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ERRATUM

Erratum to: Single nucleotide polymorphism analysis of Korean native chickens using next generation sequencing data

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Single nucleotide polymorphism analysis of Korean native chickens using next generation sequencing data

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Abstract There are five native chicken lines in Korea, which are mainly classified by plumage colors (black, white, red, yellow, gray). These five lines are very important genetic resources in the Korean poultry industry. Based on a next generation sequencing technology, whole genome sequence and reference assemblies were performed using *Gallus_gallus_4.0* (NCBI) with whole genome sequences from these lines to identify common and novel single nucleotide polymorphisms (SNPs). We obtained 36,660,731,136 ± 1,257,159,120 bp of raw sequence and average 26.6-fold of 25–29 billion reference assembly sequences representing 97.288 % coverage. Also, 4,006,068 ± 97,534 SNPs were observed from 29 autosomes and the Z chromosome and, of these, 752,309 SNPs are the common SNPs across lines. Among the identified SNPs, the number of novel- and known-location assigned SNPs was 1,047,951 ± 14,956 and 2,948,648 ± 81,414, respectively. The number of unassigned known SNPs was 1,181 ± 150 and unassigned novel SNPs was 8,238 ± 1,019. Synonymous SNPs, non-synonymous SNPs, and SNPs having character changes were 26,266 ± 1,456, 11,467 ± 604, 8,180 ± 458, respectively. Overall, 443,048 ± 26,389 SNPs in each bird were identified by comparing with dbSNP in NCBI. The presently obtained genome sequence and SNP information in Korean native chickens have wide applications for further genome studies such as genetic diversity studies to detect causative mutations for economic and disease related traits.

Keywords Korean native chicken · Genome sequence assembly · Next-generation sequencing · Single nucleotide polymorphism

Introduction

The cost for genome sequencing has markedly decreased, enabling the determination of the genome sequences of pig, chicken, cattle, and horse [1–6]. The chicken genome sequence published in 2004 indicated that the chicken genome is about one-third that of the human genome and

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can be used for the model animals, especially evolution, development and disease studies [6]. After releasing draft genome sequences obtained from red jungle fowl, re-sequencing was performed and the results were used to construct single-nucleotide polymorphism (SNP) chips [7, 8]. For the genomic studies in chicken, 60 and 600 K SNP chips were used for the identification of qualitative trait locus (QTL) regions and SNPs identified to be associated with production traits were used for the genomic selection [7, 8]. This result is mainly due to the benefits of low cost for the individual genome re-sequencing, along with the high accuracy of reference assembly method [9]. Nowadays, the next-generation sequencing (NGS) platform has become widely used and can analyze a large amount of sequencing data at a time, which is the very useful tool for genome-wide analysis [10–12]. NGS technology has been widely used for *de novo* genome sequencing, re-sequencing and SNP discovery [10, 12, 13]. Also, the accumulated sequencing data can be applied for identifying genetic markers, especially SNPs and insertion and deletion (InDel). For this reason, NGS-based genome assembly can be widely used for model and domestic animals such as mice, rats, cattle, pigs, dogs, cats and chickens together with the human sequence data.

Recently, the consumption of chicken meat has been increasing rapidly and constitutes more than 23 % of the total meat consumption in Korea [14]. However, more than 90 % of breeding stocks in Korea are imported from foreign countries. Korean native chickens (KNCs) originated 2,000 years ago in Korea [15]. Even though KNCs have good quality traits, based on the sensory evaluation, odor, taste, and overall acceptance, most native chicken breeds became almost extinct due to the Second World War, Korean War and rapid industrialization in Korea [16]. Also, the low productivity of native breeds in comparison with imported breeds has contributed to their demise. As a result, KNC meat is 2–3 times more expensive in price than the commercial broilers [16].

In 1994, a native chicken restoration project was launched and as the results, the five lines of KNC have been restored and preserved in the National Institute of Animal Science (NIAS) in Korea. In this point of view, genetic variation study of KNC is very important because they are unique and representative chicken resources in Korea. However, the genetic variation study in genome-wide level using KNC has not been reported yet. Some studies investigated associations of SNP variation in mitochondrial DNA (mtDNA) with economic traits in KNC and microsatellite marker analysis for diversity studies and discrimination of Korean native chicken lines [17–21]. In this study, we used the five lines of KNC for whole genome sequence assembly and reference assembly to investigate novel SNPs and InDels, which will be useful for genetic diversity and for the search for causal mutations or candidate gene studies in the future.

