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Review article

Joanna GRUSZCZYŃSKA, Beata GRZEGRZÓŁKA, Agnieszka MORAWSKA

GENOME COMPARATIVE STUDIES IN THE *Phasianidae* FAMILY PART I. GENOME COMPARATIVE STUDIES IN THE *Phasianidae* FAMILY BETWEEN DOMESTIC CHICKEN *(Gallus gallus domesticus)* AND WILD TURKEY *(Meleagris gallopavo)*

Department of Genetics and Animal Breeding, Warsaw University of Life Sciences – SGGW, Poland

Abstract. In studies aimed at understanding the genome of turkey, the great facilitation was the use of genetic sequences and markers previously used to study the chicken genome. This solution was possible due to the fact that domestic chicken and wild turkey are phylogenetically related species with a common ancestor. In numerous analyses using chicken sequence, positive results of amplification of the turkey sequence were obtained, which accelerated the recognition of the genome of this species.

Key words: domestic chicken, wild turkey, genetic markers, physical and genetic mapping.

INTRODUCTION

The oldest traces of domestication of domestic chicken (*Gallus gallus domesticus*), originating in northern China, reach 8,000 years BC. Studies of mitochondrial DNA confirm that the immediate ancestor of the domestic chicken was the red jungle fowl, which all populations have a monophyletic origin due to the existence of one common ancestor (ICGSC 2004). Both domestic chicken and turkey belong to the same order of burrowing (*Galliformes*), phasianid family (*Phasianidae*). The common turkey belongs to the genus *Meleagris* (containing 6 subspecies); while phylogenetically it has been included in the *Phasianidae* family, which includes also pheasant, quail, guinea fowl (Reed 2007).

Domestic chicken is a model organism; it has many features that are used in biological research and shows similarity to other species of birds. A great facilitation in research on understanding the genome of the studied animal species is the possibility to use known microsatellite sequences of other, closely related phylogenetically species. However, due to the species specificity, it is necessary to check the informativeness of the genetic markers used.

The aim of this article was to present domestic chicken like a model organism which sequences and genes are useful in to investigations genomes other birds species.

Corresponding author: Joanna Gruszczyńska, Department of Genetics and Animal Breeding, Warsaw University of Life Sciences – SGGW, Jana Ciszewskiego 8, 02-786 Warszawa, Poland, e-mail: joanna_gruszczynska@sggw.pl

GENOMES OF DOMESTIC CHICKEN AND WILD TURKEY

The domestic chicken karyotype consists of 39 pairs of chromosomes: 10 pairs of large chromosomes (autosomes 1–10) and sex chromosomes (W and Z), 28 pairs of microchromosomes (autosomes 11–38) (Burt 2002; Masabanda et al. 2004). Chromosomes 3, 5, 7, 9 are telocentric, chromosomes: 1, 2, 8 and Z and W are metacentric, and 4 and 6 submetacentric (Fechheimer 1990). The chicken genome (Genbank No. GCA_000002315.3 – last update 2015/12/16) consists of approximately 1230258 nucleotides. It is estimated that the total number of genes is 25062, and proteins 46393 (National Center for Biotechnology Information, http: //www.ncbi.nih.gov).

In December 2015, the International Chicken Genome Consortium announced a new map of the 5.0 domestic chicken genome. The chicken genome currently published in the NCBI database consists of 33 autosomes, LGE64 chromosome and Z and W chromosomes.

In relation to mammals, bird genomes contain a greater number of chromosomes. There is also a low content of DNA sequence repetitions, only at the level of 11%, while in mammals the repeatability is 40–50% (Burt 2002). The chicken genome (*Gallus gallus domesticus*) has characteristics of other genomes of birds belonging to primitive birds (*Palaeognathae*), archaic *Neognathae* (*Anseriformes, Galliformes*), as well as of many species belonging to the higher *Neognathae* (Christidis 1990; Rodionov 1997). The size of the genome is small, as it is 1.03 Gb or 96% of the size of the predicted chicken genome (Schmid et al. 2015). Microchromosomes present problems in correct karyotyping, because they are not distinguished by G-band, which is a conventional method used in cytogenetic mapping. Microchromosomes contain about 50% genes of the entire avian genome, and also behave like other chromosomes: they are kept stable during meiosis and mitosis and have functional centromeres and telomeres. The frequency of recombination in avian microchromosomes is 10 times higher than in case of mammalian chromosomes. This high rate of recombination is due to the need to ensure proper pairing of microchromosomes during mitosis and meiosis (Burt 2002).

