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REVIEWS AND THEORETICAL ARTICLES

Studies in Chicken Genetics. Commemorating the 120th Anniversary of the Outstanding Soviet Geneticist A. S. Serebrovsky (1892–1948)

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Abstract—The paper highlights the research of A.S. Serebrovsky in chicken genetics, including gene mapping and inheritance of morphological traits. Genetic formulas for several breeds are presented.The data of genetic surveys for local chicken populations from 23 regions of the former Soviet Union are also reviewed. The personal data of the authors on the morphotypological characteristics of different chicken breeds are given and discussed.

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INTRODUCTION

In 2012 we mark the 120th anniversary of the birth of Aleksandr Sergeevich Serebrovsky, an outstanding scientist in the history of national and world genetics. The milestones of his biography, scientific heritage, and the application of his ideas in modern genetics were widely addressed in numerous scientific and popular editions [1–18 and many others]. His life has been described in detail in encyclopedias, from the Great Soviet Encyclopedia to the modern global Internet resource Wikipedia. Among the recent works dedicated to the 120th anniversary of A.S. Serebrovsky, we should mention the paper by R.A. Fando in the *Russian Journal of Genetics* [19] and the paper by M.N. Romanov et al. in the journal *Priroda* [20]. In the present review, we focus on the research in chicken genetics and touch briefly on his studies concerning the problems of genetics and breeding of farm animals. Unfortunately, the significant contribution of Serebrovsky to this area of research has not been very often addressed in reputable journals. We have made an attempt to fill in this gap. We also considered our duty to remind the readers of the great importance of Serebrovsky's works on specific genetics and to pay tribute to this remarkable researcher. Our personal interest in publishing the materials of Serebrovsky on chicken genetics is explained by the fact that we often used his data, ideas and developments in our studies of genetic diversity of chicken breeds.

BIOGRAPHY

A.S. Serebrovsky started his studies on the genetic bases of livestock and poultry breeding in 1918 after the end of World War I. During two years, beginning in 1916, he participated in military operations at the Caucasus front, and after demobilization he continued his research work in Moscow under the supervision of his university mentor, N.K. Kol'tsov as an assistant editor of the journal *Uspekhi Eksperimental'noi Biologii*. Kol'tsov paid proper attention to the problems of national livestock and poultry breeding. Even in the period of the Civil War, he wrote about the necessity to preserve the Orloff and Pavlov chicken breeds and foreign breeder stocks. In those days, good specimens of the Orloff and Pavlov breeds were very rare.

At the end of 1918, a small farm was allotted for experimental works on chicken genetics 60 km from Moscow in the Zvenigorod uezd. The farm was later referred to as Anikovo by the name of the neighboring settlement. Its full name was the Anikovo Genetic Station of Narkomzem (People's Commissariat for Agriculture) of the RSFSR. The works at the station were funded by the Russian Academy of Sciences (RAN) through its Commission for the Study of Natural Productive Forces (KEPS). In 1919 this Commission allocated funds for the second station (Tula Genetic Station) in the settlement of Slobodka, which was organized on the basis of the former estate of A.S. Khomyakov. Serebrovsky was appointed as the head of the Station. Research in animal genetics was carried out on the basis of 78 purebred chickens, incubator, rabbit hutch, and stud farm [19] that remained from the estate. The

[*] The authors have made equal contributions to the work.

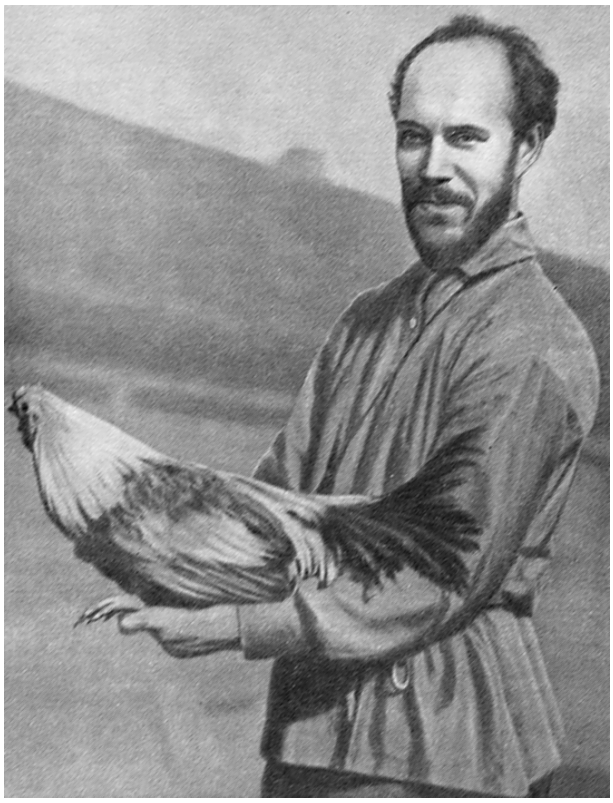

Fig. 1. A. S. Serebrovsky at the experimental station in Anikovo, 1925 [8].

first work by Serebrovsky on hereditary variability of farm animals appeared here, and it opened up a new area in livestock breeding in Russia [21]. In 1921 the Tula Genetic Station was moved onto the territory of the Anikovo Genetic Station. Studies in chicken genetics were later performed at the Anikovo Station and then at the Central Genetic Station in Nazar'evo, not far from Anikovo (Fig. 1).

The works of Serebrovsky dealing with genetic studies of chicken breeds and with the development of poultry breeding in our country occupied an important place in his scientific activity during all his life. In 1921–1923, Serebrovsky headed the Poultry Department at the Anikovo Genetic Station; in 1923–1930, he was Professor of the Poultry Department at the Moscow Zootechnical Institute; and in 1926–1928, he was the head of the Department of General Genetics and the Department of Poultry Genetics at the Central Genetic Station in Nazar'evo. In 1929 Serebrovsky organized the Laboratory of Genetics at the Timiryazev Biological Institute; and in 1931 he organized the Sector of Genetics and Breeding at the All-Union Institute of Animal Breeding of the Lenin All-Union Academy of Agricultural Sciences (VASKhNIL).

In 1926–1933, Serebrovsky guided and took part in expeditions embracing 23 regions of the USSR territory to examine local chicken populations.

In 1930 Serebrovsky participated in the World Poultry Congress in England. He made a report on the problem of gene geography (distribution of characteristic genetic traits in populations depending on the geographical place of origin and breeding) and presented the results of surveys of chicken populations in the Soviet Union. During his stay in England, he visited the laboratory of the English geneticist F. Crow, made a trip to Scotland and Ireland, and examined the largest poultry farm, where a total mechanization was implemented. This permitted him later to propose the most proper organizational structures and methods for developing poultry breeding under the economical conditions existing in the USSR. Serebrovsky tried to use his visits abroad to best advantage. Being in Berlin in 1927 at the 5th International Congress of Genetics, the scientist visited the zoological museums in Berlin, Hamburg and Hanover and examined their collections. He examined stuffed specimens of domestic chickens, wild *Galliformes* species, and different interspecific and intergeneric hybrids (including domestic chicken, wild chicken species, guinea fowl, peacock, pheasant, capercaillie, and grouse). He not only studied them, but very soon published the results in one of the leading foreign scientific journals [22]! This focus on research, on gaining new knowledge in any conditions, and on the conversion of the acquired information into a scientifically significant result characterizes Serebrovsky in the best way possible as an outstanding scientist.

In 1930–1948, Serebrovsky headed the Department of Genetics organized by him at the Moscow State University. The years of 1931–1937 were a period of the highest activity of Serebrovsky as the head of the Sector of Genetics and Breeding at the All-Union Institute of Animal Breeding aimed at seeking ways for developing animal breeding in our country.

At the age of 41, Serebrovsky was elected a Corresponding Member of the USSR Academy of Sciences within the Department of Mathematical and Natural Sciences (specialization genetics, 01.02.1933); and at the age of 43, he was elected a full Member of VASKhNIL (1935). This was an obvious recognition of his scientific authority. Serebrovsky died on June 26, 1948 in a sanatorium of the settlement of Bolshevo, Moscow oblast, at the age of 56. A month later, on July 31, the infamous August VASKhNIl Session began. It is difficult to say what might have happened to Serebrovsky, but, were it not his early death. The name of Professor Serebrovsky was many times mentioned at the 1948 Session and, unfortunately, in no case positively.

