome diversity; Single nucleotide polymorphism (SNP) analysis; Gene pool; Global ancestry; Phylogeny; Demographic history

1 Introduction

The assessment of the genetic diversity landscape is of great importance for preserving genetic resources, performing the genetic identification of breeds, studying the history of their genetic divergence, and improving the efficiency of breeding in farm animal populations (Moiseyeva et al., 1993; Tixier-Boichard et al., 1999; Sulimova et al., 2005). Domestication and subsequent artificial divergent selection for economically important or aesthetic (ornamental) traits led to the formation of many different chicken breeds, which contributed to a significant rise in genetic diversity (Weigend et al., 2004a; Dementieva et al., 2022b). Poultry industry progress in recent decades and intensive breeding, relying on a limited number of highly productive

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commercial lines, may have led to reduced genetic variability. They may also have led to a lower qualitative assortment of the products and a displacement of local gene pool breeds that could be carriers of valuable genetic variants. The architecture of the genomes of poultry species and the genetic cost of domestication can be revealed by large-scale genomic analysis (Andersson, 2001; Wang et al., 2021).

According to the Food and Agriculture Organization of the United Nations (FAO) (Baumung and Wieczorek, 2015), of 1729 chicken breeds registered worldwide, only 212 are not yet at risk of extinction. Thirty years ago in Russia, there were 26 native chicken breeds (Moiseeva, 1995; Moiseyeva, 1996), but currently many local breeds exist only as small populations and are preserved mainly in two gene pool collection farms. The first of these was established at the All-Russian Poultry Research and Technological Institute (ARPRTI; Sergiev Posad, Moscow Oblast, Russia) and embraces various breeds of chickens, geese, and other poultry species (Bondarenko et al., 1986). The second collection was created for the conservation of numerous chicken breeds at the Russian Research Institute of Farm Animal Genetics and Breeding (RRIFAGB; Pushkin, St. Petersburg, Russia) (Dementieva et al., 2020b). These poultry genetic resources could be crucial for improving adaptation to local conditions and resistance to diseases in commercial lines, as well as facilitating application of innovative genomic technologies (Ryabokon et al., 2005; Baumung and Wieczorek, 2015; Tereshchenko et al., 2015).

Previously used anonymous genetic markers, e.g., mini- and microsatellites, have now given way to single nucleotide polymorphism (SNP) markers (Romanov and Weigend, 1999; Weigend et al., 2004a, 2004b; Mohammadabadi et al., 2010; Dementieva et al., 2022b). Exploring genetic variation across multiple SNP loci in concert has allowed efficient searches for gene variants associated with economically important traits for use in genomic selection (VanRaden, 2008; Christensen and Lund, 2010; Plemyashov et al., 2021b; Pocrnic et al., 2023). Using high-density SNP chips, many genome-wide association studies (GWAS) showed that variants of SNP loci can be effectively used as genetic markers for various chicken selected traits such as body weight, egg production, and shell thickness (Zhang et al., 2012; Felício et al., 2013; Romé et al., 2015; Dementeva et al., 2018; Kudinov et al., 2019; Perini et al., 2023; Sallam et al., 2023). Examination of genetic variation is a necessary step for the subsequent successful prediction of the breeding effect (i.e., assessment of breeding value and genomic selection) (Jensen et al., 1997; Christensen and Lund, 2010; Plemyashov et al., 2021a; Tan et al., 2022; Pocrnic et al., 2023). It also contributes to our understanding of selection signatures and the biological mechanisms of adaptation and other breed features (Qanbari et al., 2015; Beissinger et al., 2016; Abdelmanova et al., 2021; Mastrangelo et al., 2023; Ren et al., 2023; Romanov et al., 2023). With the advent of SNP technology, there is also the possibility of segregation of quantitative trait loci (QTL) with different frequencies in diverse breeds. These can be used to identify genes responsible for economically useful traits in both meat and egg production (Romanov et al., 2009; Qanbari et al., 2015; Romé et al., 2015; Beissinger et al., 2016; Bondarenko and Khvostik, 2020).

In genetic and phylogenetic studies of chickens, lower-density SNP arrays such as the Chicken 60K SNP iSelect BeadChip (Groenen et al., 2011) manufactured by Illumina (San Diego, CA, USA) are often used. Using this array, Wragg et al. (2012) genotyped 36 chicken breeds and populations and produced estimates of their heterozygosity and phylogenetic relationships. However, only a small number of individuals (2 to 11) from each breed were analyzed and this reduced the reliability of the resulting phylogenetic tree. For instance, the only Russian breed used in that study, Yurlov Crower (YC), turned out to be the closest by genotype to local Kenyan chickens, raising questions about the plausibility of the established interbreed relationships. Thus, when performing a sufficiently comprehensive, broad, and in-depth study of the molecular architecture, genetic variation, and detailed structure of numerous chicken breeds and populations at a new technological level, care is needed to produce verifiable and consistent results. In the present study, we planned a large-scale genome-wide SNP genotyping analysis to explore the landscape of global ancestry (Alexander et al., 2009) and phylogeny and demographic history of 49 chicken breeds and populations from the RRIFAGB gene pool collection farm using the whole genome Illumina SNP array.

2 Materials and methods

2.1 Chicken breeds and samples

The study used samples obtained from the Genetic Collection of Rare and Endangered Breeds of Chickens included in the Network Bioresource Collection of Farm Animals (Dementieva et al., 2022b; Vakhrameev et al., 2023). SNP variants were studied in 822 chickens from 49 native and imported breeds and populations kept at the RRIFAGB gene pool farm (Table 1). The studied gene pool set included both old and traditional Russian, European, Chinese, and other breeds, as well as new promising breeds and populations. Known native Russian breeds included OMF (Oyun et al., 2015a, 2015b; Moiseyeva et al., 2016), PS, PW (Moiseyeva et al., 2009a; Corti et al., 2010), YC (Moiseyeva et al., 2007a, 2009b, 2011), and RW (Dementeva et al., 2017, 2018; Kudinov et al., 2019; Dementieva et al., 2020a; Abdelmanova et al., 2021), as well as UM of Southern Russian and Ukrainian descent and PC of Ukrainian origin (Romanov and Bondarenko, 1994; Moiseyeva et al., 2006, 2007b; Kulibaba and Tereshchenko, 2015). Among the old breeds, the Pavlov chickens, FS (of French descent) and SW (of Chinese origin) are remarkable for their polydactyly trait (Moiseyeva et al., 2009a; Corti et al., 2010). Three traditional Chinese breeds, SW, CBm, and CBl, were included in this investigation. Details regarding individual breeds and subpopulations are given in Table S1.