The turkey karyotype consists of 40 pairs of chromosomes (2 n = 80). The macrochromosomes include: 9 pairs of autosomes and sex chromosomes, while microchromosomes are represented by 30 pairs (Bloom et al. 1993). The following types of macrochromosomes can be distinguished in turkey's genome: one of them is a metacentric chromosome, five acrocentric chromosomes and three chromosomes with shorter arms (Schmid et al. 2005). The metacentric Z chromosome is the fourth largest chromosome, and the size of the metacentric W chromosome is roughly compared to the size of the chromosome 6 (Krishan and Shoffner 1966). The karyotype contains an additional chromosomal pair relative to the chicken due to the presence of at least two fission/fusion differences (GGA2 = MGA3 and MGA6 and GGA4 = MGA4 and MGA9). Given these differences involving the macrochromosomes, an additional fission/fusion must also exist between the species involving the microchromosomes if the diploid numbers are valid. Other rearrangements have been identified through comparative genetic maps (Axelsson et al. 2005; Reed et al. 2007), physical maps and whole genome sequencing (Dalloul et al. 2010).

Turkey genome sequencing project began in 2008 with scientists from the University of Virginia and in 2010 scientists published the results of the study, which presented the results

of sequencing 93% of the genome. During the study, 16 000 genes were discovered, most of the data came from 10 macrochromosomes. The turkey genome was known much faster, and at a lower costs than the chicken genome, which was published in 2004 (Dalloul et al. 2010). In GenBank information on the genome of turkey was published under number GCA_000146605.3, 30 autosomes and chromosomes of sex Z and W were examined, with a total sequence length of 1128.34 Mb, 21672 genes and 33329 proteins were described (National Center for Biotechnology Information, http://ncbi.nih.gov – last updated on December 23, 2016). It is believed that the size of turkey genome is comparable to the size of chicken genome, representing one third of the human genome. Repeated sequences in turkey genome have not been extensively characterized, but are similar to 10–15% tested in the chicken (Wicker et al. 2005). Stability of the genomes of species of the genus *Galliformes* has been found. Research on the sequencing of the turkey genome confirmed and expanded high level of co-linearity between chicken and turkey genomes. Genomes of these two species can be distinguished from each other by rearrangements (mainly small inversions).

Repeats in turkey genome account for 7% (Dalloul et al. 2010). Ultra short telomere repeats (TTAGGG)n were reported in domestic chicken as well as in other bird species, including turkey (Chaves et al. 2007). These repetitions seem to enrich the W sex chromosome and numerous microchromosomes. The reduced amount of repeated DNA in chicken genome compared to the mammalian is reflected in the frequency of microsatellite repeats (Primmer et al. 1997). In the domestic chicken genome the most common repeating sequences are motifs (CA)n and (GA)n, in turkey the situation is similar (Dranchak et al. 2003). In the latter a significant number of a three-nucleotide repeating motif (GGA)n can be seen (Reed 2009).

In later studies, Reed et al. (2007) and Reed (2009) demonstrated that the similarity between chicken and turkey genomes exceeded 90%. A study by Griffin et al. (2008) proved that despite the above-described differences, avian genomes compared to their mammalian equivalents, have remained relatively stable during evolution.

DOMESTIC CHICKEN GENOME SEQUENCING

Great progress in work on the chicken genome was possible due to sequencing of the entire genome of this species with the use of bacterial artificial chromosomes (BACs), plasmids and fosmids. Despite the fact that the chicken genome is characterized by small size and a relatively small number of repeating elements, a relatively high quality sequence was obtained. Its total size was 907 mega base pairs (Mbp). The second version of the sequence (Genome Built 2.1), which is widely available, contains autosomal chromosomes from the first to 28, as well as chromosome 32 and chromosomes of sex Z and W, mitochondrial DNA and two additional linking groups. Researchers succeeded in sequencing 2.8 million single nucleotide polymorphisms (SNPs), based on comparing the genome sequence of the red jungle fowl with sequence fragments of different breeds of both meat and layer hens and also of fancy ones (ICPMC 2004).