THE STUDY OF DOMESTIC CHICKEN GENETICS

After the brief review of the biography of A.S. Serebrovsky and his research dealing with genetics and breeding of farm animals, let us dwell in more detail on his scientific contribution to this research area. He is

justly considered to be a pioneer and a coryphaeus in the field of specific genetics of chicken, the species that is not only of economic value for humans, but is also a classical object of biological research. The works of Serebrovsky in chicken genetics were not restricted only to discrete and visually distinguishable external traits, but also involved physiological parameters, egg productivity, weight and size of eggs, body weight (quantitative traits), as well as plumage fullness, rate of feathering and many other characteristics.

There may be little information about that in literature, but we should be proud that the first chicken genetic map in the world was constructed in the Soviet Union by Serebrovsky and his team, who determined the topography for a number of genes known at that time on some chicken chromosomes.

When embarking on mapping chicken genes at the beginning of his scientific career, Serebrovsky had to start studies practically from scratch, while in the West the chicken genetics had been rather actively developing over 20 years by the efforts of W. Bateson, R. Punnett, T. Morgan, A. Sturtevant, J. Haldane and other scientists. Being unaware of the results of the Western colleagues in view of the hard wartime, Serebrovsky sent the results of his first mapping of three sex-linked chicken genes (i. e., genes on the sex Z chromosome) to the journal *American Naturalist*. The paper of the young Russian researcher [23] was accepted and published with the comment that the data of Serebrovsky support the findings of the American scientist H. Goodale [24] and the English scientist J. Haldane [25] of which the author did not know because of the absence of information exchange.

When Serebrovsky started large-scale genetic studies on chickens, he submitted in 1926 in co-authorship with his colleague E. T. Vasina (later Vasina-Popova) another paper to the English journal *Journal of Genetics* on mapping sex-linked genes [26]. In 1928 the American journal *Journal of Heredity* published his work in coauthorship with his disciple Sergei Gavrilovich Petrov[1], in which the authors inform of the first known case of linkage of autosomal genes [30]. This meant that the Soviet researchers took up firm positions of leaders in mapping chicken genes.

In 1930 a major work on the construction of the first chicken genetic map was published in the Soviet journal *Zhurnal Experimental'noi Biologii*. This map is also the first in the world for domestic animals. Serebrovsky and Petrov generalized the previous data obtained by the team of Serebrovsky and abroad as well as the results of new studies. The first classical map included 12 chicken genes located on four linkage groups (three autosomal groups and one sex chromosome); other four genes remained unlinked relative to any of these groups according to the results of analytical crosses [31].

Accuracy of assignment of the genetic loci to the linkage groups in chickens by Serebrovsky and Petrov, who used usual crosses between specially chosen individuals, strikes us even today. For instance, the naked neck locus (*NA*) was usually assigned to the third classical group corresponding to chicken chromosome 1 until it has recently been localized with the use of molecular markers on chromosome 3 [32]. The results of the Soviet scientists did not support the assignment of *NA* to chromosome 1, too. Other two genes, *MC1R* (solid black) and *BCDO2* (white and yellow skin), were traditionally localized to chicken chromosome 1, despite the fact that Serebrovsky and Petrov supposed these loci to belong to independent linkage groups. Contemporary researchers have mapped these two genes to chromosomes 11 [33] and 24 [34], respectively. According to Serebrovsky and Petrov, the fourth linkage group included the genes of pentadactyly (polydactyly) and duplex comb. This fact again was supported 70 years later as a result of molecular mapping of these genes to chromosome 3 [32].

As follows from the caption to the original figure (Fig. 2) by Serebrovsky and Petrov, the genetic map or "plan of chromosomes" of chicken was built according to the data (as of December 1, 1929) of the Central Farm Animal Genetic Station. We see a cluster of four genes in the second linkage group, which in later foreign works were divided in two independent groups. However, for reasons unknown to us, these works did not have references to two notes added to the initial map of 1929 by Serebrovsky's colleagues in 1931 and 1933, in which the existence of two linkage groups instead of one was made clear [35, 36].

According to the information of S.G. Petrov [35] and A.N. Sungurov [36], the genes of dominant white (PMEL), crest (*CR*), and frizzling (*F*) formed one new linkage group; the genes for creeper (*CP*) and rose comb (*R*) formed another group; and linkage between the genes for solid black (*MC1R*) and fibromelanosis (*FM*) was also very likely. In these works, some other information was added to the chicken chromosomal map; as a result, it had six linkage groups and 15 genes. Using the numeration of the linkage groups accepted in classical chicken genetics, we summarize the results of chicken genome mapping in the Soviet Union in the table.

[1] S.G. Petrov (1903–1999), Dr. Sci. (Biol.), Prof., is, unfortunately, almost forgotten by the scientific community. Early in his career (1920s) he worked under the direction of N.K. Kol'tsov and A.S. Serebrovsky and participated in expedition surveys of local chicken populations organized by Serebrovsky. A.A. Nikiforov, a former worker of the Vavilov Institute of General Genetics, studied the materials of the expeditions in the RAS Archives and testified that the records made by Petrov were precise and academically accurate. His book *Genetika dlya ptitsevodov* (Genetics for Poultry Breeders) [27] became the first manual on chicken genetics in the USSR, and his Dr. Sci. degree thesis *The Origin and Evolution of Domestic Fowl* [28] defended at the Institute of Genetics of the USSR Academy of Sciences still remains the best work in this field by the scope of material and thoroughness of analysis. In 2011 a book about poultry researchers and breeders in our country [29] was issued, in which justice is done to S. G. Petrov. His name is mentioned six times in this book, which we certainly appreciate.

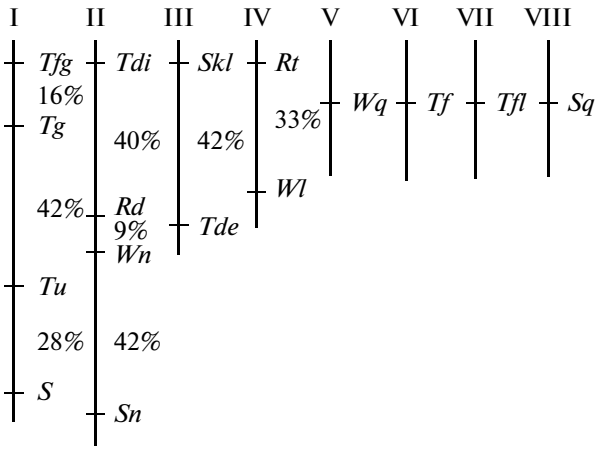

Fig. 2. The first chicken chromosome map [31]. It is based on the data as of December 1, 1929, obtained at the Central Farm Animal Genetic Station, Anikovo. The genes on the map are designated according to the nomenclature of A.S. Serebrovsky. The modern chromosome and locus symbols are given below in brackets and parentheses, respectively: Linkage group I [GGAZ]: *Tfg (ID)—Tg (BARR)—Tu (SLC45A2)—S (K)*. Linkage group II *Tdi (PMEL)* [E22C19W28_E50C23 (classical group II)]—*Rd (CP)* [GGA4? (classical group I)]—*Wn* (R) [GGA4? (classical group I)]—*Sn* (CR) [E22C19W28_E50C23 (classical group II)]. Linkage group III: *Skl (NA)* [GGA3]—*Tde (BL)* [?]. Linkage group IV [GGA2 (classical group IV)]: *Rt (LMBR1)—Wl (D)*. Chromosome V [GGA1]: *Wq (P)*. Chromosome VI [GGA11]: *Tf (MC1R)*. Chromosome VII [GGA24]: *Tfl (BCDO2)*. Chromosome VIII [GGA1 or GGA24]: *Sq (MB)*.

