Genome-wide genetic structure and selection signatures for color in 10 traditional Chinese yellow-feathered chicken breeds

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Abstract

Background Yellow-feathered chickens (YFCs) have a long history in China. They are well-known for the nutritional and commercial importance attributable to their yellow color phenotype. Currently, there is a huge paucity in knowledge of the genetic determinants responsible for phenotypic and biochemical properties of these iconic chickens. This study aimed to uncover the genetic structure and the molecular underpinnings of the YFCs trademark coloration.

Results The whole-genomes of 100 YFCs from 10 major traditional breeds and 10 Huaibei partridge chickens from China were re-sequenced. Comparative population genomics based on autosomal SNPs revealed three geographically based clusters among the YFCs. Compared to other Chinese indigenous chicken genomes incorporated from previous studies, a closer genetic proximity within YFC breeds than between YFC breeds and other chicken populations is evident. Through genome-wide scans for selective sweeps, we identified RALY heterogeneous nuclear ribonucleoprotein (RALY), leucine rich repeat containing G protein-coupled receptor 4 (LGR4), solute carrier family 23 member 2 (SLC23A2), and solute carrier family 2 member 14 (SLC2A14), besides the classical beta-carotene dioxygenase 2 (BCDO2), as major candidates pigment determining genes in the YFCs.

Conclusion We provide the first comprehensive genomic data of the YFCs. Our analyses show phylogeographical patterns among the YFCs and potential candidate genes giving rise to the yellow color trait of the YFCs. This study lays the foundation for further research on the genome-phenotype cross-talks that define important poultry traits and for formulating genetic breeding and conservation strategies for the YFCs.

Background

Different cultures and ethnicities around the globe have developed unique cuisines, into
which chickens are incorporated in diverse ways. Chicken consumption is popular globally, with the preference for chicken meat eclipsing that of red meat [1, 2]. Yellow-feathered chickens, otherwise known as “three-yellow chickens” because of their characteristic yellow beak, feathers, and feet [1], and herein abbreviated as YFCs, are a favorite choice for traditional broths and soups in Asian countries, particularly in Korea and southern China. YFCs have been described in the ancient Chinese agricultural text “Qimin Yaoshu” written around 540 C.E. [3], and their importance is evidenced by the incredible leap in their demand. For instance, the production of YFC meat in China reached 4,445 kilotons in 2015, representing 31.8% of the national broiler meat yields [4]. The YFCs’ unique meat flavor and color appeal are important factors driving this strong consumer preference. In addition to serving as a traditional nutritional and commercial mainstay for millions of people living in China and its purlieus, YFCs are reported to have contributed to the recent breeding of European chickens [5], indicating a broadening utility of the YFCs. At the present, more than 15 traditional breeds of YFCs are dispersed widely in China [6]. However, these attributes are threatened by the aggressive genetic selection for rapid growth and high feed conversion efficiency in China and other Asian countries [7].

Previous research on YFCs primarily focused on understanding the chemical properties of meat and soups [2, 8–10], or their genetic diversity compared to commercial breeds using low-density markers [1, 11, 12]. Hardly any genome-wide investigations of the population structure and genetic basis of the unique YFC phenotypic traits have been conducted, a major drawback in rational improvement and conservation of these chickens.

In this study, we sought to accomplish an extensive sequencing of YFC populations across China to support their in-depth studies into their evolutionary biology. We also aimed to implement comparative population genetic analyses to determine the genetic structure of the YFCs and retrieve the footprints of selection for their unique color property. This study
provides vital resources and insights to facilitate effective avicultural strategies.

Results

Characteristics of the genome datasets

We performed an initial in-depth characterization of the genomes of the 100 YFCs from 10 different breeds and 10 Huaibei (HB) partridge chickens (used for comparisons) sequenced in this study (Figure 1a; Additional file 1). An average of 86,155,900 clean reads per genome are obtained after quality control protocols, which were then aligned to the reference genome, yielding a mean mapping rate at 87.12% (Additional files 2 and 3, Additional file 4: Fig. S1). The total average base coverage across the genome is 96.35% at a sequencing depth target of 1X, 86.81% at 4X, 41.87% at 10X, and down to 0.36% at 30X (Additional file 4: Fig. S2). The average number of nucleotides in each genome is 11,916,810,290 after filtration, with an average GC content at 44.53% (Additional file 5).