Each breed was assigned to a group based on its main purpose of use as described within the traditional classification model of domestic chickens: (1) egg-type; (2) dual-purpose (egg-meat and meat-egg); (3) meat-type; (4) game; and (5) ornamental or fancy (Table S1) (Larkina et al., 2021). By geographical origin (Fig. S2-5 in Data S2), the populations were subdivided into 31 chicken breeds from Europe (LLB, MB, RW, WC, RWD, ZS, Pu, LMF, LGG, CG, PB, ABS, AB, Ar, NN, Pm, PC, SL, FS, Ts, YC, OMF, MG, RC, UM, BMF, HSSD, PWB, F, PS, and PW), seven from Asia (UG, CBl, BB, BL, SW, CBm, and F), seven from North America (RIR, NH, Ar, PRB, CBl, BB, and BL), and one from Oceania (AoB), with a few having been successively developed in two continents (e.g., Ar, BB, and BL).

Individual samples for genotyping were collected from unrelated birds, depending on the size of a gene

Table 1 List of chicken breeds, their codes, and subpopulations

Breed	Code	Subpopulation
Amrock	Ar	
Aurora Blue	AB	
Australorp Black	AoB	
Australorp Black Speckled	ABS	
Bantam Mille Fleur (or Russian Korolyok)	BMF	
Brahma Buff	BB	
Brahma Light	BL	
Cochin Bantam (or Pekin Bantam)	CBm	CBm1, CBm2, and CBm3
Cochin Blue	CBl	
Czech Golden	CG	
Faverolles Salmon	FS	
Frizzle	F	
Hamburg Silver Spangled Dwarf	HSSD	
Leghorn Light Brown (or Italian Partridge)	LLB	
Leningrad Golden-and-gray	LGG	
Leningrad Mille Fleur	LMF	
Minorca Black	MB	
Moscow Game	MG	
Naked Neck	NN	
New Hampshire	NH	
Orloff Mille Fleur	OMF	
Pantsirevka Black	PB	
Pavlov Spangled	PS	
Pavlov White	PW	
Pervomai	Pm	Pm1 and Pm2
Plymouth Rock Barred	PRB	
Poland White-crested Black	PWB	
Poltava Clay	PC	
Pushkin	Pu	
Red White-tailed Dwarf	RWD	
Rhode Island Red	RIR	
Russian Crested	RC	
Russian White	RW	RWS, RWP, and RWG (Fig. S1-1 in Data S1)
Silkie White	SW	
Sussex Light	SL	SL1 and SL2
Tsarskoye Selo	Ts	
Ukrainian Muffed	UM	
Uzbek Game (or Kulangi)	UG	
White Cornish	WC	WC1, WC2, and WC3 (Fig. S2-1 in Data S2)
Yurlov Crower	YC	
Zagorsk Salmon	ZS	

pool population. Blood samples for genomic DNA isolation were harvested from a wing vein. To study and establish the fine breed structure, up to 32 samples from each population were taken. DNA was isolated using commercially available kits (Thermo Scientific, Waltham, MA, USA). DNA quality was controlled using a NanoDrop 2000 instrument (Thermo Scientific). Samples with an absorption ratio at 260 to 280 nm (A_{260}/A_{280}) greater than 1.8 and a concentration greater than 50 ng/μL were used in further analysis.

2.2 SNP genotyping and post-genotyping analyses

Genotyping was executed using Illumina Chicken 60K SNP iSelect BeadChips generated for the Genome-wide Marker-assisted Selection (GWMAS) Consortium (Groenen et al., 2011) and designed for 24 samples each, following the procedure described elsewhere (Dementieva et al., 2020b; Abdelmanova et al., 2021; Larkina et al., 2021). In short, DNA samples were filtered using the GenomeStudio program (Illumina, USA) with a threshold of >80% genotyped SNP loci. Further quality control adjustment and analysis of genotyping results were performed using PLINK 1.9 software (Purcell et al., 2007). To eliminate the influence of sex on this evaluation, SNP markers located on the sex chromosomes were excluded. Based on the obtained SNP genotypes, bioinformatic analyses were carried out. These involved determining such population genetic parameters as metrics of inbreeding (F_{IS}), heterozygosity (H_o), linkage disequilibrium (LD), run of homozygosity (ROH; including the respective index of genomic inbreeding F_{ROH}) (Biscarini et al., 2019), and effective population size (N_e) (Barbato et al., 2015) (Table S2). Through multidimensional scaling (MDS; available in PLINK 1.9), principal component analysis (PCA), and the ADMIXTURE 1.3 program (Alexander et al., 2009), within and between breeds (subpopulations) heterogeneity and clustering analyses were implemented. Genetic distances between populations for PCA were identified using the EIGENSOFT 6.1.4 software (Patterson et al., 2006). To visualize the obtained MDS results, the ggplot2 library in R was used (Wickham, 2009). The number of ancestral populations (K) was determined using a common ADMIXTURE-assisted cross-validation (CV) method (Weir and Cockerham, 1984). In comparison to alternative K values, the assumed number of K corresponded to the CV error with the lowest value. The implementation of the ADMIXTURE program enabled estimation of global ancestry, defined as the percentage of ancestry from each contributing population, taken as an average over each individual's complete genome (Alexander et al., 2009).

In addition, for a general analysis of the genetic diversity and phylogeny of all 49 breeds and populations, pairwise values of fixation index (F_{ST}) were computed and used as measures of genetic distance (kinship). Using the PHYLogeny Inference Package (PHYLIP) (Felsenstein, 1989, 2005) software, the neighbor joining algorithm (Saitou and Nei, 1987), and F_{ST}-based distances, a rootless phylogenetic tree was generated and graphically plotted using iTOL v4 (Letunic and Bork, 2019).

3 Results

3.1 Genetic diversity and genomic variability in small chicken populations

Based on the results of SNP genotyping, values of F_{IS}, H_o, LD, and ROH metrics were generated as the main parameters characterizing the state of genomic diversity in the studied populations (Table 2; Table S2-1 and Fig. S2-2 in Data S2). The H_o level fluctuated from 0.002 (in NN) to 0.162 (in CBm). Breeds with higher F_{IS} tended towards slightly lower H_o values (CBm, PWB, and CG). HSSD, RWS, BMF, CBm, PW, BL, and CG also had higher F_{ROH} values. Higher F_{IS} and lower H_o values may have been due to the smaller size of some studied populations, such as CBm and PWB. Although the CG population was large enough, a lower genetic diversity in this breed could be explained by a limited number of males involved in breeding. The LD measure in the studied breeds was higher in RWS, SL2, HSSD, and BMF. A small population size in these breeds, as well as reduced reproduction rates, could suggest a possible increase in inbreeding in future generations. On the whole, the presence of a large number of SNP markers that were in non-equilibrium linkage suggested a limited population size or a small number of effectively working roosters in a group.

Table 2 shows data on the extent and number of homozygous regions in the main gene pool breeds. Overall, ROH scores (Table 2) varied significantly

across the breeds and populations studied. Higher scores were indicative of a higher proportion of ROHs in the genome of individuals, as in HSSD, RWS, CBm, BMF, LLB, CG, and PWB. An unevenness in the number of ROHs among individuals in a population suggested a possible emergence of random crossbreds or traces of gene flow from unrelated groups of the same breed.