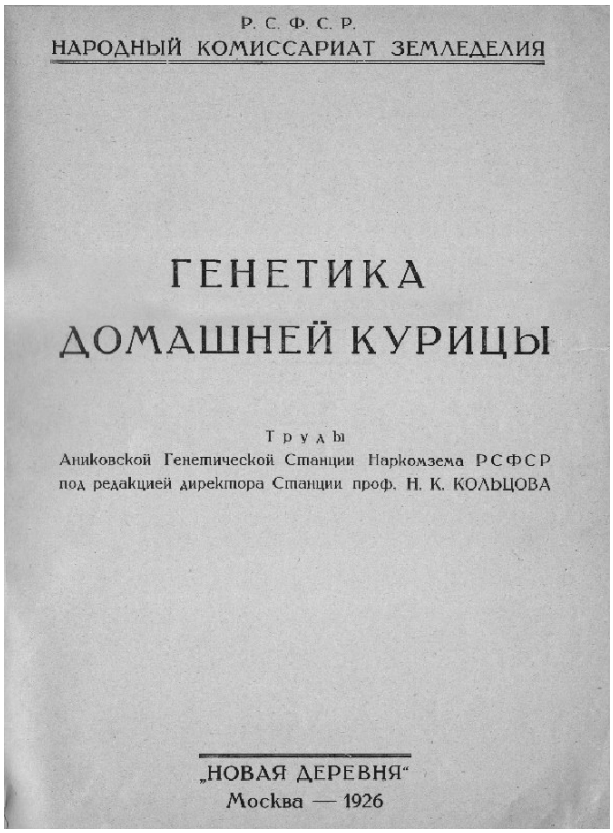

Fig. 3. The book *Genetika Domashnei Kuritsy* (1926) [38].

However, until recently this discovery was ascribed in the foreign literature to F. Hutt despite the fact that his work was published only in 1936 [37]. Only owing to the efforts of the authors of the present article aimed at popularization of the scientific heritage of Serebrovsky and his colleagues, it became possible in the 2000s to restore to some extent justice as to the priority in chicken genetic mapping in favor of the Soviet group of researchers guided by Serebrovsky.

Let us consider in more detail the data presented in the book of collected articles under the title *Genetika Domashnei Kuritsy* (Genetics of Domestic Fowl) [38], which is a bibliographic rarity today (Fig. 3). The book is a result of the collective work of the staff of the Anikovo Genetic Station since the time of its establishment. It is lavishly illustrated by A.N. Martynov and N.N. L'vova. Both of them were teaching at the Moscow State University and perfectly combined their knowledge in zoology with the drawing skill. They have left us a legacy of finely depicted watercolor portraits of cocks and hens and other illustrations. Twenty eight original pictures made by L'vova are kept in the collection of the Memorial Museum of Academician N.I. Vavilov at the Vavilov Institute of General Genetics (IOGen), RAS. They were a gift to the Museum from R.A. Fando, a researcher of the S.I. Vavilov Institute of History of Natural Science and Technology, RAS. All original pictures in the collection are made in color. Part of them was not presented in the book, and part of the illustrations shown in the book has been lost and is not available in the Museum collection. The book *Genetika Domashnei Kuritsy* [38] has 31 pictures of chicken breeds and hybrids (nowadays better called crossbreds); of them 11 are colored and the remaining ones are black-and-white; seven pictures depict purebred cocks and hens, and 24 show hybrids between the Orloff and Pavlov breeds and hybrids of these breeds with foreign breeds (Indian Game, Plymouth Rock, Faverolle, Buff Orpington, Minorca, Houdan, and Bantam). We see from the choice of breeds for crossing that Serebrovsky used chicken breeds belonging to different evolutionary types (game, meat/dual-purpose, egg, and Bantam). This allowed him to follow the inheritance of not only discrete morphological traits, but also of the type of constitution or traits associated with it. The book contains descriptions of each chicken gene Serebrovsky examined, it also provides hereditary formulas for the Black-Breasted Red Orloff cock, Spangled Orloff hen, Silver Pavlov cock and for some other hybrids between these and other breeds. These formulas were a result of the hybridological analysis of inheritance of the traits in the crossbreds studied. It should be taken into account that the existence of some genes studied by Serebrovsky was not

Summarized data on chicken genome mapping according to the results of the studies in the laboratory of A. S. Serebrovsky and current views

Linkage group according to Serebrovsky (with amendments)	Classical linkage group	Contemporary linkage group/chromosome	Locus symbol			Gene name		
			according to Serebrovsky	classical	current	according to Serebrovsky	classical	current
I	I	*Z*	*Tfg*	*Id*	*ID*	*Trufege* – dark blue and white color of shanks	Dermal melanin inhibitor	Dermal melanin inhibitor
			Tg	*B*	*BARR*	*Trage* – barred feather plumage pattern	Barring	Barring
			Tu	*S*	*SLC45A2*	*Tuge* – silver plumage color	Silver	Solute carrier family 45, member 2
			S	*K*	*K*	*Suke* – slow feathering	Late feathering	Late feathering
II	I	E22C19W28_ E50C23/2, 3 or 4?	*Rd*	*Cp*	*CP*	*Rode* – short legs	Creeper	Creeper
			Wn	*R*	*R*	*Wene* – rose comb	Rose comb	Rose comb
III	III	3	*Skl*	*Na*	*NA*	*Sukli* – naked neck	Naked neck	Naked neck
	–	3, 1 or 4?	*Tde*	*Bl*	*BL*	*Tode* – blue plumage color	Blue dilution	Blue dilution
IV	IV	2, 3 or 4?	*Rt*	*Po*	*LMBR1*	*Rete* – pentadactyly	Polydactyly	Limb region 1 homolog (mouse)
			Wl	*D*	*D*	*Wele* – Y-shaped duplex comb	Duplex comb	Duplex comb
V	III	1	*Wq*	*P*	*P*	*Weque* – pod comb	Pea comb	Pea comb
VI	III	11	*Tf*	*E*	*MC1R*	*Tifa* – black plumage color, *Tine* – wild-type plumage and down color	Solid black	Melanocortin 1 receptor
	–	11 or 4?	*Tr*	*Fm*	*FM*	*Trule* – skin and periosteum fibromelanosis	Fibromelanosis	Fibromelanosis
VII	III	24	*Tfl*	*w*	*BCDO2 (APOA1)*	*Trufele* – yellow and white shank color	Yellow skin	Beta-carotene dioxygenase 2
VIII	III	1 (or 24?)	*Sq*	*MB*	*MB*	*Suque* – muffs and beard	Muffs and beard	Muffs and beard
IX	II	E22C19W28_ E50C23/2, 3 or 4?	*Sn*	*Cr*	*CR*	*Sune* – crest	Crest	Crest
			Tdi	*I*	*PMEL*	*Todi* – dominant white plumage and down color	Dominant white	Premelanosome protein
				F	*F*	*Sule* – frizzling	Frizzling	Frizzling
–	–	1		*c*	*TYR*	*Tedu* – plumage coloration	Recessive white plumage color	Tyrosinase (oculocutaneous albinism IA)
–	III?	1 or 24?		*PTI1*	*PTI1*	*Susta* – dominant shank feathering	Dominant shank feathering (I)	Dominant shank feathering (I)
–	III?	1 or 24?		*PTI2*	*PTI2*		Dominant shank feathering (II)	Dominant shank feathering (II)
–	–	–		–	–	*Suso* – recessive (Pavlov) shank feathering	Recessive shank feathering	Recessive shank feathering

confirmed later on, and their names do not correspond to those accepted nowadays. For the sake of convenience, we present the hereditary formulas, when it is possible, with the modern gene symbols given in parentheses and with the names of the traits according to Serebrovsky. The names of the genes and alleles are capitalized, the first is the gene name with an asterisk; *N* is normal, wild type. In some cases, the authors indicate homozygosity of the trait in the gene symbol judging from the expression of the trait itself and its recessivity, irrespective of the fact that Serebrovsky himself might not have indicated that.