For comparative analyses, we merged the 100 YFC and 10 Huaibei partridge chicken genomes with 104, 10, and 1 previously published Chinese chicken, red junglefowl (Gallus gallus; RJF), and green junglefowl (Gallus varius; GVF) genomes, respectively, retaining a total of 3,065,814 autosomal SNPs.

Genome variants in the Yellow-feathered chickens

After filtration, 16,817,111 single nucleotide polymorphisms (SNPs) and 1,289,024 InDels (insertion or deletion of bases) (≤ 50 bp) were retained. The structural variations (SVs) and the increase or decrease of the copy number of large (>1 kb) genomic fragments were analyzed. All these genomic variants in the newly generated dataset are summarized in Additional file 4: Fig. S3. Briefly, most of the SNPs are located in intergenic followed by intronic genomic regions (Additional file 4: Fig. S4a). Those located within coding sequences are mainly associated with synonymous or nonsynonymous coding attributes.
There are more transitions (11,943,736; 71.02%) than transversions (4,873,375; 28.98%) in the dataset. G→A and C→T substitutions are the common transitions at 28% while A→G and T→C substitutions are around 21%.

Different transversions show a low but relatively uniform distribution rate in the dataset. The total average ratio of transitions to transversions is 2.53 in this dataset. On average, there are 208,737 and 88,832 novel transitions and transversions per genome, respectively, with respect to the reference dbSNP annotation, yielding a novel transition to transversion ratio at 2.35. Analysis of the clean SNPs in the dataset shows that averagely 2,033,275 and 2,259,628 SNPs per genome are homogenous and heterozygous hybrids, respectively. Of these, 63,995 and 233,575 are novel homogenous and heterozygous hybrids, respectively.

Among the high quality InDels, there are more deletions than insertions (785,806 (60.96%) versus 503,218 (39.04%)). The genomic locations of these InDels are summarized in Additional file 4: Fig. S6a, where most InDels are located in non-coding (i.e. intergenic and intronic) regions. Additionally, the four most common genomic consequences of the InDels include frameshift or non-frameshift insertions and deletions.

InDels causing loss or gain stop codons are present in these genomes but in lower proportions.

Besides SNPs and InDels, the SVs, which represent a large range of chromosomal variations encompassing large genomic regions, are evaluated. These include large fragment deletions (DEL), insertions (INS), inversions (INV), translocations, and duplications. A predominance of intrachromosomal translocations (65%) and deletions (26%) is observed in the YFC genomes. Inversions and interchromosomal translocations are also present but in comparatively low proportions.
**Fig. S7a.** Analysis of copy number variations (CNVs; 95,918 in total), divided into deletions and duplications, reveals an overall higher proportion of deletions (56.5%) than duplications (43.5%) (Additional file 4: Fig. S7b).

**Population structure**

Principal component Analysis (PCA) was performed for all the 100 YFC genomes, revealing a general separation of YFCs from Henan (Zhengyang, ZY) and Hubei (Jianghan, JH) (**Fig. 1b and c**) into a northern cluster. The YFCs from Guangxi (Guangxi Yellow, GX), Guangdong (Huaixiang, HX, Huiyang bearded, HY, and Wuhua Yellow, WH), and Hainan (Wenchang, WC) form a southern cluster, while those from Hunan (Huanglang, HL), Jiangxi (Ningdu Yellow, ND), and Fujian (Hetian, HT) group into a central cluster. This finding is supported by ADMIXTURE analysis (**Fig. 1d and e**). At the lowest cross validation error value, corresponding to $K=2$, the northern (blue) and southern (red) clusters show a complete separation, whereas the central cluster exhibits a signal of admixture with the northern and southern clusters. These three clusters were verified when $K=3$, with HL and WC showing admixed ancestries. When $K=4$, both HT and HY harbor the same ancestry component, which also contribute to WC.