Materials and methods

Sample preparation

Male KNC samples were collected for DNA extraction. Broiler care facilities and procedures met or exceeded the standards established by the Committee for Accreditation of Laboratory Animal Care at National Institute of Animal Science (NIAS) in Korea. The study also was conducted in accordance with recommendations described in The Guide for the Care and Use of Laboratory Animals" published by the institutional Animal Care and Use Committee (IACUC) of NIAS (2012-C-037) in Korea. The five chicken lines were mainly classified on the plumage colors of white, black, red, yellow and gray (Supplementary Fig. 1). One representative sample, the core animals for the QTL study, was selected from each line for DNA extraction from blood. Genomic DNAs were extracted using a manual extraction method [22] and stored at −20 °C until use.

Genome sequencing

A genomic DNA library with an insert size of 250 bp was constructed from each sample using TruSeq™ DNA Sample Preparation Kit v2 (Illumina, San Diego, CA, USA) following the manufacturer's protocols. Raw sequence data were obtained by paired-end sequencing using HiSeq 2000 sequencing platform (Illumina) from each genomic library. All raw sequence data were deposited in a public database [i.e., Sequence Read Archive (GenBank:Study_id)].

Reference assembly

The raw sequence read from five lines of sample were pre-processed according to its quality scores. The sequence bases with less than Q20 were changed to "N". The sequences with less than 90 base pairs (bps) or with "N"s more than 10 % of their total lengths were removed (Table 1). Quality-trimmed sequence reads were aligned to the chicken reference genome, *Gallus_ gallus_4.0* using CLC Assembly Cell software 4.1.06 [23] with the default settings, i.e. 80 % identity and 50 % high-scoring pairs (HSP) coverage (Table 2).

SNP discovery

SNPs and small InDels were identified using the 'find_variations' program in CLC Assembly Cell from

Table 1 Raw sequence data from five Korean native chicken lines

Line	Raw data		Processed high quality data (>q20)		
	No. of read	Total, bp	No. of read (%)	Total, bp (%)	Depth (X)
Gray	375,424,656	37,917,890,256	281,536,451 (75.0)	27,992,800,244 (73.8)	27
Black	354,548,474	35,809,395,874	259,765,759 (73.3)	25,995,380,609 (72.6)	25
Red	350,530,416	35,403,572,016	277,166,653 (79.1)	27,620,520,396 (78.0)	26
White	367,190,708	37,086,261,508	293,172,162 (79.8)	29,332,112,305 (79.1)	28
Yellow	369,509,968	37,320,506,768	289,084,995 (78.2)	28,789,201,753 (77.1)	27

Table 2 Reference genome assemblies with *Gallus_gallus_4.0* (NCBI) for the five Korean native chicken lines

Line	No. of mapped read (%)	Depth (X)	Mapped nucleotide (bp)	Coverage (%)
Gray	280,034,588 (99.47)	26.49	1,019,536,924	97.38
Black	258,348,412 (99.45)	24.59	1,019,542,120	97.38
Red	275,718,319 (99.48)	26.14	1,018,743,154	97.31
White	291,583,125 (99.46)	27.76	1,019,672,009	97.40
Yellow	287,566,463 (99.47)	27.25	1,015,226,270	96.97

reference-assembled sequences with parameters as follows: minimum depth = 10; minimum mismatch count = 10; limit fraction ≥35 %. To reduce the erroneous SNP callings caused by uncertainty of multiple sequences mapping to high sequence similarity regions among genome, we filtered out the low quality mappings which failed to satisfy 95 % identity and 100 % HSP coverage. To compare our findings with dbSNP database, all chicken rsSNP sequences from dbSNP build 131 were mapped to *Gallus_gallus_4.0* genome with 98 % identity and 100 % HSP coverage, since the dbSNP set was originally localized to the *Gallus_gallus_ 2.1* assemblies.

SNP analysis

To further characterize the features of the SNPs, we categorized them into genic versus intergenic SNPs. About half of the SNPs (47 %) were localized into genic regions, and the rest was mapped in intergenic regions. In addition, non-synonymous SNPs in the exon region were analyzed concerning whether its amino acid character was changed (e.g., hydrophobic to basic or stop codons), since the compositional change of amino acids in proteins can result in changes of structural conformation or enzymatic activities and give phenotypic diversity or critical functional variations. First, 20 amino acids were clustered into several character groups. Then non-synonymous SNPs causing an amino acid change from one group to another were searched. Among all of the SNPs, common SNPs in five birds representing each line were classified.