Hereditary formula of the Black-Breasted Red Orloff cock no. 57 (Fig. 4a): diguo—deep voice; fora—hatching instinct; $gidu_2$—homozygosity for normal development of nostrils and nasal processes of intermaxillary bones; aqoqua—normal form of the left lobe of the liver; rane—absence of spurs or their development at the old age; arano—one spur (*M*N/M*N*); arete—tetradactyly (*LMBR1*N/LMBR1*N*); $sudi_2$—homozygosity for the presence of tail (*RP*N/RP*N*); asuke—early feathering (*authors' note*: it is probable that this particular cock no. 57 was a carrier of the early feathering allele, but the Orloff breed was originally characterized by late feathering— *K*K*, or there is a misprint here: "asuke" should be changed into "suke"); asuki—autosomal early feathering; asukli—feathered neck (*NA*N/NA*N*); asule—nonfrizzling (*F*N/F*N*); asuli—loose plumage; asuma—absence of henny feathering (*CYP19A1*N/CYP19A1*N*); asune—absence of crest (*CR*N/CR*N*); $sunu_2$—homozygosity for the absence of full crest; $suque_2$—homozygosity for the presence of muffs and beard (*MB*MB/MB*MB*); $suso_1$—heterozygosity for the absence of shank feathering; asusu—absence of dominant shank feathering; asusta—absence of a more frequent form of dominant shank feathering (*PTI1*N/PTI1*N*); asusti—absence of vulture hocks, i. e., of a small number of feathers on the inner side of the shank at the base of the tibia (*V*N/V*N*); asuti—short tail in contrast to long-tailed Japanese chicken (*GT*N/GT*N*, *MT*N/MT*N*); $tedu_1$—homozygosity for the presence of plumage coloration (*TYR*N/TYR*C*)); $tefa_2$—homozygosity for the presence of the secondary plumage color trait; atifa—absence of the solid black plumage color (i. e., of the *MC1R*E* allele); atine—absence of the wild-type pattern of chick down (i. e., of the *MC1R*N* allele); atode—absence of the black pigment dilution factor (*BL*N/BL*N*); atodi—absence of inhibition of plumage coloration (*PMEL*N/PMEL*N*); atofa—presence of the black pigment on the breast of cocks (*MH*MH*); atofe—absence of henny plumage color; atuge—gold plumage color (*SLC45A2*N/ SLC45A2*N*); tule—black-breasted red plumage color in the cock, rust-colored plumage in the hen; atrage—absence of sex-linked barring (*BARR*N/ BARR*N*); trakia—light color of the feather stem, mainly in the hackle and saddle feathers of cocks and in the hackle feathers of hens; atrale—absence of color dilution in the hackle and saddle feather edge; $trase_1$ —heterozygosity for the solid feather color; $trasi_2$ —homozygosity for the presence of feathers tipped with a spangle, mainly on the head and in the upper part of the hackle, in the primary flight feathers and wing coverts, and in the shank; $trate_2$ —homozygosity for the presence of feathers tipped with a spangle (*MO*MO/MO*MO*); atrudune—red face color; $trufege_2$ —homozygosity for the yellow shank color (*ID*ID/ID*ID*); atrufele—absence of the epistatic white color of the shank (*BCDO2*W/ BCDO2*W*) (*authors' note*: it is considered at present that the shank color depends on the combined action of two genes, *ID* and *BCDO2*); *truklade* —creamy-white eggshell color; atruklage—absence of the brown eggshell color; atruklake—absence of the epistatic white eggshell color; atrule—absence of the black pigment in the skin (*FM*N/FM*N*); $trunu_2$ —homozygosity for the red eye iris color; awele—absence of duplex comb (*D*N*); $wene_1$—heterozygosity for rose comb (*R*R/R*N*); $weque_2$—homozygosity for pea comb (*P*P/P*P*); genes of the characteristic form of the head and beak, and of a peculiar plumage were not identified.

Note how thoroughly Serebrovsky worked: in the Black-Breasted Red Orloff cock No. 57, he examined 44 traits/genes, of which 15 were analyzed for zygosity: 10 appeared to be homozygous (foot number 2 after the gene name) and five displayed heterozygosity (1), i.e., 67 and 33%, respectively.

The hereditary formula for the Spangled Orloff hen no. 173 (Fig. 4b): gidu—normal development of nostrils and nasal processes of intermaxillary bones; $siso_2$—homozygosity for shank nonfeathering; $sunu_1$—heterozygosity for full crest; $tedu_2$—homozygosity for the presence of plumage coloration (*TYR*N/TYR*N*); $trakla_1$(?)—heterozygosity (?) for the light feather color; atrase—nonsolid feather color; $wele_1$—heterozygosity for duplex comb (*D*D/D*N*); $wene_2$—homozygosity for rose comb (*R*R/R*R*); the remaining traits are like in cock no. 57.

As we see, the examined individuals did not display homozygosity for all genes under study. Such a situation is probably observed in all our national breeds, which presents rather great difficulties for amateur poultry breeders: it is not always that phenotypically "perfect" individuals can produce the same progeny. Here we should cite Kol'tsov's words about how the search for individuals of the Orloff and Pavlov breeds for genetic studies was made. That is what he writes in the preface to the book *Genetika Domashnei Kuritsy* [39]: "This breed has almost disappeared in our country. Not a single full nest of Orloffs was presented at exhibitions that took place in Moscow since 1918. During our expeditions organized in the autumn of 1923 to Nizhni Novgorod and Pavlovskoe, where we obtained our breeder birds, we found that these birds turned out to be extinct at all farms where they had been raised earlier. We observed evidence for a very

s42Fig. 4. Chicken breeds and hybrids studied by A.S. Serebrovsky (a–d). (a) Black-Breasted Red Orloff cock [38]; (b) Spangled Orloff hen [38]; (c) F_2 hybrid (Pavlov × Orloff) hen [38]; (d) Silver Pavlovs [42].

barbarous attitude to the last remains of the breed. A whole Orloff breeder farm was eaten in the winter of 1922, and the family that had to exterminate its fowl learned from their own bitter experience of high meat qualities of this breed. Further search for remains of this breed in the USSR is necessary, or we will have to turn back to their import from England, as the economical value of the breed cannot be finally estab-

lished on the basis of the progeny of those rare accidental reproducers that we succeeded to find in 1917 and 1918 as well as in 1923 in the N. Novgorod guberniya". This remark of Kol'tsov explains a rather high degree of heterozygosity of the Orloff cock and hen used to deduce their hereditary formulas. This is also observed for hybrids of the mentioned breeds, when the same parental pair produced a differently looking progeny.

Hereditary formula of the Silver Pavlov cock no. 157 (purebred according to Serebrovsky): adiquo—high-pitched voice; agidu—open high nostrils; agoqua—normal left lobe of the liver; rane—absence of spurs or their development at the old age; arano—one spur (*M*N/M*N*); arete—tetradactyly (*LMBR1*N/LMBR1*N*); $sudi_2$ —homozygosity for the presence of a tail (*RP*N/RP*N*); asuke—early feathering (*K*N/K*N*); asuki—autosomal early feathering; asukli—feathered neck (*NA*N/NA*N*); asule—nonfrizzling (*F*N/F*N*); asuli—loose plumage; asuma—absence of henny feathering in the cock (*CYP19A1*N/CYP19A1*N*); $sune_2$ —homozygosity for the presence of a crest (*CR*CR/CR*CR*); asunu—the crest is not full, but upright and squeezed on the sides; $suque_2$—homozygosity for the presence of muffs and beard (*MB*MB/MB*MB*); asuso—recessive shank feathering; asusu—absence of dominant shank feathering; asusta—absence of a more frequent form of dominant shank feathering (*PTI1*N/PTI1*N*); asusti—absence of vulture hocks (*authors' note*: the Pavlov breed has vulture hocks, and this is seen in the figure in the book [38]. It is more correct to write as follows: susti—presence of vulture hocks (*V*/V**)); asuti—short tail (*GT*N/GT*N*, *MT*N/MT*N*); $tedu_2$ —homozygosity for the presence of plumage coloration (*TYR*N/TYR*N*); $tefa_2$—homozygosity for the presence of the secondary plumage color trait; $tifa_2$—homozygosity for the solid black plumage color (*MC1R*E/MC1R*E*); atine—absence of the wild-type pattern of chick down (i. e., of the *MC1R*N*) allele); atode—absence of the black pigment dilution factor (*BL*N/BL*N*); atodi—absence of the inhibitor of plumage coloration (*PMEL*N/PMEL*N*); $tofa_2$—homozygosity for the absence of the black pigment on the breast of cocks (*MH*N/MH*N*); atofe—absence of henny plumage color; tuge—silver plumage color (*SLC45A2*S*); tule (?)—red plumage color in cocks, rust-colored plumage in hens; atrage—nonbarred plumage (*BARR*N/BARR*N*); atrakia—dark color of the feather stem; trale (?)—color dilution in the feather edges, mainly in the hackle and saddle feathers in cocks and in the hackle feathers in hens; $trase_2$—homozygosity for solid plumage color; atrasi—absence of solid black plumage color, presence of a black spot on the tip of the feather (*DB*DB*, *PG*PG, ML*ML*) (*authors' note*: it is considered at present that this trait is a result of the action of three genes); atrudune—red color of the face; atrufege—colored shank (*ID*N/ID*N*); $trufele_2$—homozygosity for the epistatic white shank color (*authors' note*: there is probably also a misprint here. It should be written $trufele_2$ instead of $atrufele_2$, then the name of the trait will be: absence of the epistatic white shank color (*BCDO2*W/BCDO2*W*); it is considered at present that the shank color depends on the action of two genes, *ID* and *BCDO2*); atruklage—absence of the brown eggshell color; $truklake_2$ —homozygosity for the epistatic white eggshell color; atrule—absence of the black pigment in the skin (*FM*N/FM*N*); $trunu_2$ —homozygosity for the red color of the eye iris (*authors' note*: the eyes of the Pavlov chicken are considered to be black or dark); $wele_2$ —homozygosity for duplex comb (*D*D/D*D*); awene—single comb (*R*N/R*N*); aweque—non-pea comb (*P*N/P*N*); awera—absence of extra spikes at the back of the comb. This cock proved to be homozygous in all 12 established cases. Unfortunately, this remarkable breed was almost lost at the end of the 20th century.