Using MDS, expected genetic differences and the possibility of genetic identification of the examined breeds and (sub)populations were demonstrated (Fig. 1; Fig. S2-3 in Data S2). In all, the between-breed diversity was determined by the type of utility and the respective phenotypic traits of a particular chicken breed/population available in the Bioresource Collection. MDS analysis of the 49 breeds and populations revealed the subdivision of the studied individuals into four main clusters (Fig. 1). The first cluster consisted of European layer and related breeds of light type: RWG, RWS, RWP, LLB, CG, and HSSD. Chickens

Table 2 Characteristics of runs of homozygosity (ROHs) on average for the populations of the main chicken breeds

Breed (subpopulation)[a]	Origin region (country)	Total number	ROH number	Total ROH length (bp)	Mean ROH length (bp)	F_{ROH}[b]
AB	Europe (Russia)	20	19.7±1.3	118 278.6±8387.0	6240.8±457.2	0.064±0.006
AoB	Oceania (Australia)	9	11.9±1.5	94 335.9±11 666.7	8508.3±1246.7	0.037±0.008
ABS	Europe (USSR)	20	24.5±1.4	138 977.0±12 045.2	5878.1±499.3	0.082±0.008
CBm	Asia (China)	20	58.6±2.3	358 763.2±16 152.2	6191.3±240.2	0.257±0.014
CBl	Asia (China)/North America (USA)	18	19.5±1.4	168 315.6±9865.9	9010.0±449.6	0.137±0.008
CG	Europe (Czech Republic)	16	48.5±3.9	283 378.3±25 909.2	5819.2±142.4	0.193±0.022
FS	Europe (France)	20	37.1±1.9	239 154.6±12 154.9	6584.8±284.6	0.160±0.010
LGG	Europe (USSR)	20	33.3±1.3	179 247.0±14 980.9	5291.9±337.9	0.120±0.009
LMF	Europe (USSR)	21	20.6±1.3	115 576.7±8600.1	5771.1±414.0	0.066±0.004
MB	Europe (Spain and UK)	19	10.3±1.7	88 304.6±12 503.7	8708.5±1192.0	0.036±0.008
MG	Europe (Russia)	20	8.6±0.9	96 100.2±8105.5	12 513.1±1292.0	0.111±0.019
NN	Europe (Romania)	19	19.3±0.9	157 204.4±7541.5	8326.3±389.7	0.079±0.005
NH	North America (USA)	19	8.6±1.1	65 059.3±10 586.3	7686.2±1264.8	0.022±0.004
OMF	Europe (Russia)	20	23.5±1.8	140 857.2±14 926.9	6096.6±460.5	0.079±0.010
PB	Europe (USSR)	17	14.1±1.3	98 695.1±13 409.5	7222.9±866.2	0.048±0.007
PS	Europe (Russia)	20	32.3±0.9	183 943.2±8991.1	5696.5±236.4	0.111±0.005
PW	Europe (Russia)	15	35.9±1.8	221 749.9±17 941.7	6122.9±303.9	0.214±0.064
Pm1	Europe (USSR)	20	23.7±1.7	154 585.5±16 390.1	7095.9±874.8	0.132±0.042
Pm2	Europe (USSR)	8	26.9±1.0	181 040.4±17 256.1	6696.7±495.2	0.126+0.009
PRB	North America (USA)	19	20.9±1.3	155 533.0±12 302.8	7500.9±466.1	0.126±0.010
PWB	Europe (The Netherlands and Poland?)[c]	18	37.4±6.1	250 244.1±36 797.6	8340.8±881.9	0.166±0.032
PC	Europe (USSR)	17	13.6±1.9	109 415.4±14 016.7	8874.3±942.6	0.052±0.010
RWD	Europe (England)	18	31.8±1.6	209 453.9±13 452.8	6656.8±292.1	0.131±0.012
RIR	North America (USA)	24	15.6±1.2	89 653.2±8833.4	5902.9±565.6	0.048+0.005
RC	Europe (Russia)	20	12.4±1.4	113 488.5±8278.6	11 144.7±1154.7	0.044±0.007
RW	Europe (Russia)	11	12.0±1.4	108 649.3±12 443.2	9573.3±1111.4	0.088±0.010
SW	Asia (China)	19	33.2±2.8	203 476.9±25 218.7	5840.5±504.1	0.167±0.020
SL	Europe (England)	5	45.6±4.7	229 088.0±28 271.8	5036.2±273.7	0.153±0.033
UM	Europe (Ukraine)	18	11.8±1.4	97 294.7±13 322.9	8300.1±795.7	0.042±0.009
WC2	Europe (UK and Russia)	18	16.3±1.2	97 605.7±9825.6	6084.7±525.0	0.079±0.008
WC3	Europe (UK and Russia)	19	17.6±0.9	101 565.6±8690.8	5820.4±473.0	0.083±0.007
YC	Europe (Russia)	20	12.4±1.9	123 421.5±21 749.7	10 746.5±1305.3	0.100±0.018
ZS	Europe (USSR)	18	40.5±1.3	209 098.3±14 269.0	5117.0±240.6	0.142±0.010

[a] The expanded breed codes are given in Table 1; [b] F_{ROH}, genomic inbreeding derived from ROHs; [c] The exact origin country of this breed is unknown. There is only a speculation that this could be The Netherlands and Poland. USSR: (the former) Union of Soviet Socialist Republics.

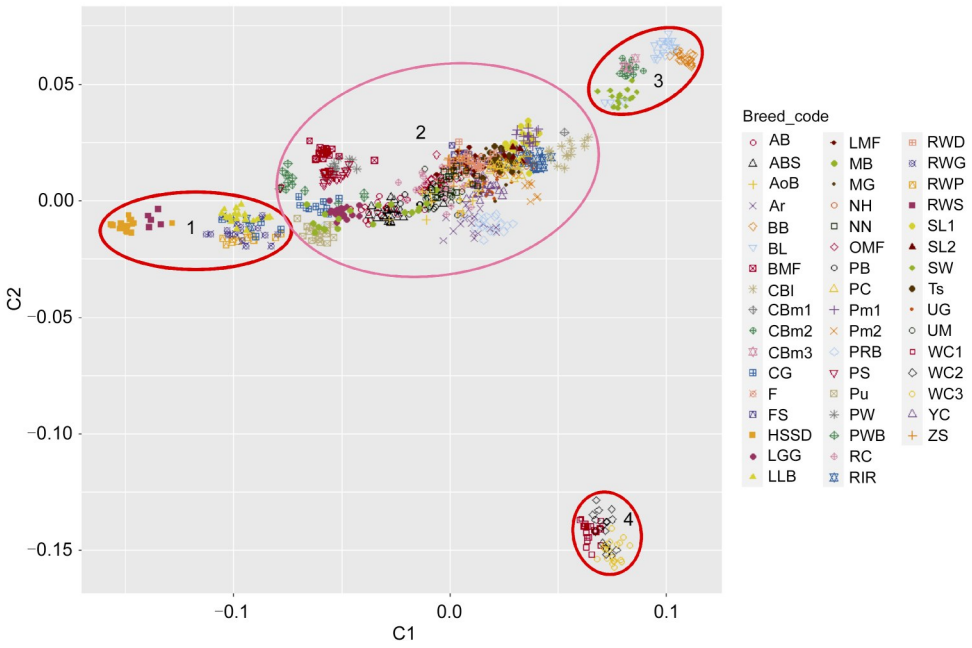

Fig. 1 Genetic identification and clustering of populations by multidimensional scaling (MDS) in all 49 breeds and subpopulations distributed among four clusters: (1) European layer and related breeds of light type; (2) dual-purpose breeds and those close to them; (3) Asiatic breeds (subpopulations) related to fancy and Bantam breeds; and (4) European meat-type chickens of heavy-type. The expanded breed codes are given in Table 1.