Results

Sequences of KNCs

Five birds representing each line of KNC were subjected to the NGS using Hiseq 2000 sequencing platform (Illumina). The results indicated that more than 350,530,416 (350 M) of 100 bp paired-end short reads were obtained in each animal and total sequence lengths were more than 35,403,572,016 (35 G) bp (Table 1). After quality trimming analysis, total 259–293 million short reads (73.3–79.8 % of the total reads) having 90–100 bp of length and average depth of 26.6× were obtained (Table 1). Thus, total lengths after quality-trimming were from 25 to 29 billion (G) bp, which represents between 72.6 and 79.1 % of the raw sequence length (Table 1). The shortest sequence length was 25 Gbp from black KNC and longest sequence length was 29 Gbp from white KNC (Table 1). Reference assembly with *Gallus_gallus_4.0* Genome in NCBI was obtained using quality trimmed sequence data. The results indicated that 99.466 % reads were identical between the sequences obtained in this study and the NCBI database. Also, the results of mapped sequences indicated that 97.288 % of reference genome was covered in this study and the average depth was 26.4× (Table 2).

Detection and analysis of SNPs and InDels

The SNPs identified in this study were compared with the dbSNP in NCBI. As the results, 3,813,253–4,103,602 SNPs were obtained from 29 autosomes and Z chromosome (Table 3). Among the identified SNPs, the number of common SNPs is 752,309 across lines. Of these, 80.75 ± 1.15 % were homozygous SNPs and 19.25 ± 1.15 % were the heterozygous SNPs in KNC. These SNPs were further classified as base substitution, insertion, and deletion. The base substitution, insertion, and deletion were 93.8 ± 0.2, 2.45 ± 0.05 and 3.75 ± 0.15 %, respectively (Table 3). Also, the ratio of insertion and deletion was calculated as 1:1.54. Among the location known SNPs, the number of previously identified SNPs and novel SNPs were estimated

1,005,238–1,062,907 and 2,800,268–3,030,062, respectively. Also, the number of SNPs that were not assigned on the chromosome was 1,022–1,331 and 6,725–9,302 for known SNPs and novel SNPs, respectively (Table 4). When we compared the numbers of known SNPs with those of novel SNPs, the novel SNPs in KNC were three times more than previously known SNPs. Also, the SNPs in the genic region were investigated. The synonymous SNPs, non-synonymous SNPs, and SNPs having character changes were counted as 24,810–27,722, 10,863–12,070 and 7,722–8,638, respectively. Among the SNPs, large number of SNPs (1,772,392–1,899,860 SNPs) in the genic region were mapped in the intron regions (Table 5). Also, SNPs having character changes were further analyzed (Supplementary Table 1). Moreover the genes that lost stop codon(s) or gain the stop codon(s) were listed in Supplementary Table 2.

Table 3 The variation types of identified SNPs with the comparison of reference sequence

Line	Total no. of SNP	Variation type		
		Substitution	Insertion	Deletion
Gray	4,044,996	3,796,757	98,370	149,869
Black	3,813,253	3,585,756	91,059	136,438
Red	3,905,285	3,666,396	94,444	144,445
White	4,103,602	3,839,466	103,855	160,281
Yellow	4,006,068	3,761,049	97,107	147,912

Table 4 The comparison of identified SNPs with the SNP data from dbSNP in NCBI

Line	Total No. of SNP	Localized on chr		Unlocalized on chr	
		Known	Novel	Known	Novel
Gray	4,044,996	1,052,155	2,983,262	1,181	8,398
Black	3,813,253	1,005,238	2,800,268	1,022	6,725
Red	3,905,285	1,021,413	2,875,467	1,070	7,335
White	4,103,602	1,062,907	3,030,062	1,331	9,302
Yellow	4,006,068	1,047,951	2,948,648	1,186	8,283

When we investigated the SNPs among native chicken lines, these five animals representing each line had the similar number of SNPs, ranged from 416,659–469,436 SNPs (Fig. 1, Table 6).