Of great interest for those who like the Pavlov breed and especially for those who are involved in its restoration and breeding is the work of Serebrovsky *Geneticheskii Ocherk Pavlovskoi Porody Kur* (1940), in which he describes in detail genetic characteristics of Pavlov chicken and the results of crosses of this breed with other breeds. The Pavlov breed, like the Orloff breed, is considered to be the pride of national breeding. S. G. Petrov [41] characterized the Pavlov breed as follows: "Pavlov chicken are the masterpiece of the beauty of chickens in the 19th century." To confirm the words of Petrov, we present a picture (Fig. 4d) from the Album of 1905 [42], since among the pictures prepared for the book *Genetika Domashnei Kuritsy* [38] this breed is presented only in the black-and white image.

Serebrovsky also could not but pay attention to the national breed Yurlov Crower and on its distinctive features; long crowing, voice quality, large eggs, and a greater body weight. Since 1921, Yurlov Crowers became an object of genetic studies performed under the direction of Serebrovsky. He came to the conclusion that the last long note in Yurlov cocks dominates in crosses with other breeds, although he considered this conclusion not finally tested [38]. Serebrovsky also actively participated in the work on the improvement by Yurlov cocks of the local fowl in the Shabalinskii raion of the Kirov oblast, to where 662 Yurlov cocks were brought from the Livenskii raion in 1928. The first examination of the obtained crossbreds was made in 1930 by D.V. Shaskol'sky (1908–1990), a former IOGen researcher. The second was performed in 1938 by a team from the Poultry Research Institute. It was established that Yurlov cocks improved the weight and body size characteristics of the local chicken populations [43, 44].

The close inspection of the obtained F_1 and F_2 hybrids, whose images are presented in the book *Genetika Domashnei Kuritsy* [38], showed that, in addition to the their use as a test system for studying inheritance

of traits, they, being a potential gene pool of future breeds, are important *per se* in searching for ways for creating new forms of chicken populations and thus for increasing the genetic resources of chicken breeds (Fig. 4c).

Expeditions to survey the local chicken populations were made from 1926 to 1933 under the guidance and with a direct participation of Serebrovsky to 23 regions of the USSR territory: Armenia; South Dagestan, North Dagestan; Ossetia I, Ossetia II; Baksan, Balkar, and Chegem ravines in Balkaria; Kabarda (regions of North Caucasus and Transcaucasia); Kirovograd, Aleksandria, Kremenchug, Poltava, Chernigov (Ukranian SSR); Livny, Yelets, Ryazan,Yaroslavl, Nizhnii Novgorod, Vyatka, Bashkiria (RSFSR); Samarkand and Fergana (Uzbek SSR). These expeditions provided an abundant material for a careful description of the known morphological mutations. Comparison of 58 chicken populations was made for the allelic frequencies of 14–16 genes controlling discrete morphological traits, such as the presence of crest, muffs and beard, comb form, color pattern, and others. Such wide-range surveys of the aboriginal fowl were not repeated later in our country; they are also unknown abroad. Therefore, the evidence about the distribution of morphological traits in local chicken populations is available only for the Russian territory and is lacking for other countries. As always, the creative mind of Serebrovsky did not allow him to be restricted only to the registration of the frequencies of traits/genes in populations and regions, but using this material he substantiated the role of the migration and stochastic (later referred to as the genetic drift) processes in the concentration of genes in populations, and proposed and established a new area of knowledge, gene geography, closely associated with the notion of gene pool. Both terms have come into common use in the scientific practice and are already inseparable from the name of Serebrovsky [45].

The scope of Serebrovsky's interests included not only the problems of hybridization of chicken breeds, but also of other animal species. We have already touched upon chicken hybrids above. In 1931 in accordance with the proposal of A.S. Serebrovsky and E.F. Liskun and on the basis of the program developed by them, the USSR Narkomzem adopted a resolution about a wide development of interspecific hybridization among animals. As a result of this initiative, the Institute of Agricultural Hybridization and Steppe Acclimatization of Animals (in the later years it changed its name several times) was founded in Askania-Nova. The Institute has further on grown into a large scientific center, a unique reserve of rare plants and animals. Its initial basis was a private reserve established in 1875 by Friedrich Falz-Fein. Serebrovsky supervised some studies at this Institute up to 1937. Not concentrating only on practical tasks, he managed to analyze the world hybridization resources and proposed their classification [46, 47].

Dealing with the problems of genetics and breeding of farm animals, Serebrovsky said a new word in this research, too: he advanced the *theory of leaders*, i. e., the identification of breed improvers coupled with an obligatory use of *artificial insemination*. He drew attention of scientists to the investigation of *lethal genes*, to the methods of breeding for a group of traits, and formulated the idea of *signaling genes*. However, in this research he, like many other representatives of classical genetics, did not take into account the environmental influence on economically valuable traits. At a later time, Serebrovsky himself admitted the fallacy of these views [17].

MODERN RESEARCH ON GENETICS OF MORPHOLOGICAL TRAITS IN CHICKENS

Studies of discrete morphological traits in chicken breeds have been carried out for approximately twenty years in the Laboratory of Comparative Animal Genetics, IOGen, under the direction of the RAS Corresponding Member I.A. Zakharov-Gezekhus [10–14, 16, 18, and others]. When starting these studies, the authors (I.G. Moiseyeva, A.A. Nikiforov, M.N. Romanov, et al.) used the data of Serebrovsky himself and his colleagues obtained in the already mentioned expeditions. Until now, not all results of these surveys of chickens have been published, some are available in field diaries and draft notes in the RAS Archives. Nikiforov gained access to the materials of Serebrovsky in the Archives and carried out a laborious work on writing out the values of the frequencies of occurrence of morphological traits characterizing the chicken populations of South Dagestan, North Ossetia, East Bashkiria, and some regions of Russia and Ukraine. These data have thus been introduced to the academic community. By using the values of the gene frequencies for each population in the regions calculated by us according to the data of Serebrovsky and his colleagues, both published [50–53] and taken from the RAS Archives [54–58], the above-mentioned authors calculated a distance matrix, performed a cluster analysis, and constructed a dendrogram of population similarity (Fig. 5). Three large clusters are distinguished in the dendrogram, in which the chicken populations are grouped in the following way: the first cluster includes chickens from Russia; in the second cluster the Ukrainian chicken populations are grouped with the chickens from Ossetia and South Dagestan; the third cluster contains the Asian populations (Samarkand and Fergana) together with the remaining chickens from the Caucasus, i. e., from Armenia and North Dagestan, from the Baksan, Balkar and Chegem ravines, and from Kabarda. We can also observe the unique character of the local chickens from Bashkiria. It can be stated here that the chicken populations show a rather close association of their frequencies of genes controlling discrete morphological traits with definite closely located geographic