The avian genome is about three times smaller than the genome of any mammal species; this is due to reduction in the number of repetitive elements, pseudogenes, as well as

segmental duplication and duplication of genes in the avian genome. Such a significant reduction in size is caused by evolutionary adaptations of birds to flight. The ability to fly requires intensive oxygen metabolism, which can be achieved with the large surface area of gas exchange and the reduction of cell size. Thus, the mass of the cell nucleus was reduced, which resulted in reduction in the mass of genomic DNA (Huges and Piontkivska 2005). The reduction in the genome caused reduction in the size of chromosomes and negative correlation of the size of the chromosome with the recombination rate, the number of CpG islands, the number of guanine (G) and cytosine (C) bases with gene content. Thus, it is known that genetic rich regions are found in microchromosomes from eleventh to 38, which constitute 18% of the chicken genome and contain approximately 31% of genes (ICGSC 2004).

USE OF MICROSATELLITE SEQUENCES

Short tandem repeats or simple sequence repeats (STRs or SSRs) have variable numbers of tandem repeats (VNTRs). Microsatellite sequences are present in all chromosomes, and also show strong polymorphism in terms of length and number of base sequence repeats. Their occurrence is more frequent in the area of euchromatin than heterochromatin, while clusters of microsatellite sequences have been detected in centromeres and telomeres. They are developed for each species individually because they have high genomic specificity. Microsatellite sequences are used for compaction of genetic maps, and are also used to search for linkage between functional traits. In homologous chromosomes, two fragments of DNA that differ in length of the repetition will be the next alleles of a given microsatellite sequence.

The repeated motifs in homologous chromosomes occupying the same site can be of different lengths. In these regions the efficiency of the control and repair system is reduced due to high rate of mutation in these regions and because these sequences are usually located in introns and are not transcribed. The presence of microsatellite sequences located in the region of DNA repeats (the region of repeats between two flanking regions) lead to so-called polymerase slip (during DNA replication) or unbalanced crossing over (during meiosis). The length of the sequence, the type of repetition and the location in the chromosome has an impact on the frequency of mutations in microsatellite sequences. The addition or deletion of a single copy of the basic motif results in about 1.2% of new alleles of the microsatellite sequences.

GENETIC MAPPING

Several types of markers have traditionally been used for genetic mapping: encoded sequences (ESTs or type I) and highly polymorphic markers such as microsatellites (type II markers). Significant progress in genetic mapping has been made thanks to the development of molecular techniques (Groenen et al. 2000). The basis for creating a genetic linkage map of chicken genome was the recombination rate between microsatellites, and three available reference populations (East Lansing, Compton and Wageningen) were used to create it (Groenen et al. 2000). The map was composed of 1889 *loci*, and 480 of them form its

framework; they were grouped in 50 linkage groups, while the remaining 1409 *loci* were located in relation to the frame *loci*. The estimated size of the consensus genetic map is approximately 3800 cM. The resolution of the map was significantly increased by 12945 SNP markers, which were grouped in 34 linkage groups in 29 autosomes. In this way a new map was obtained and it is much smaller than the previous one, the size of 3228 cM. It was found that the level of recombination varies, but is not sex-dependent (Groenen et al. 2000).

In 1992, the first gene sequences for turkey were registered / deposited in the GenBank, while in 1995 the first microsatellite sequences were published (Burt 2003). The first linkage map of the turkey genome was published by Harry et al. (2003). Over 300 markers were examined, of which 277 were new microsatellite sequences and also 111, which turned out to be polymorphic and used for mapping (Burt et al. 2003).

In total, 20 linkage groups (including the Z chromosome) containing 74 markers and 34 markers that could not be assigned to any linkage group were examined. The number of markers per linkage group ranged from two to six and the largest of them was 76.3 cM.

According to research carried out by Reed and colleagues (2003), the genomic map contained 138 loci and comprised 113 loci arranged in 22 linkage groups and additional unrelated 25 loci. The total map distance within the linkage groups was 651 cM. Further studies have shown that in 20 linkage groups the total genetic distance is 700 cM and is estimated to be 25% of the turkey genome and is based on chicken genetic map (3800 cM). 20 cM were assigned to unlinked markers, which extended the coverage of the map to approximately 70% of the genome (Reed 2009). An average length obtained between the linked markers was 6 cM and the largest distance between the markers (17 *loci*) was 131 cM (Reed 2009).

The genetic map for turkey was created based on the analysis of the segregation of genetic markers in backcrosses. Based on these studies, a similarity was found between 23% of the turkey sequence and the mRNA sequence reported to the GenBank for the domestic chicken.