of the second cluster included the largest number of dual-purpose breeds or those close to them. In the upper right corner, there was a third cluster with Asiatic breeds (subpopulations) related to fancy and Bantam breeds: BL, BB, CBm2, CBm3, and SW. The group most distant from all others was the European heavy-type (i.e., meat-type) chickens that belonged to WC (subpopulations WC1, WC2, and WC3), forming the fourth cluster in the lower right corner.

The dual-purpose breeds (Fig. 1; Fig. S2-3a in Data S2) were clearly separated from each other, with PRB and Ar forming one cluster, which conformed to the origin of Ar from PRB. On the MDS plot (Fig. S2-3b in Data S2) that included the game (UG and MB) and related breeds (YC and OMF), OMF and most of the YC birds were clearly distinguishable from UG and MB. UG and MB overlapped and were merged into a common cluster, which was also mixed with a few YC chickens. We also analyzed several individuals of another variety of Orloff chickens, namely Mahogany, that significantly overlapped with OMF (Fig. S2-3b in Data S2). Finally, there was a clear distinction between egg-type (RW), meat-type (WC), and dual-purpose (RIR) breeds (Fig. S2-3c in Data S2). The three RW subpopulations were well separated among themselves according to their origin: the modern RWG subpopulation was located closer to RWS from which it is descended, while RWG was more distant from the unrelated and independent RWP subpopulation. Some RWG individuals were closer by genotype to the dual-purpose breed (RIR), which may indicate a small extent of gene flow from dual-purpose breeds to RWG. The three meat-type WC subpopulations were clearly separated on the MDS plots (Fig. 1 and Fig. S2-3d in Data S2). Moreover, WC2 and WC3, related by origin, constituted one subcluster, overlapping with each other, whereas WC1 was clearly different by genotype and descent and was significantly removed from the other two subpopulations. Also, when creating prospective two- and three-way interbreed crosses (using dual-purpose, game, and meat-type (WC) breeds), which would have higher productive traits, the crossbreds had lower homozygosity rates than purebred birds (Table S2-2 and Fig. S2-2 in Data S2). On the MDS plot (Fig. S2-3e in Data S2), crossbred combinations occupied a position equidistant from the parent breeds. F_{ST} values for interbreed offspring were greater than those calculated between parent breeds (Table S2-3 in Data S2). In addition, using the SNP scan, the fine population structure of the RW breed was explored by

PCA and MDS (Figs. S1-2 and S1-3 in Data S1, and Fig. S2-3c in Data S2), and F_{ST} values in pairwise comparisons of RW subpopulations were identified (Table S1-1 in Data S1). Using bioinformatic criteria for assessing the genetic characteristics of small populations, a methodology was developed for planning their breeding strategy, including genomic selection (Fig. S1-4 in Data S1).

3.2 Effective population size

Considering that not all individuals were involved in reproduction, the effective population size, N_e (Fig. 2), which is important for the process of population evolution, differed from the total number. By itself, the maintenance of large populations may not prevent the loss of genetic variation, unless N_e is also large enough. According to our genome-wide SNP analysis, the populations similar by phenotype, when kept in groups, could have been subject to some inadvertent or accidental crossbreeding (Table S2-4 in Data S2), and had a higher N_e as, for example, in the following breed/subpopulation pairs and trios: RWG–RWP; RIR–NH–PC; and PB–MB–AB. With extensive and prolonged mixing of breeds, even further isolated propagation and breeding will not lead to significant divergence (note that strong selection pressure is rarely possible in small gene pool groups). Genome-wide analysis enables the identification of crossbred individuals and then selection of only those individuals that are genotypically similar or identical to the overall population under preservation.

Breeds with a lower N_e both 25 and 3200 generations ago, e.g., BB, SL2, and RWS (Table S2-4 and Fig. S2-4 in Data S2; Fig. 2), at some stage of their demographic history, may have come from a limited stock of ancestors or experienced strong selection pressure over many generations. Breeds such as LMF, RC, and RW, which have developed more recently or by crossing of several breeds or by telic "blood-refreshing" mating of a breed with another purebred population, had a higher N_e 25 generations ago. An abrupt decline in N_e over a wider period of demographic history was observed in the PRB, NH, and RWG populations (Fig. S2-4 in Data S2). To assess a population's current state and demographic history, one needs to know not the total number of individuals in the population, but only the number that participated in the reproduction process. Therefore, N_e is an important indicator.

3.3 ADMIXTURE analysis

By implementing the ADMIXTURE analysis of global ancestry, more generalized results were obtained enabling us to compare the fine genetic structure and demographic history of breeds and (sub)populations representing a large sample of the worldwide

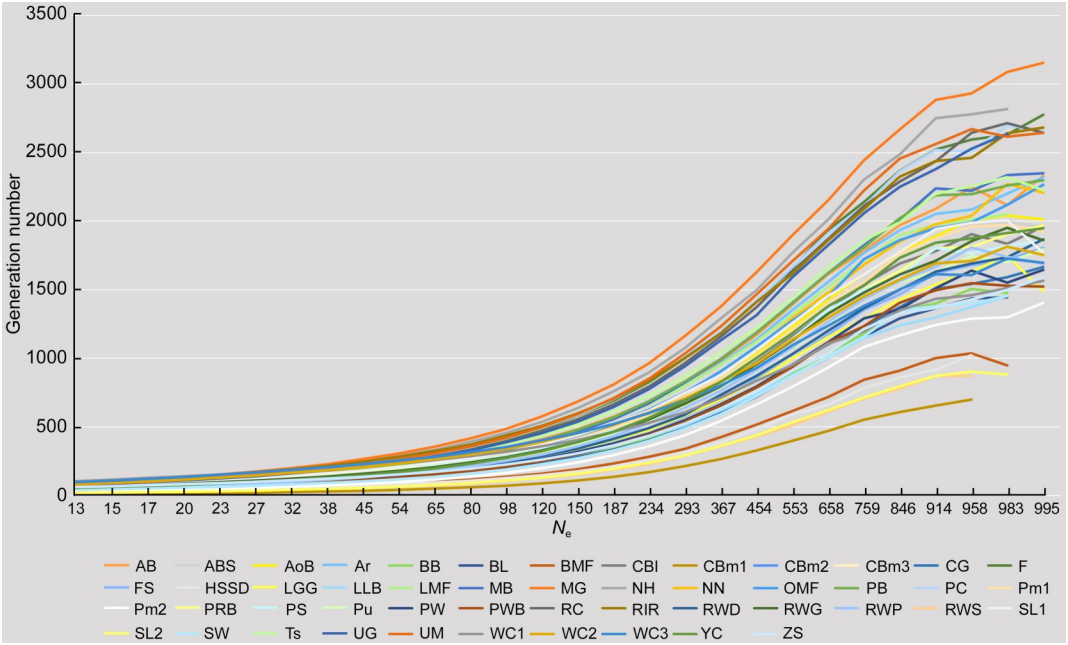

Fig. 2 Effective population size (N_e) in all 49 chicken populations. The expanded breed codes are given in Table 1.