We implemented comparative population genetic analyses the YFCs against other indigenous chickens from China, RJF, and GVF. In the PCA (**Fig. 2a**), YFCs tend to cluster together and appear to be in close proximity to HB partridge chickens and a few indigenous chickens from Sichuan and Tibet. These patterns imply a close congruity in the total genomic architecture of the YFCs. Yuanbao bantams are grouped in a distant cluster from the YFCs and other chickens, underscoring the genomic effects of differential breeding trajectories [15, 16]. Neighbor joining (NJ) phylogeny (**Fig. 2b**) and ADMIXTURE (**Fig. 2c and d**) corroborates the findings of the PCA and further clarifies the northern, central, and southern YFC clustering pattern inferred from **figures 1b-d**.
Detection of selective sweeps

Genome-wide scans for signals of selection in YFCs revealed several analytical windows within the top 1% of the selection tests, corresponding to 366 and 504 positively selected genes (PSGs) in the Locus-specific branch length (LSBL) and π-ratio tests, respectively. A total of 28 PSGs were concurrently identified in the top 1% by the two selection tests (Fig. 3a). Among the 28 genes are genes that are associated with pigmentation including: RALY heterogeneous nuclear ribonucleoprotein (RALY), leucine rich repeat containing G protein-coupled receptor 4 (LGR4), ryanodine receptor 2 (RYR2), RYR3, solute carrier family 23 member 2 (SLC23A2), and SLC2A14. Functional enrichment assessment showed significant gene ontology (GO) terms including vitamin transport activity (GO:0090482; Fig. 3b), intersecting with SLC23A2 and SLC2A14, which play roles in pigmentation. There are additional genes that had top 1% significant signals in either of the selection tests and are of important for understanding the color trait and other properties of interest like meat quality of the YFCs. These include BCDO2, IL-18, FBXO5, COL1A2, COL4A2, COL6A1, COL6A2 in LSBL; and GDF8, HSPA5, SHISA9, COL4A1, and COL23A1 in π-ratio tests (Fig. 4).

BCDO2 haplotype differentiation

The assessment of the haplotype pattern of BCDO2 gene in all the chicken populations revealed a general commonality across the 10 YFC breeds sequenced in this study (Fig. 5). Interestingly, HB partridge chickens, initially showing an overall population genomic closeness to the northern cluster YFCs, clearly exhibit a BCDO2 haplotype pattern similar to other Chinese indigenous chickens rather than to the YFCs. Overall, the haplotype differentiation pattern of the BCDO2 gene is synonymous with the selection of this gene as a candidate PSG for the yellow pigmentation phenotype among the YFCs.

Discussion

We provide the first comprehensive whole-genome sequencing data and genomic variants
for the YFCs. We also describe the genetic structure and molecular background of the distinguished color phenotype of these chickens. YFCs are a traditional nutritional and commercial mainstay for millions of people living in China and its purlieus, and are believed to have contributed to the recent breeding of European chickens [5]. Next generation sequencing has augmented scientific research into the molecular foundations of various complex phenotypic poultry traits such as body size in chicken [15], body size and plumage color in ducks [17], as well as maturation and plumage color in domestic quails [18], among others. In this study, we characterize not only the SNPs in the genomes of the YFCs but also other variants including InDels, structural variations (SV), and copy number variations (CNV) to facilitate research of these chickens. Particularly, SVs are increasingly gaining research interest as they can lead to the birth of new genes, change gene copy number as well as their expression profiles, eventually affecting phenotypic evolution and adaptation of organisms to local environments [19-22], hence will be an important resource to extend the SNP-based genetic analyses [23, 24]. Similarly, CNVs are linked with phenotypic evolution and have supported high-impact evolutionary investigations on complex diseases and economically important traits [25, 26]. For instance, in chicken, sequence duplication proximal to the first intron of SOX5 gene is linked with the chicken pea-comb trait [27], an inverted duplication covering EDN3 gene leads to dermal hyperpigmentation [28], and a partial duplication of PRLR gene is associated with late feathering [29].