All the SNPs in this study have been submitted to NCBI's dbSNP and their accession numbers are KG53_chr : 804271016–808268271, KG53_unChr : 825085054–825133198, KL40_chr : 808268284–813196753, KL40_unChr : 825133199–825178737, KR16_chr : 813196754–817057774, KR16_unChr : 825178737–825223372, KW03_chr : 817057775–821109537, KW03_unChr : 825223373–825275664, KY24_chr : 821109538–825066221, KY24_unChr : 825275665–825325506.

Discussion

The KNC was subjected genome sequencing using NGS platform and the SNPs and InDel were investigated in this study. Recently, many studies focused on the improving

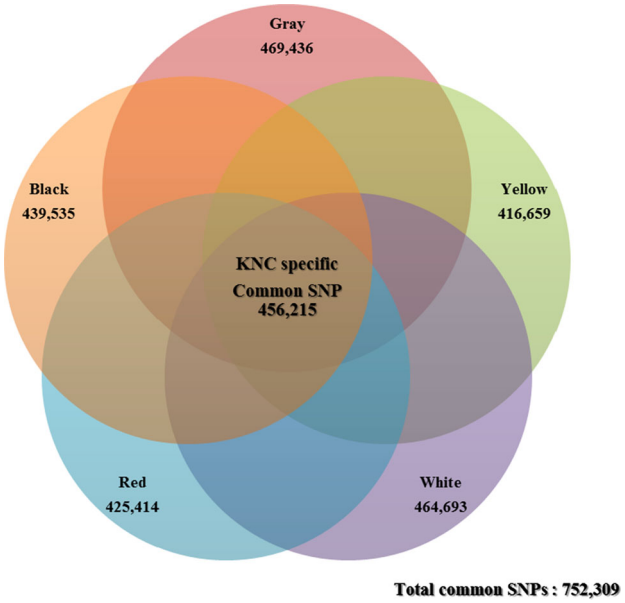

Fig. 1 The identified SNPs in the Korean native chicken

Table 5 The classification of identified SNPs in genic regions

Line	Total no. of SNP	Coding sequence				Intron
		Synonymous	Non-synonymous	Character change	No. of gene affected	
Gray	4,044,996	27,461	11,852	8,496	1,600	1,872,161
Black	3,813,253	24,810	10,863	7,722	1,606	1,772,392
Red	3,905,285	25,193	11,146	7,987	1,526	1,812,877
White	4,103,602	27,722	12,070	8,638	1,670	1,899,860
Yellow	4,006,068	26,816	11,651	8,271	1,683	1,855,701

Table 6 The classification of SNPs identified in this study

	Gray	Black	Red	White	Yellow	Common
Total No. of SNP	469,436	439,535	425,414	464,693	416,659	456,215
Intergenic	250,668	232,549	228,363	248,029	222,121	246,382
Intron	213,218	202,323	192,819	211,137	189,853	20,5212
Gene	270	209	208	300	296	199
CDS	5,280	4,454	4,024	5,227	4,389	4,422
Synonymous	3,639	3,020	2,701	3,593	2,982	2,910
Non-synonymous	1,641	1,434	1,323	1,634	1,407	1,511
Character change	1,182	1,030	962	1,194	997	1,098
Substitution	418,110	391,767	378,259	409,368	369,603	437,278
Insertion	33,453	31,094	30,861	36,443	30,682	9,372
Deletion	17,873	16,674	16,294	18,882	16,374	9,565

the quality of native chicken meat for wider use in the Korean poultry industry [17–20]. This result is the first report for the release of the genome sequence information of native chickens and the related SNPs and InDel information in the public domain. In this study, 25–29 Gbp sequences were obtained, covering 26.6× of the chicken genome. Previously, Groenen et al. [7] obtained 12× coverage and 14.6 Mbp sequences and subsequently developed 60 K SNP chips. Also, Kranis et al. [8] achieved 8–17× coverage and 3.6 Gbp to prepare 600 K SNP chips. Our data generated in this study have more genome coverage and longer sequence length than the previous results. Additionally, the result of reference assembly with *Gallus_gallus_4.0* (NCBI), we obtained 97.288 % of high coverage sequence which length of sequences are similar with previous results [6, 9].