gene pool. Fig. 3 presents data on the variability of SNP markers in the 49 populations, where a lower K=29 was selected for an optimal number of ancestral populations (Fig. S1), suggesting genetic relationships between some breeds. Distinct and more homogeneous clusters were produced using genotyped individuals of the following breeds: RWS, CBl, FS, HSSD, CBm, YC, Pu, ZS, PRB, PS, SW, BL, BB, LLB, and Pm. Some had older breed histories, some, such as RWS (Dementeva et al., 2017), had passed through a population bottleneck, and some were younger breeds (Pu and PS) whose recent intensive selection has led to significant consolidation of the breed. On the other hand, footprints of the common origin of certain breeds/populations were observed, which allowed us to discern the following groups (Fig. 3):

(1) The RW group consisted of three related subpopulations of this Russian egg-type breed (RWS, RWP, and RWG).

(2) The LLB group involved European egg-type LLB, CG (similar to LLB in coloration and possibly by origin), and partly LGG, for which LLB was one of the parent breeds.

(3) The AoB group encompassed such related Russian, European (except Russian), and Australian dual-purpose breeds as Pu, ABS, AB, MB (whose population may have crossed to AoB), PB, and AoB (the ancestor of ABS and PB), as well as LGG (with ABS being one of its progenitors).

(4) A group of old (mostly Russian) game, semi-game, and related breeds including OMF, UM, NN, UG, YC, and MG.

(5) The RIR group comprised dual-purpose RIR, NH and PC breeds (descended from RIR and NH, respectively), as well as the breeds originated from them and/or formed, among other things, due to genome introgressions in the populations of MG, RC, LMF, Ts, F, and RWD.

(6) A dual-purpose group of two SL subpopulations was identical to the Pm subpopulation group in a pairwise mode: SL1–Pm1 and SL2–Pm2, with the latter pair being partly related to CBl (due to Cochin contributing to SL).

(7) The dual-purpose PRB group embraced the nearly identical PRB and Ar breeds.

(8) ZS and FS combined in one dual-purpose cluster (due to probable random mating).

(9) The fancy PS group included the almost identical PS and PW breeds, as well as PWB.

(10) The Brahma group of Asiatic fancy breeds combined BB and BL, while CBm and SW of Bantam (dwarf) type were related to them at K=2 to K=7.

(11) The WC group combined three related subpopulations (WC1, WC2, and WC3).

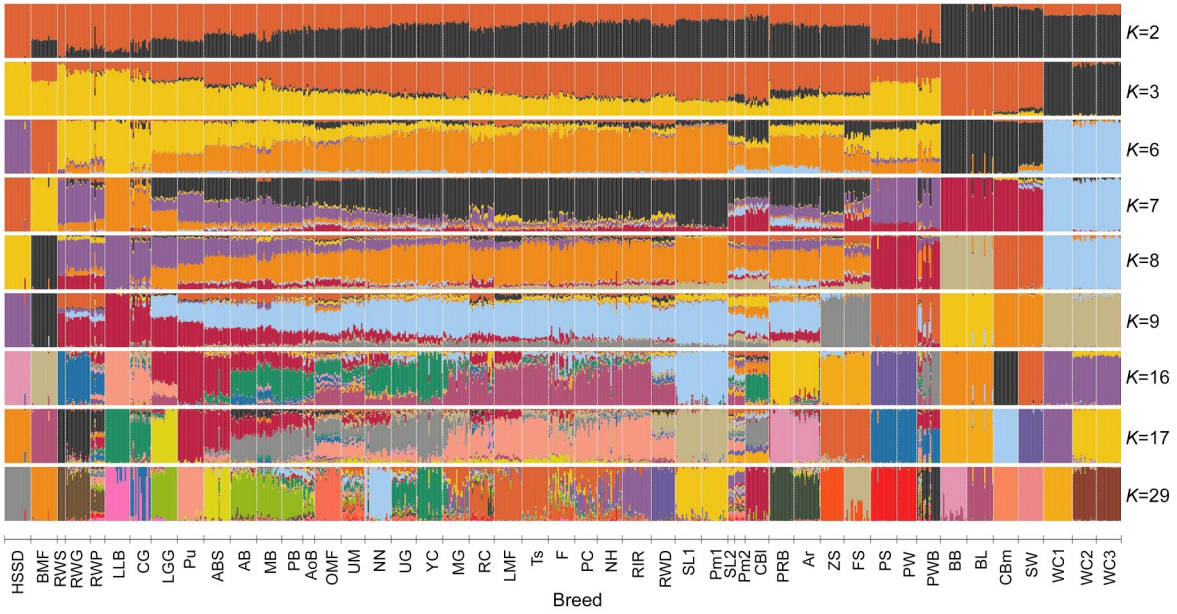

Fig. 3 ADMIXTURE-assisted rugged (and ragged) landscape of global ancestry, with the optimal number of ancestral populations being K=29 (see the respective cross-validation (CV) error plot in Fig. S1), in the gene pool breeds/subpopulations. The expanded breed codes are given in Table 1.

Each of two Bantam breeds, HSSD and BMF, had a distinct and unique genomic architecture. A few breeds seemed not to be consolidated genetically, including F and NN whose populations are preserved in the collection only as genotypes carrying the frizzle and naked neck phenotypes, respectively. We also noted the presence of "impurities" in PC that was recently collected from poultry fanciers and had a high N_e. Also, we noted a higher admixture and the presence of "impurities" of various breeds in the populations of F, NN, PC, and others. In general, the fine structure of the studied large portion of the worldwide gene pool could be characterized as a rugged (and ragged) genomic landscape of ADMIXTURE-assisted global ancestry, breed variation, and demographic history, as illustrated in Fig. 3.

3.4 Overall 49-population phylogeny analysis

Using the pairwise F_{ST} values inferred from SNP genotypes (Table S3), a phylogenetic tree was plotted (Fig. 4) that made it possible to conduct a general analysis of the genetic diversity and phylogeny of this extensive sample of the worldwide chicken gene pool.