Our current comparative population genomics analysis was anchored on genome-wide SNPs of the YFCs, other indigenous chickens, and wild ancestors. Population structure analysis revealed an overall distinctive genomic architecture of the YFCs from other Chinese indigenous chickens (PCA and NJ phylogenetic tree). Interestingly, a three-way sub-clustering pattern is consistent in PCA, ADMIXTURE, and NJ phylogenetic tree and
amazingly mirrors the geographical distributions of the YFCs. The 10 YFC populations divide into northern, central and southern clusters, agreeing with the trends earlier proposed by microsatellite-based studies of chickens from these regions of China [1, 11, 12]. This sub-structuring may be reflective of some extent of differential exchange of genetic materials in neighboring locations, breeding histories, or natural and artificial selection drivers as described in several chicken populations [16, 34]. This explains the existence of genomic grouping among populations with close phenotypic appearances such as the YFCs. A crucial point to note is the signals of admixture at K=3 and 4 in the ADMIXTURE analysis. Hetian (HT) and Huiyang bearded (HY) YFCs are historically ascribed to the Hakka Chinese [6] who are thought to have immigrated from northern China, and have preserved their distinguished cultures, languages [30], and even genetic attributes [31]. Wenchang (WC) chickens are reported to have originated from crossbreeding of chickens brought into Hainan Province by people (including the Hakka) from Guangdong and Fujian Provinces [6]. The results of PCA and ADMIXTURE (K=2 and 3) suggest that the Huaibei (HB) partridge chickens have a close relationship with YFCs of the northern cluster, consistent with their geographical proximity. Nevertheless, it is incomprehensible that HB, Huanglang (HL), and Ningdu Yellow (ND) shared dominant ancestry component at K=4. Compared to other indigenous Chinese chickens, the YFCs tend have a closer genetic semblance among themselves than with other chickens, inferring a possible overriding effect of selection for the outstanding phenotypic traits of the YFCs.

Fundamental to the genomic selection scans in this study is the identification of RALY, LGR4, RYR2, RYR3, and SLC23A2 as well as its related homologue, SLC2A14. These genes stood out as a candidate gene under selection in the YFCs, having significant signals both in LSBL and π-ratio scans. There is a known epistatic relationship bringing together RALY, ASIP, and MC1R [32]. ASIP gene codes for agouti-signaling protein, which antagonizes the
α-MSH hormone (melanocyte stimulating hormone) for the melanocyte-1 receptor (MC1R) counteracting the production of eumelanin (black/brown melanin) and favoring the synthesis of pheomelanin (yellow/red melanin) [33]. Both ASIP and MC1R are genes which continue to be synonymous with nearly all studies on pigmentation in mammalian and avian species [34-38]. Interestingly, it has been demonstrated that a >90kb deletion upstream of avian ASIP, encompassing portions of the RALY locus, places ASIP under the regulatory control of RALY promoter [39]. The resulting up-regulation of ASIP underlies the yellow feather phenotype in quails and is interestingly associated with down-regulation of SLC24A5 [39]. SLC24A5 is an important gene in pigmentation whose roles in eumelanogenesis has been clearly demonstrated in both human and zebrafish [40]. We detected two members of the solute carrier family (SLC), SLC23A2 and SLC2A14. SLC23A2 is a major mediator of the transport of ascorbic acid, an indispensable metabolite that is fundamental for survival [41]. Anomalies in the availability of this vitamin have been associated with neonatal jaundice and yellow chromophore in eye lenses of human and humanized mouse model [42, 43]. It is key to note that although the selection of neither ASIP nor MC1R did not reach significance in our analyses, genes with which they are closely related, particularly RALY and SLC family homologues such as SLC23A2 and SLC2A14 point to the possibility of a gene network encompassing the PSGs identified in this study, working in conjunction with ASIP and MC1R in the determination of the yellow color trait of the YFCs.

From the analysis of signals of selection, it was not a surprise to detect a strong selection for the BCDO2 gene and a common genetic architecture of this gene among all the YFCs. Even the HB chickens which are phylogenetically and geographically close to the YFCs in the northern cluster were clearly distinguishable based on the BCDO2 haplotype structure, depicting a possible marked differentiation of indigenous chickens at trait-linked genome
compartment under selection pressure, despite likely closeness at the total genome level. Besides the YFCs, the \textit{BCDO2} haplotype for yellow skin is also observed in Yuanbao chicken, which also have yellow skin, and at a low frequency in some indigenous chicken, consistent with the reporting of related haplotypes of this gene in southern China chickens [44].

Moreover, our results show some clues for meat quality which is a major economic feature in chicken production. \textit{RYR2} and \textit{RYR3} [45-47]; \textit{IL-18} [48]; \textit{FBXO5} [49]; \textit{COL1A2}, \textit{COL4A2}, \textit{COL6A1}; \textit{COL6A2}; \textit{COL4A1}, and \textit{COL23A1} [50]; \textit{GDF8} [51]; \textit{HSPA5} [48]; \textit{SHISA9} [52]; all bearing strong selection signals in the YFCs, are important determinants of meat quality in domestic animals. These genes provide a foundation for understanding the meat properties of the YFCs, which would attract more concerns to investigate the detailed function roles in future studies.