SNP and InDel analysis

A total of 3,258,237 rsSNPs were identical to the SNPs which are deposited in the *Gallus_gallus_4.0* genome at NCBI. The number of SNPs from KNC genome sequence indicated approximately four million SNPs. With comparison of reference genome sequence of red jungle fowl (2.8 million SNPs), the SNP data of the five lines of KNC were more polymorphic than that of red jungle fowl [6]. Also, Kranis et al. [8] performed re-sequencing of various chicken breeds for making 600 K SNP chip and investigated SNPs from 448 K to 11 M in the variable chicken species. The commercial lines were highly polymorphic, whereas inbred lines showed low polymorphism content, as expected. The KNC showed similar results with Rhode Island Red and White Rock, but lower than White Plymouth Rock, White Leghorn, and broilers. [8]. Furthermore, our SNP results revealed three times more novel SNPs than common SNPs in dbSNP (NCBI) in the five animals of KNC, which can be used for further genetic variation and diversity studies. In addition, the results indicated a homozygous and heterozygous SNP ratio of eight to two, showing four times less variation compared with the reference genome. This result may be due to the small population size of the founder population of KNC and also may due to the bottleneck effect during the recent restoration process (BS Kang, personal communication). The identified SNPs were subjected to comparative analysis using the dbSNP (NCBI), resulting in approximately 1 million SNPs which matched known SNPs, and 2.9 million SNPs, which were confirmed as novel SNPs with known chromosomal map position. Alternatively, 1,000 SNPs matched known SNPs, while 7,000 SNPs were confirmed as novel SNPs with unassigned chromosomal locations. Approximately, half of the identified SNPs were existed in the genic region, indicating that more research is needed to clarify relationships between the variation in the genic regions and phenotypic traits of interest. Also, the identified ratios of synonymous and non-synonymous SNPs among the identified SNPs were 0.66 and 0.28 %, respectively, which was fewer compared to those of a previous study (2.45 and 1.9 %, respectively) [8].

InDel mutations are very important information for the genetic diversity between and within species [23]. Also, a recent study indicated that the InDels are commonly associated genetic diseases in humans [24]. A previous report from International Chicken Genome Consortium indicated that 2.8 million SNPs were observed in red jungle fowl and about 5 % of these mutations (140,484) were small InDel mutations from 1 to 5 bp of sequences [25]. In this study, the average number of identified SNPs was 3,974,641, which was more SNPs than the SNPs identified from International Chicken Genome Consortium. Of these, 6.16 % (244,756) were InDel mutations with less than 6 bp InDels. This indicates that more InDels that were identified in this study were much more than that of the International Chicken Genome Consortium [6, 25, 26]. The difference of InDel ratio may due to the difference in evolutionary process and genome size variation among the chicken breeds. [25, 27, 28].

When we looked at the variation types, the ratio between insertion and deletion was 1 (2.44 %):1.5 (3.72 %) and deletion was slightly more and there were few variations among the KNC lines. The total number of insertions and deletions was 96 K and 147 K, respectively. Among the lines, the black line had smallest number of InDels and the white line had the largest number of InDels. The InDel distribution suggests that 1 bp InDel was highest and 5 bp InDel was relatively lowest values. Our results support the findings that were made in a previous study, reporting that the 1–2 bp InDel was predominant and relatively less number of 5 bp InDels were identified [25]. Compared the InDel locations by chromosome, generally, macrochromosomes have more InDels compared to microchromosomes. And autosomes appear to have more InDels than sex chrosmomes. It is of note that intergenic and intron regions have more InDels than 5′-UTR, upstream of the gene and the first intron [25]. Our results support previous findings that largest number of SNPs and InDels were identified in intergenic and intron regions. Also, a relatively small number of 3′-UTR and 5′-UTR variations was identified. In order to validate the SNPs and Indels from the NGS data, variations in chicken THRSP gene were investigated by Sanger sequencing. The results indicated that all the identified SNPs (15 SNPs) from the NGS data were appeared in the Sanger sequencing, indicating the SNPs that we provided are very accurate (data not shown).

In conclusion, whole genome sequencing from the five birds representing each line of KNC was conducted in this study and novel SNPs and InDels were identified. The NGS data from KNC can provide the understanding the phenotypic characteristics of native chickens and genes under selective sweeps during the domestication. These results also provide guidelines for the breed establishment and identifying causative mutations affecting economic traits. Also, the native chicken SNPs can be utilized to understand the trait relationships in the diverse native chicken populations [29]. All of these results were deposited in the public domain and these results can be widely used for the diverse research areas including genome studies, identifying causative mutations for economic and disease related traits in the future.

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