In the generated phylogenetic tree (Fig. 4), a number of remarkable patterns were identified. In particular, the 49 genotyped (sub)populations were grouped into four main evolutionary branches, one of which (blue lines in Fig. 4) was represented mainly by breeds of European origin, another (red lines) by breeds of Asiatic roots, and two others (dark and light green lines) by breeds of mixed origin. Furthermore, the tree topology, to a certain extent, was fitted into the four evolutionary lineages of chicken breed formation

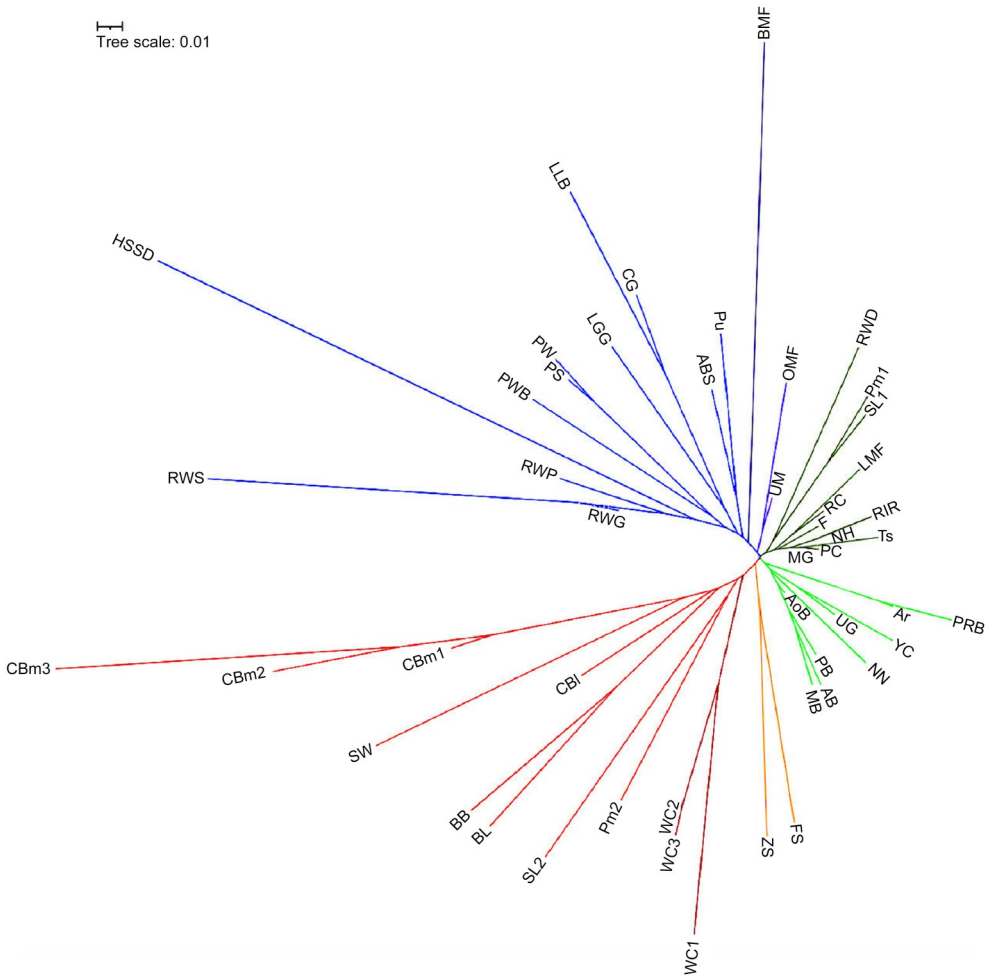

Fig. 4 A phylogenetic tree based on single nucleotide polymorphism (SNP) genotypes and visualizing relationships among 49 chicken breeds and (sub)populations. The expanded breed codes are given in Table 1. The respective Newick tree format is provided in Data S2.

postulated by Moiseyeva et al. (2003), i.e., egg-type, meat-type, game, and Bantam. For instance, BMF, a Bantam breed that, according to Moiseyeva et al. (2003), is one of the four evolutionary branches, occupied a fairly independent twig in the present study. This observation, moreover, was consistent with BMF being an old local Russian breed, also known as the Russian Korolyok, with a unique phenotype. Separate branches of blue and red colors, respectively, were formed by the breeds of European (Mediterranean) and Asiatic descents. However, Moiseyeva et al. (2003), in their data analysis, clearly overlooked another evolutionary breed lineage that formed an independent, basal branch on the kinship cladogram. This included two related American breeds, RIR and NH, developed by combining features of European and Asiatic chickens in their genomes. In our study, the respective large group of synthetic dual-purpose (egg-meat and meat-egg) breeds occupied two distinct clusters (green lines) on the dendrogram of 49 populations.

3.4.1 Egg-type and other European breeds

The plotted phylogenetic relationships (Fig. 4) provided more evidence relevant to the history of each population or breed. For example, three subpopulations of egg-type Russian Whites (RWS, RWP, and RWG) formed one subcluster, as expected. RWG is the current population of RW chickens derived from RWS using an introductory telic cross to the typical egg-type breed of White Leghorns (Table S1) (Larkina et al., 2021). Other related breeds and (sub)populations were clustered as expected, e.g., the two varieties of the Pavlov breed, PS and PW, the latter having been known in the past as the Old Pavlov and considered a derivative of the Sultan. Since the Old Pavlov was totally lost in the 20th century, birds resembling Sultans were apparently used in the last two decades, while restoring the breed and its new varieties, PW and PS. These further adjoined PWB, which also has some resemblance to Sultan and Pavlov. Two other breeds, CG and LLB, also shared similarities, i.e., a Mediterranean body type and wild plumage coloration, although a probable random mating of LLB with CG may have occurred in the past (Table S1) (Larkina et al., 2021). For the same reason (and, possibly due to intercrosses during breed development), LGG also adjoined here. Pu and ABS, which constitute another separate subcluster, are probably very close to each other by origin (both were created at the RRIFAGB) or one originated from the other.

3.4.2 Dual-purpose and other mixed breeds

The almost coincident position of the dual-purpose breeds RIR and NH (similar in appearance) on the tree is explained by their origin in two nearby Eastern American states. In addition, the probability of random mating between the two breeds, as well as between NH, MG, and PC, was assumed, which led to combining all these breeds in the same subcluster. Another American breed, Ar, was bred from PRB and introduced to Germany (Table S1) (Larkina et al., 2021). Both breeds are of dual-purpose type and have a similar build and barred plumage. These two breeds also occupied nearly identical branches on the phylogenetic tree. The similarity of YC and UG, which were in the same subcluster, could be because, firstly, some game chickens could have participated in the creation of YC, and, secondly, a probable random mating between these two breeds cannot be excluded. The following four mostly dual-purpose breeds made up one common subcluster: AoB, PB, and MB, all three having a solid black plumage, as well as AB with a blue feather color. They have a common origin and/or demographic history. AoB was bred from a few ancestral breeds including MB, and might recently have had a further probable random mating to PB and MB. PB originated from a few other breeds including AoB and was recently subject to probable random mating to AoB and MB. MB was likely to have been randomly mated to PB and AoB. AB was derived from ABS with a probable recent random mating to AoB (Table S1) (Larkina et al., 2021).