Conclusions

In summary, this study provides an invaluable resource for further research on the molecular mechanisms conferring complex traits that are of high economic and nutritional value. Through genomic insights regarding key genes behind the unique traits of YFCs and a comprehensive data resource, this study paves way for reconstructing the breeding history and formulating future conservation and breed improvement strategies for YFCs.

Methods

\textbf{Samplings and sequencing of the Yellow-feathered chickens}

Wing-vein blood samples were collected from 100 birds of 10 major YFC breeds, 10 chickens per breed, including Guangxi Yellow (GX), Hetian (HT), Huaixiang (HX), Huanglang (HL), Huiyang bearded (HY), Jianghan (JH), Ningdu Yellow (ND), Wenchang (WC), Wuhua Yellow (WH), and Zhengyang Yellow (ZY) (\textbf{Additional file 1}). Ten Huaibei
partridge (HB) chickens were also sampled for comparison. Sample selection was referred to the records for each breed [6]. All samples were collected from conservation farms based on the informed consent of the farm owners. The study was approved by Jiaying University. Genomic DNA was extracted using the standard phenol-chloroform method and checked for quantity and quality using agarose gel electrophoresis and NanoDrop spectrophotometer 2000 (NanoDrop, Wilmington, DE, USA). Whole genome sequencing for these 110 samples was carried out to a median depth of 12.22X (ranging from 9.34 to 18.66) (Additional file 1) using the Illumina HiSeq X10 platform at the Genedenovo Biotechnology Co., Ltd (Guangzhou, China).

**Identification and annotation of whole-genome variants**

To obtain high quality clean reads, stringent quality filtering procedures were applied as follows: 1) removing reads with ≥ 10% unidentified nucleotides (N); 2) removing reads with > 50% bases having phred scores of ≤ 20; and 3) removing reads aligned to the barcode adapter. The clean reads were then aligned to the chicken reference genome (Galgal5) [53] using the BWA-MEM alignment algorithm [54] implemented in the BWA [55] with options ‘mem 4 -k 32 -M’. Further quality control processes were performed using the SortSam and MarkDuplicates tools in the Picards package (picard-tools-1.56) to sort and remove possible duplicates in the aligned BAM files, and the RealignerTargetCreator, IndelRealigner, and BaseRecalibrator tools in the Genome Analysis Toolkit (GATK 2.6-4) [56] for local realignment and base quality recalibration. The bedtools software (v.2.25.0) [57] was employed to generate sequencing coverage statistics.

Variant calling was performed using the GATK’s Unified Genotyper. SNPs and InDels were filtered by the GATK’s VariantFiltration with options “-Window 4, -filter "QD < 2.0 || FS > 60.0 || MQ < 40.0 ", -G_filter "GQ < 20"”, excluding those exhibiting segregation distortions or sequencing errors. The ANNOVAR [58] was used to align and annotate the
SNPs and InDels with reference to ENSEMBL chicken gene annotation database (version 92.5). The structural variations (SVs) in these 110 chicken genomes were assessed using the BreakDancer package (Max1.1.2.) [59, 60], and the CNVnator program (v.0.3.2) [61] was employed to classify copy number variations (CNVs).

**Analysis of population genetic structure**

The evolutionary interactions among the 100 YFCs were examined using principal component analysis (PCA) following the GCTA approach [62] and maximum-likelihood-based ADMIXTURE [63] at K=2 to 9. The PLINK package (v.1.90) was used to obtain pruned data with parameters “--indep-pairwise 50 10 0.1” [64] for the PCA and ADMIXTURE analyses. To perform a comparative analysis of the YFC genomes generated in this study against those of other chicken populations, 104 previously published whole genomes [15, 65] of Chinese indigenous chickens (Sichuan, n = 50; Tibet, n = 20; Qinghai, n = 2; Yunnan, n = 8; and Yuanbao bantams, n = 24), as well as 10 RJF and 1 GVF genomes were included. After merging our dataset of the 110 chicken genomes with the additional 115 genomes, 3,065,814 common SNPs were retained for subsequent analyses. The PCA was performed as stated above and a neighbor joining (NJ) tree rooted to RJF was constructed using the RapidNJ program [66] with 100 bootstrap replications.