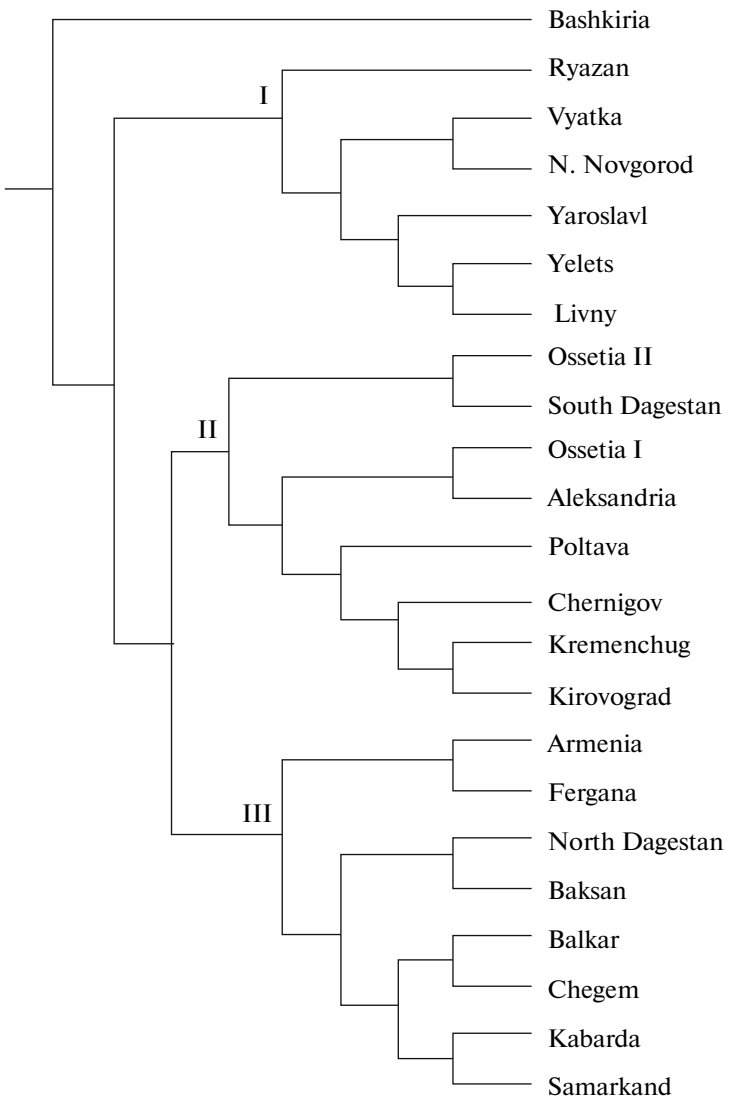

Fig. 5. A dendrogram of genetic similarity of the local chicken populations from 23 regions of the USSR territory based on the frequencies of 14 genes controlling discrete morphological traits [14].

regions, and we can also trace the distribution of domestic chickens from the east to the west and from region to region taking into account the history of nations and settlements.

On the basis of the graphic presentation of the frequencies of two genes (for crest, *CR***CR*, and for silver, *SLC45A2***S*) in the same regions of North Dagestan, Serebrovsky demonstrated the effect of parallel changes of their frequencies called by him *parallelism of genes* [59]. Using the same data, Nikiforov calculated the coefficient of correlation between the frequencies of these two genes in the same regions and obtained an even clearer demonstration of this phenomenon (Fig. 6) [14]. This discovery made by Serebrovsky means that these two mutant genes often found in different linkage groups occur simultaneously either more frequently or less frequently in different settlements. Such linkage of the traits can depend on the preference the local inhabitants could have in selecting individuals with these traits as well as on stochastic processes and a subsequent isolation of these regions.

The series of genogeographic studies includes the work with the use of the data of Serebrovsky on the distribution of the rose comb gene *R***R* in chickens [49]. The map constructed by using computer cartography clearly demonstrates that the concentration of the *R***R* gene increases from the north of the European part of the USSR towards the southern regions. The result obtained shows a high similarity with the maps of the third major component of the gene pool of the Eastern European nations constructed from the data about the frequencies of occurrence of classical autosomal DNA markers.

There are two approaches to study morphological traits: the method used by Serebrovsky for chickens,

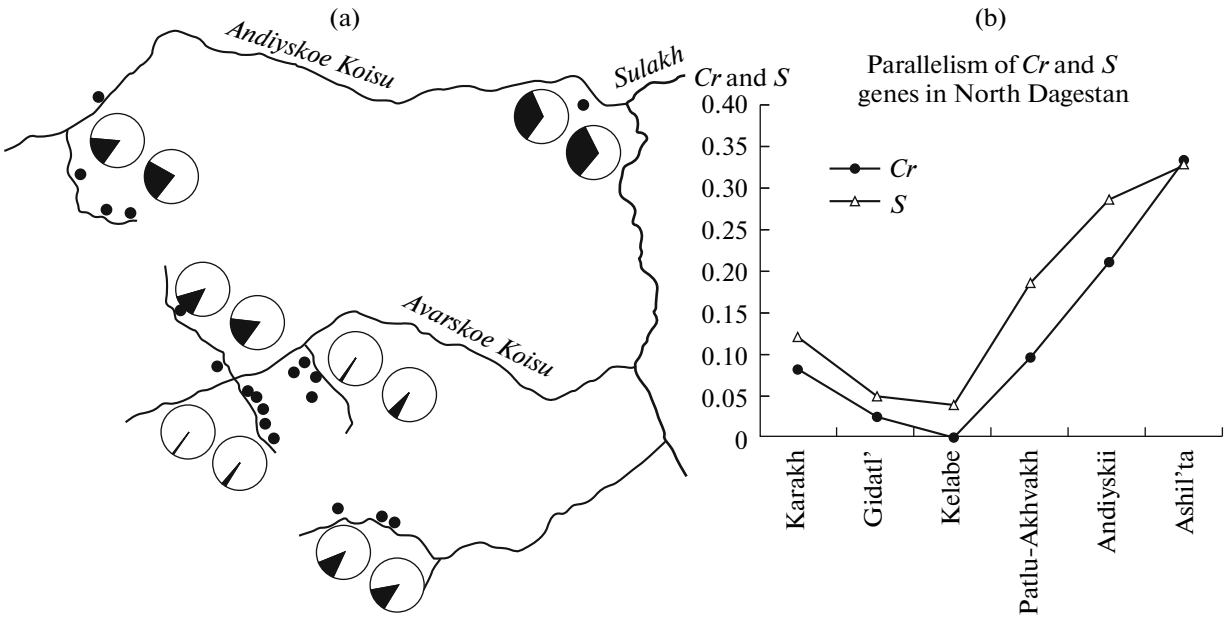

Fig. 6. An example of parallel distribution of alleles at the loci for crest (*CR*) and silver plumage color (*S*, or *SLC45A2*) in North Dagestan: (a) a drawing made by A.S. Serebrovsky. In each pair of circles depicting the allele concentration (black sector), the left circle is the crest locus allele (*CR***CR*), the right circle is the silver color locus allele (*SLC45A2***S*). The dots show the examined auls; (b) a diagram constructed on the basis of the same data. Ordinate is the allele frequency [14].

when the frequency of a trait is determined in different populations; and the method of morphological (or, as called by us, morphotypological) characterization of each breed on the basis of the presence or absence of a trait taking into account some quantitative parameters. In the latter case, the trait was represented by several states: low, medium, and high values. The second method was rather successfully developed for chickens in the Laboratory of Comparative Animal Genetics, IOGen. An active part in this work, as well as in the analysis of the materials of Serebrovsky, was taken by M.N. Romanov.