3.4.3 Meat-type and other Asiatic breeds

All three subpopulations (WC1, WC2, and WC3) of the meat-type White Cornish (Table S1) (Abdelmanova et al., 2021; Larkina et al., 2021) formed a single and distinct subcluster. Although this heavy-type breed is of European descent, the Aseel or Malay fowls of Asiatic origin were originally used for WC development (Table S1) (Abdelmanova et al., 2021; Larkina et al., 2021). Note that there was a very significant similarity in SNP genotypes between WC2 and WC3 (from the 2006 sample bank) that were related lines A and B, respectively. WC1 was noticeably different from WC2 and WC3, since it had a different

origin, being the descendants of a three-line cross (from the DNA sample bank). All three CBm subpopulations (CBm1, CBm2, and CBm3) also formed one subcluster and were joined by the related CBl as well as SW, all these traditional strains being of Chinese origin. Also, a pair of two Brahma populations, BB and BL, of Indian origin joined the same subcluster. All of these breeds are traditionally regarded as Asiatic, being moderately close to each other. Intriguingly, two subpopulations of the Light Sussex (SL1 and SL2) and two subpopulations of Pervomai chickens (Pm1 and Pm2), which are relatives to the Light Sussex, ended up on different branches of the tree. Moreover, SL1 and Pm1 formed a close subcluster on the green (dual-purpose) branch, while SL2 and Pm2 were very close to each other on the red (meat-type) branch. This may be evidence of some parallel genetic divergence of these two pairs of subpopulations, with a probable simultaneous introgression of meat-type SNP variants into the SL2–Pm2 pair. The SL2 and Pm2 subpopulations were represented by banked samples obtained from amateur breeders and were the offspring of crossbreds with BL (Table S1). Indeed, in some SL2 and Pm2 chicks a slightly feathered metatarsus was observed. This suggests that to increase body weight in SL2 and Pm2 birds there was a probable introductory crossing with BL, the breed that, like SL and Pm, has the Colombian plumage color. Therefore, the SL2–Pm2 twig went into the Asiatic (meat-type) supercluster. Thus, in the case of SL and Pm chickens, the pairs of subpopulations SL1–Pm1 and SL2–Pm2 were discriminated from each other, proving that different demographic histories of subpopulations of disparate origins, even those seemingly belonging to the same breeds, can lead to significant genetic divergence between them.

3.4.4 Ambiguous breeds

Some breeds (populations) landed up on the phylogenetic tree with an ambiguous position relative to other breeds. For example, F was bred only with the preservation of the curled feather trait, that is, crossbreeding with other breeds was possibly used. Some other similar breeds also appeared to admix. Returning to the Bantam (dwarf) breeds, including BMF, HSSD, CBm, SW, and RWD, note that they were mostly scattered along different tree branches. This suggests that the presence of the dwarfism gene (alleles) in these breeds was not a determining factor for their phylogenetic position, but their origin and general genomic architecture played a certain role. The merger of ZS and FS into a distinct subcluster could have been due to the supposed random mating between the two breeds. This subcluster occupied an intermediate and ambiguous position between dual-purpose and meat-type breeds, prompting a further and closer examination of the ZS and FS genomes. Note the isolated position of the subcluster of two breeds, OMF and UM, very close to the center of the phylogenetic tree. Both are old indigenous Russian breeds developed in the European part of Russia in the 18th–19th centuries and exhibiting cold tolerance, which warrants further study (Romanov et al., 2023).

Collectively, by plotting and describing the phylogenetic tree, both in general and specific terms, the evolutionary divergence and relationship of worldwide chicken breeds were investigated in detail, taking into account data on their descent and demographic history.

4 Discussion

The issues of assessment, monitoring, conservation, and usage of genetic resources currently remain acute and highly relevant (Moiseyeva et al., 1993; Bondarenko and Kutnyuk, 1995; Bondarenko and Podstreshny, 1996; Ryabokon et al., 2005; Tagirov et al., 2006; Baumung and Wieczorek, 2015). Monitoring the gene pools of animal populations is tightly linked to breeding aims and phylogeny studies (Zakharov-Gesekhus et al., 2007). Hereby, we determined the degree of genetic diversity, differentiation, and potential of chicken gene pool populations for further genomic selection (Fig. S1-4 in Data S1). Also, our analysis showed that the chicken gene pool itself not only is a carrier of peculiar phenotypic features (such as adaptability to local conditions, resistance to certain diseases, and unique productive, ornamental, and other traits), but also has peculiar features of intra- and interpopulation genetic variability. Genome-wide SNP genotyping appeared to have a sufficient resolution and discriminative power to identify, for instance, a remarkable divergence of SL2 and Pm2 (cross-hybridization descendants) from their purebred counterparts, SL1 and Pm1.

In terms of demographic history patterns evaluated using N_e (Fig. 2), there was an abrupt decrease in the

effective size of some populations due to the accumulation of linked loci and long-term selection of sires for certain economically important traits. Breeds with higher N_e, such as NH, MG, F, RIR, UM, RC, and PC, can be used as a genetic reserve for crossing with other breeds to maintain genetic diversity among modern poultry breeds and populations. Because of SNP genotyping limitations, breeds with higher N_e values would require further study using whole genome sequencing.

MDS analysis (Fig. 1) showed the breed distribution by region of origin. Clusters of Asiatic breeds, European light egg-type and ornamental breeds (RWS, RWP, RWG, LLB, CG, and HSSD), and commercial meat-type WC subpopulations all separated out from the main core of breeds in distinct ways. The implementation of the global ancestry concept using ADMIXTURE-assisted analysis (Fig. 3) revealed more details on genomic signatures of chicken breed origin, development, and admixture. The genetic structure discovered reflected the evolution of breeds and (sub)populations that make up a sizable portion of the worldwide gene pool. The information provided showed that there were fewer ancestral populations (17 of the 49) and suggested how the breeds were related. Breeds having a longer history, such as CBl, FS, HSSD, CBm, YC, SW, BL, BB, and LLB, produced distinct and more uniform clusters. Recent extensive breeding led to significant breed consolidation in younger breeds (Pu and PS) and bottlenecked populations (e.g., RWS). The results of the MDS and ADMIXTURE analyses were in good agreement with each other and also correlated with the phylogenetic analysis (Fig. 4). Significant evolutionary genome divergence observed in chicken breeds has been developed under environmental influences (especially extreme ones) and artificial selection (Li et al., 2019). Our current study presents the divergence of a wide range of breeds of various origins. Previously, we demonstrated evolutionarily determined changes in the phenotype and genotype of diverse chicken breeds (Larkina et al., 2021; Vakhrameev et al., 2023). This work provides further and more detailed information on the genotypic differentiation and divergence of breeds, which determines the heterogeneity of the genome of chickens during their domestication. The built phylogenetic tree (Fig. 4) kept the proportionality of genetic distances between populations. For example, RW and HSSD had long branches relative to each other and eventually formed one subcluster. However, this did not indicate their immediate relatedness; they belonged only to European breeds and were on a large blue branch, on which other European breeds were shown. Similarly, a large red cluster was represented by Asiatic breeds, and between them were two green "bushes" that encompassed breeds of mixed (synthetic) origin including the American breeds RIR, NH, PRB, and Ar, as well as the Australian AoB. We also demonstrated that in some cases the subpopulations formed one branch (RWS–RWG–RWP, CBm1–CBm2–CBm3, and WC1–WC2–WC3), and, in others, they were on different branches of the phylogenetic tree (SL1–SL2 and Pm1–Pm2). Thus, multilocus SNP genotyping enabled elucidation of the intricate demographic histories of some breeds, implying gene flow and gene introgression between populations.