PHYSICAL MAPPING

Cytogenetic mapping was one of the first methods of physical mapping of chicken genome, in which classical techniques of staining or methods of molecular cytogenetics were used. As microchromosomes form the majority of chicken genome, it is difficult to identify them. In cytogenetic mapping, specific molecular probes for the chromosome and FISH technology were used. These probes mark the entire chromosome, but they are also specific to a given *locus* (Masabanda et al. 2004).

Radiation hybrid (RH) panel has higher resolution than cytogenetic maps. It is composed of a set of cell hybrids that were created by fusion of chicken embryo fibroblasts. They were irradiated with a dose of 600 rads with $Wb3hCl_2$ cells, and did not display hypoxanthine--guanine phosphoribosyltransferase (HPRT) activity. DNA was isolated from 452 clones of cellular hybrid and microsatellite marker panel analysis was performed. With this analysis, it was possible to reconstruct the radiation map based on the presence of chromosomal cracks.

This led to the separation of markers to individual cell hybrids, which gave the opportunity to determine the distance between markers on the radiation map (Morisson et al. 2002).

Nucleotide map has the highest resolution. In order to obtain the genome sequences, DNA expressed sequence tags (EST), were to be subjected to mass sequencing. The expressed DNA sections were deposited in cDNA libraries. Functional elements in the chicken genome were identified in result of identifying about 20,000 cDNA fragments. Thanks to this data, expression macro arrays were constructed to analyse the functionality of genes.

Interspecies physical mapping of the genome of the turkey also used hybridization of the artificial bacterial chromosome clones (BACs) to turkey metaphase chromosomes (Robertson et al. 2005) and chromosomal labelling. To locate turkey BAC turkey clones, *in situ* fluorescence hybridization (FISH) was used for these analyses (Reed 2010).

In Romanov and Dodgson's studies (2006), CHORI-260 filter sets were used to perform interspecific hybridization of comparative mapping. A positive hybridization result was obtained from 81% of Overgo probes (total number of probes – 415), and 336 markers or genes were assigned to 3772 artificial turkey bacterial chromosomes (BACs).

Creating turkey maps and comparing them with the chicken genome was based on genetic markers, which include microsatellites and SNPs. BLAST analysis made it possible to build a physical map of chicken genome by comparing the sequences of turkey markers with the sequences of the whole genome of the domestic chicken. The result of segregation of genetic markers was the development of a linkage map of the genome of turkey based on data from the University of Minnesota / Nicholas Turkey Breeding Farms, in which up to 29 linkage groups were assigned to 314 *loci*. The distance between the linkage groups was 2.011 cM, the longest segment of the linkage group measured 413.3 cM and was made up of 47 *loci* (Reed et al. 2005). Aslam et al. (2010) developed a linkage map containing 531 markers in 28 linkage groups, and the total distance between the groups was 2.324 cM. The largest distance between linkage groups (81 *loci*) was 326 cM.

CONCLUSIONS

Research by Aslam et al. (2010), Zhang et al. (2011) and others demonstrated that the differences between chicken and turkey genomes result from the chromosomal rearrangements, which, as shown by phylogenetic analysis, could occur over a period of 20 million to 40 million years back on the result of the progressing evolutionary separation of both species.

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BADANIA PORÓWNAWCZE GENOMÓW W RODZINIE *Phasianidae.* CZĘŚĆ I. BADANIA PORÓWNAWCZE GENOMÓW W RODZINIE *Phasianidae* NA PRZYKŁADZIE KURY DOMOWEJ (*Gallus gallus domesticus*) I INDYKA ZWYCZAJNEGO (*Meleagris gallopavo*)

Streszczenie. W badaniach, których celem było poznanie genomu indyka, wielkim ułatwieniem było zastosowanie sekwencji i markerów genetycznych wcześniej wykorzystywanych do poznania genomu kury. Takie rozwiązanie było możliwe, ponieważ kura domowa i indyk zwyczajny to gatunki spokrewnione filogenetycznie, posiadające wspólnego przodka. W wielu analizach z wykorzystaniem sekwencji kury uzyskano pozytywne wyniki amplifikacji sekwencji indyka, co przyspieszyło poznanie genomu tego gatunku.

Słowa kluczowe: kura domowa, indyk zwyczajny, markery genetyczne, mapowanie fizyczne i genetyczne.