Morphotypological characterization of the chicken breeds, subsequent statistical analysis, and the methodology of these investigations as a whole presented serious difficulties, the more so as we had no precedents in this respect. We started with the use of different variants in choosing breeds for the statistical analysis (from a random sample to the choice of breeds representing their evolutionary roots or the specialization of their use by man), identification of traits that are most significant for characterization of a breed with the establishment of their states, and the application of various techniques of statistical analysis.

We performed a series of studies and compared the morphological features of different breeds. These studies differed in the choice and number of breeds and traits, and the calculation of the matrices of distances between the populations and their clusterization were made by different methods. In our first work [10], we used the cladistic method for calculating the distance matrices and corresponding programs [60, 61]. Creative assistance in the employment of the cladistic method for calculating distance matrices was provided by Lyudmila V. Bannikova, a former IOGen researcher. The authors of the present publication express their great gratitude to her.

The grouping of 30 randomly chosen populations for 24 discrete morphological traits (their 48 phenotypical variations) showed that the chicken breeds were clustered in two large classes. The first included meat type, dual-purpose, and game breeds of chickens. This cluster contains a subcluster formed of game breeds only: Kulangi, Red Orloff, Gilan, Old English Game, and Malay (Fig. 7). In the second cluster, we see light-type breeds and the main wild ancestor of domestic chickens, Red Jungle Fowl. An exception is Kuchino Jubilee belonging to dual-purpose breeds. It is important to note here that the breeds of common origin are separated by a minimal distance from each other. These are New Hampshire and Rhode Island, Orloff and Gilan, and Russian White and White Leghorn.

Now let us turn to the study [12], in which 31 morphological traits were compared in 36 chicken populations representing four evolutionary branches of domestic chickens. The traits used in the work and their states are presented in the supplement to the book *Genofondy Sel'skokhozyaistvennykh Zhivotnykh* (table a2, p. 417) [16]. The MATRIX computer program developed by E.M. Myasnikova and I.A. Zakharov (1994, data unpublished) was used to estimate similarity between the populations and to calculate the distance matrices for the morphotypological characteris-

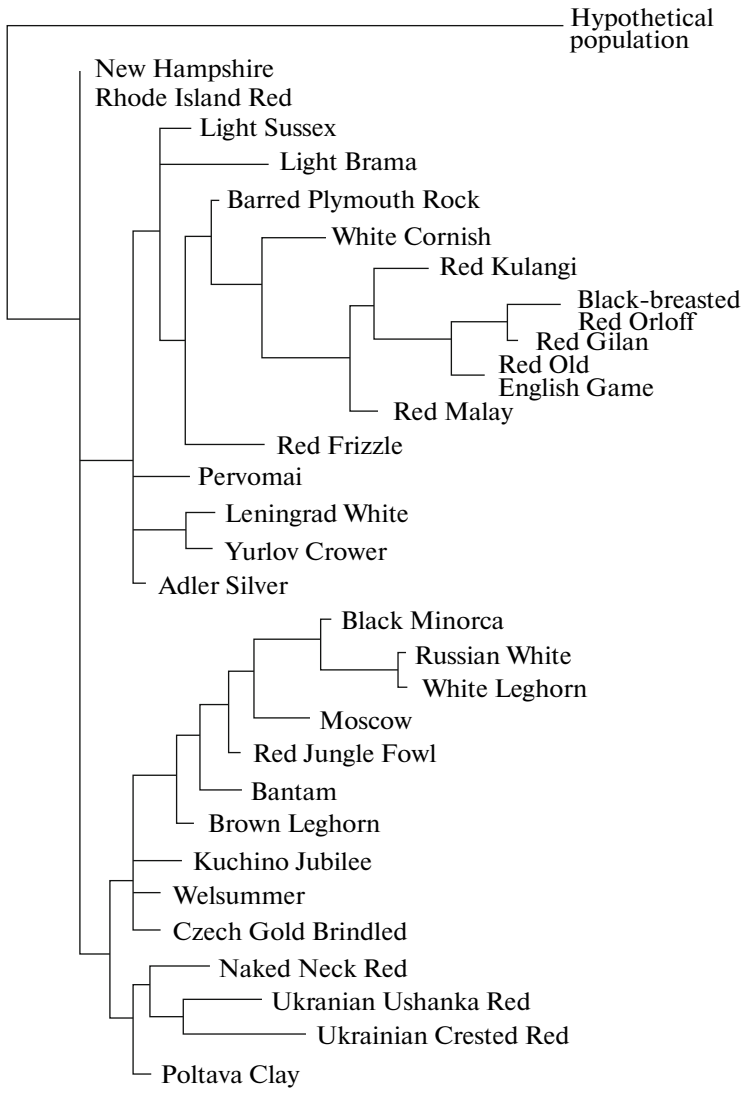

Fig. 7. A cladogram of relationship between 30 chicken populations based on the presence or absence of 48 morphological traits [10].

tics. The method is described in detail in the work by Moiseyeva et al. [11]. The sample of chicken breeds also included their varieties that differed in one trait: Leghorn, Ushanka, Russian Crested, Yurlov Crower, Livny, Liyang (Chinese meat type breed), and Chabo. Fig. 8 [16] shows five well distinctive clusters: the first cluster includes all game breeds; the second cluster groups breeds of the egg type and the wild ancestor of domestic chickens, except the Xiaoshan breed (Chinese dual-purpose breed); the third cluster is represented by breeds of the meat and dual-purpose types; the fourth cluster contains meat type breeds; and breeds of the bantam type form the fifth cluster. The analysis of these data showed that the breeds examined were distinctly clustered according to their evolutionary types. As we see in this figure, the varieties of one and the same breed displayed very close similarity. Information on the Chinese breeds was obtained by us from Zhang Yugou, a former postgraduate of the Laboratory of Comparative Animal Genetics, IOGen, who translated Chinese texts into Russian and helped in understanding the specificity of chicken breeding in China and the ancient Chinese customs associated with the chicken theme.

The comparison of all our studies on the registration of morphological traits in chicken breeds demonstrated a good agreement between the results obtained and their correspondence to the direction in which breed groups are known to be used by man in practical poultry breeding or to their attribution to common phylogenetic roots.

The question arises as to what extent different criteria are effective for differentiation of chicken populations and estimation of their genetic diversity. In different studies we used morphological traits, biochemical markers, blood groups, microsatellites, esterase