The original Moiseyeva et al. (2003) model covered four main evolutionary lineages of chicken breed formation. Larkina et al. (2021) added to the model two more evolutionary branches of dual-purpose and fancy breeds, based on multiple phenotypic data for breeds from the RRIFAGB bioresource collection. Underrepresentation of dual-purpose breeds in the study by Moiseyeva et al. (2003) may have led to the oversight of the dual-purpose branch. In our comprehensive survey, which was based solely on genome-wide SNP-derived comparisons of numerous breeds of the world's gene pool, we clearly confirmed the presence of dual-purpose breed type, mixed in origin and divided into two large subclusters. We also demonstrated stable clustering at the phylogenomic level for two large traditional evolutionary branches of chicken breeding, i.e., egg-type (European) and meat-type (Asiatic). Notably, representatives of the Bantam type were scattered across different branches, suggesting that the reduced body size itself (under the influence of the dwarfism gene) cannot serve as a clear criterion for clustering these breeds together, as might be expected based on the models of Moiseyeva et al. (2003) and Larkina et al. (2021). The same can be said of the game breeds, whose specific conformation resulted from appropriate selection for a compact fighting type, although this was not reflected at the phylogenomic level. In addition, there were several ambiguous breeds, including one Bantam (BMF), whose position on the general phylogenetic tree was characterized by obvious isolation. These findings give us grounds to postulate the following four evolutionary branches of chicken breed

formation: (1) egg-type (European) and related breeds; (2) Asiatic, including meat-type and related breeds; (3) dual-purpose (with two large subclusters); and (4) ambiguous breeds not clearly belonging to the other three main branches.

The vast and distinctive Russian chicken gene pool was represented by native breeds located on different branches of the phylogenetic tree, depending on their original breeds, their divergent selection objectives, and demographic history. Among them, however, there were both old (OMF, BMF, and UM) and younger (ZS) ambiguous breeds, which were characterized by more unique genome-wide genotypes and did not fit strictly into the three main evolutionary branches. In our current and previous studies, some Russian breeds of importance for use in breeding programs have been examined in more detail in terms of genome-wide associations and candidate genes. One of these breeds, RW and its snow-white subpopulation, differs from others in tolerance to low temperatures and has been selected for use in the production of viral vaccines (Kudinov et al., 2019; Abdelmanova et al., 2021; Fedorova et al., 2022; Romanov et al., 2023). Another dual-purpose breed, Pu, is used by farmers for the production of organic products and was subject to whole genome genotyping and analysis of the accumulation of ROHs (Dementieva et al., 2022a).

As a result of this study, it was found that one of the bioinformatic population criteria for planning the selection strategy in populations is the occurrence and length of LD regions (Data S1). To plan the breeding strategy, as well as to preserve breeds (especially rare and small ones), we recommend the use of SNP scanning and clustering analyses for comparing their fine structure, homozygosity, and admixture to reveal connections between them and important events in their demographic history (Guo et al., 2022; Gao et al., 2023).

5 Conclusions

In the present study, we used whole genome genotyping of more than 820 birds from 49 chicken breeds and populations originating from Europe, Asia, North America, and Oceania. The results of their phylogeny corroborated the finding in MDS and ADMIXTURE-assisted global ancestry analyses. This enabled determination of the genomic landscape of genetic diversity and the differentiation of breeds that were similar or different by phenotype, and consideration of their prospects for use in genomic selection. A refined evolutionary model of breed formation of the worldwide chicken gene pool was also proposed. Thanks to the implementation of this study, the knowledge of genetic resources in the Russian poultry industry has significantly increased. In particular, this genome-wide assessment of the genetic potential of breeds and populations of chickens, which are a national treasure, provides a solid foundation for further use in genomic selection.

Data availability statement

The proprietary SNP genotyping data produced and analyzed in this study were generated using the 60K chicken SNP chip produced by Illumina Inc. for the GWMAS Consortium represented by Cobb-Vantress Inc. (Siloam Springs, AR, USA) and Hendrix Genetics B. V. (Boxmeer, The Netherlands). As such, the datasets generated using this chip are confidential and protected as intellectual property or as trade secrets. As a consequence, the SNP genotyping information used in this study was not made public but rather is kept in a secure database at the RRIFAGB. However, the data can be provided upon reasonable request and can be shared with the third parties upon approval with the GWMAS Consortium. The authors affirm that all data necessary for confirming the conclusions of the article are present within the article, figures, and tables.

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Author contributions

Natalia V. DEMENTIEVA: conceptualization, methodology, software application, investigation, writing – original draft, project administration, and funding acquisition. Michael N. ROMANOV: conceptualization, methodology, software application, investigation, writing – original draft, visualization, project administration, and writing – review & editing. Olga A. NIKOLAEVA, Anna E. RYABOVA, and Artem P. DYSIN: validation. Yuri S. SHCHERBAKOV and Tatiana A. LARKINA: formal analysis. Olga I. STANISHEVSKAYA, Olga V. MITROFANOVA, and Anastasiia I. AZOVTSEVA: resources. Anatoly B. VAKHRAMEEV

and Grigoriy K. PEGLIVANYAN: data curation. Darren K. GRIFFIN: writing – review & editing and supervision. Natalia R. REINBACH: visualization. All authors have read and approved the content of the manuscript, and therefore, have full access to all the data in the study and take responsibility for the integrity and security of the data.

Compliance with ethics guidelines

Natalia V. DEMENTIEVA, Yuri S. SHCHERBAKOV, Olga I. STANISHEVSKAYA, Anatoly B. VAKHRAMEEV, Tatiana A. LARKINA, Artem P. DYSIN, Olga A. NIKOLAEVA, Anna E. RYABOVA, Anastasiia I. AZOVTSEVA, Olga V. MITROFANOVA, Grigoriy K. PEGLIVANYAN, Natalia R. REINBACH, Darren K. GRIFFIN, and Michael N. ROMANOV declare that they have no conflict of interest.

All applicable institutional and/or national guidelines for the care and use of animals were followed. The experiments on chickens were carried out following the ethical approval by the institutional review board of the RRIFAGB, Branch of the L. K. Ernst Federal Research Center for Animal Husbandry (Protocol No. 2020-4 dated 3 March 2020).

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Supplementary information

Tables S1–S3; Fig. S1; Data S1 and S2