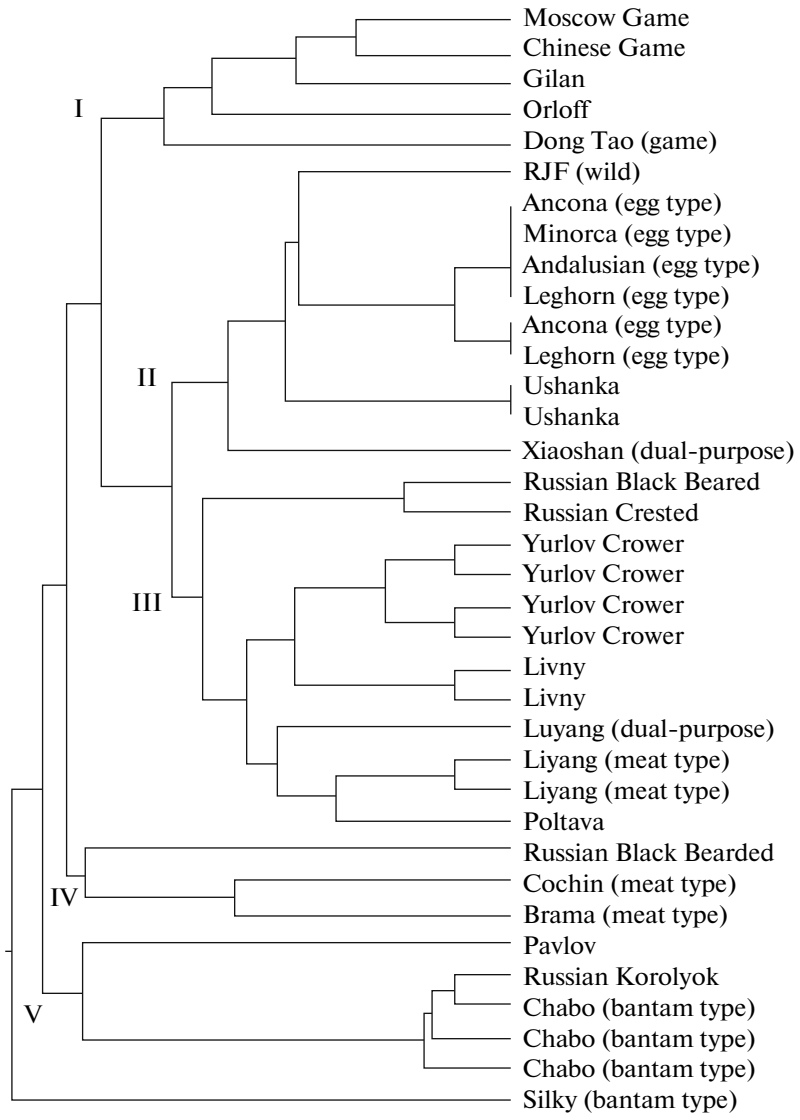

Fig. 8. A dendrogram of the chicken breeds and the wild species *Gallus gallus* (RJF) constructed on the basis of their similarity for different states of 31 morphological traits. The types of their economical use are given in parentheses. I–V are clusters [12].

activity, and body measurements. The details of their comparison are presented in the works by Moiseyeva et al. [48] and Moiseyeva [16]. Here, we will only note that the general tendencies in the differentiation of breeds with the use of the characteristics studied by us proved to be similar with a few exceptions. The similarity of the breeds was higher in the cases they were sampled taking into account the evolutionary types. The ranges of genetic diversity in the groups of breeds of the common evolutionary root also showed sufficient similarity.

Serebrovsky also worked out the approach of graphical presentation of the concentration of genes in populations of one or another region (wing rose), which was further elaborated in the works of Yu.G. Rychkov and Yu.P. Altukhov in the form of frequency polygons [62, 63 and their other works]. We also often used this method in our chicken studies. It enables one to visually demonstrate differences in the concentration of genes between breeds, to construct an ancestral population on the basis of averaged frequencies of genes of all breeds involved in the work, and to identify populations that are distant from or close to the ancestral form [16, 64, 65]. The same method is also successfully applied by Yu.A. Stolpovsky to other animal species [66].

Together with the appearance of new breeds and populations and the loss of the old ones, the quantitative and qualitative traits characterizing them also occur or disappear. As stated at the beginning, domestic chickens have a broad diversity of external morphological traits, of which most are inherited monogenically; therefore, at the initial stages of genetics development chickens were favorite objects in genetic

research. With the use of discrete morphological traits of chickens some fundamental laws of genetics were discovered (e. g., the phenomenon of epistasis). However, chicken, as objects for studying inheritance of morphological traits, have not been used for a rather long time. And wrongfully. These traits and objects have many advantages and can be successfully used even in the epoch of a wide introduction into research of molecular markers.

In the case of morphological traits, it is possible to work with museum objects, photos, drawings, verbal descriptions, and breed standards. If the original breed is cleared of traits characteristic of its varieties (chicken breeds have up to ten and more varieties differing mainly in plumage color), it is possible to create a "generalized" breed (its archetype) that is more ancient than its varieties, since the differentiation of breeds into smaller taxonomic units took place undoubtedly later. The possibility to compare hypothetic (generalized) breeds provides a great advantage in the case of using morphological traits. Other criteria do not give such possibilities. The features of the biological material (body measurements, blood groups, biochemical markers, and DNA) always characterize either a particular individual and reflect its individual genetic variability or a particular population when mixed samples of blood or some other biological material are used. In both cases, they can sometimes represent an atypical variant of a breed.

The use of morphological traits proved to be very suitable for determining phylogenetic relations between breeds or with the main wild ancestor of domestic chickens (Red Jungle Fowl). By characterizing breeds for morphological traits it is possible to estimate the loss of traits/genes under the influence of various factors, particularly the anthropogenic influence [65]. For instance, it is seen from a simple visual examination of commercial fowl crosses that they do not display an abundant diversity of morphological traits, i. e., they are rather similar in appearance. To estimate the losses in this connection, information was collected for 40 chicken breeds (including six commercial breeds) employed in the creation of commercial fowl lines on the basis of the presence or absence of 37 well recorded traits (comb form, neck feathering, crest, muffs and beard, rate of feathering, some colors and patterns of plumage, etc.). The commercial breeds appeared to lack 13 traits (13 genes) of the mentioned 37 ones (35.1%). We do not discuss here the expediency of introducing the missing traits into the breeding process, which is a special theme [65].

Now we will digress from the chicken theme. Recall that the System of Nature by Carl Linnaeus was developed mainly on the basis of morphological characters and since that time has not undergone significant changes with the introduction of molecular studies in our century. N.I. Vavilov worked with different cereal species and studied them mainly for morphological and several physiological criteria using 91 traits! This work permitted him to formulate the law of homologous series in hereditary variability [67]. After all, whole sciences (zoology, botany) exist that involve studies of morphological features of varieties, species, and taxa of higher ranks. The laws of Gregor Mendel are also based on discrete qualitative characters of pea. As far as animals are concerned, there are followers and supporters of this approach in our time, too. In his PhD thesis, Yu.A. Stolpovsky characterizes Ukrainian Grey Steppe Cattle not only for molecular markers, but also for morphological traits (phenes) [68].

However, we should also indicate the drawbacks of the use of discrete morphological traits. First of all, they are suitable and informative in the case of a high degree of intra- and interspecific variability for these traits. When such variability is absent (sibling species, visually indistinguishable populations within a species), the application of these traits does not seem to be efficient. This, however, is true of other markers as well. There are opposite cases existing in nature, when species differ from one another just in a few structural genes (chimpanzee and man), but nevertheless are phenotypically very unlike. We can hypothesize here that in such cases the analysis of morphological features of species might help to estimate the share of variability depending on the interaction of elements both within the genetic system and also on the interaction of this system with external factors, since this variability is likely to be most responsible for the mentioned differences.

Another serious disadvantage of morphological traits that is known to geneticists is their not always identifiable genetic control and the recessivity of alleles determining different traits that are not expressed phenotypically in the heterozygous state. Thus, in this case we study a trait sometimes not knowing its genetic determination, while when using molecular markers we know genetics, but often do not know what trait they determine. Let us state here three common truths. The first is that the choice of traits must depend on the purposes of a researcher. Some traits are more informative for one purpose, and other traits for another purpose. The second truth is that similarity does not yet mean relationship. The third is that it should always be remembered that one or another category of traits is only a part of the organism, i. e., of a system. Unfortunately, these truisms are not always addressed in scientific works.

The idea that the genetic system of a single organism and of a population as a whole (gene pool) is a complex and variable unit was graphically formulated by Serebrovsky himself: "We are standing jn the shore of a vast sea. Thousands of various or harmful substance-like genes are dissolved in that sea. And the sea is surging. Every minute mutations are blowing up in it as silent explosions presenting us with new values or poisoning the sea with new toxic substances. Through diffusion processes, these genes are slowly spreading, seizing more and more new areas. *Like complex flows,*

the iridescent streams are playing, mixing, and whirling, bearing new combinations of genes, often yet unknown to man, which we lose without catching... The name of that sea is the gene pool of domestic animals. *To learn, understand and master its disturbed highly complex life is our noble task"* [45] (our italics).

As we could see, the fundamentals of the genetic science developed by Serebrovsky are far from being exhausted. There still are pathways to be followed and things to work at and think of.

It is difficult to cover in one review all areas of research Serebrovsky was involved in during his rather short life and even his studies in only one field—particular and population genetics. In all his studies he strived to achieve remarkable scientific results. The life of Serebrovsky can be briefly characterized in one honorable and capacious word, devotion. Despite his uneasy life full of heroic efforts at achieving and defending scientific truth and overcoming adversity of life, he can be considered a happy man. He did much for the time allotted to him and worked throughout all his life constantly and purposefully for the sake of Science, Homeland, and Humankind. To him can be applied the words of V.V. Mayakovsky: "We are going through barking revolver shots to be incarnated into the names of ships and into the lines and other long-term deeds."

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