**Genomic targets of selection in Yellow-feathered chickens**

To retrieve the genetic foundation for the outstanding phenotypic properties of the YFCs, we performed genome-wide scans for signals of selection using locus-specific branch length (LSBL) statistics [67] and π-ratio. The comparative genomic analysis approach involved the genomes of the YFCs against 24 chickens with outstanding non-yellow phenotypes (non-YFCs), i.e. black-phenotype Chinese chickens (five Emei black fowl, four Miyi fowl, five Muchuan black-bone fowl, and five Tuanfu black-bone fowl; **Additional file 1**) and RJF. In the LSBL, we computed LSBL(A;B,C) = (F_{ST(AB)} + F_{ST(AC)} - F_{ST(BC)})/2 to assess
the population differentiation between YFCs and other chickens, set as ‘YFCs;non-YFCs,RJF’. $F_{ST}$ values were calculated as described elsewhere [68] with a 50-kb sliding window and 25-kb stepwise increments. $\pi$-ratio was performed by first calculating the genetic diversity ($\pi$) for YFCs and the 24 non-YFCs populations using VCFtools [69] in 50-kb windows with 25-kb stepwise increments, then computing $\pi$-ratio ($\pi_{\text{non-YFCs}}/\pi_{\text{YFCs}}$). An empirical cutoff of 99th percentile was used to retrieve candidate selective sweeps, which were then annotated using variant effect predictor (VEP) to identify the putative positively selected genes (PSGs) [70].

We performed functional enrichment analysis using g:Profiler [71] to obtain a global overview on the biological functions of the candidate PSGs with concordantly significant selection signals in the two genomic selection scans employed. A Benjamini-Hochberg false discovery rate (FDR) significance threshold was set at 0.05.

**Assessment of the classical yellow skin gene, BCDO2**

BCDO2 gene, located in chromosome 24: 6,110,301-6,130,965 reverse strand (Galgal5, [53]), is believed to be substantially associated with yellow skin pigmentation in chickens following a possible introgression from grey junglefowl (Gallus sonneratii) in South Asia [72]. We evaluated the haplotype variability of BCDO2 gene in all indigenous chickens and RJFs. Haplotypes for each chromosome were phased using the BEAGLE software (v.3.3.2) by the default parameters [73] and viewed as heatmaps.

**Abbreviations**

**BCDO2**: Beta-carotene dioxygenase 2  
**CNV**: Copy number variation  
**FDR**: False discovery rate  
**GO**: Gene ontology
GVF: Green junglefowl

InDel: Insertion or deletion of bases

INS: Insertions

INV: Inversions

LGR4: Leucine rich repeat containing G protein-coupled receptor 4

LSBL: Locus-specific branch length

NJ: Neighbor joining

YFC: Yellow-feathered chicken

RALY: RALY heterogeneous nuclear ribonucleoprotein

RJF: Red junglefowl

RYR2: Ryanodine receptor 2

SLC23A2: Solute carrier family 23 member 2

SLC2A14: Solute carrier family 2 member 14

SNP: Single nucleotide polymorphism

SV: Structural variation

PCA: Principal component analysis

PSGs: Positively selected genes

VEP: Variant effect predictor

**Declarations**

**Availability of data and materials**

All new sequencing data generated in this study have been deposited in the NCBI sequence read archive (SRA) under accession number SRP155577.

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**Authors’ contributions**

X.H.H. and B.W.D supervised the project. X.H.H, Z.X.W, W.N.L, J.B.C, M.Z, F.S.Z, S.H.J, Z.Y.G, W.L. and D.L.H collected samples, and X.H.H and Z.X.W prepared samples for sequencing. Y.P.Z. provided genomic data for comparison. N.O.O, M.P, and X.H.H. performed data analysis, interpretation of results, and writing of the manuscript. J.L.H., M.C., S.C.O., Y.P.Z. and X.Q.Z. revised the manuscript. All authors read and approved the final manuscript.

**Ethics declarations**

**Ethics approval and consent to participate**

Animal handling and experimentation was conducted according to the animal experimental procedures and guidelines approved by the Animal Ethics Committee of Jiaying University, China.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare no conflicts of interest.

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Additional File Legends

Additional file 1: Individual sample characteristics of all chickens sequenced in this study.

Additional file 2: Reads filtering statistics for the chicken sequenced in this study.

Additional file 3: Genome alignment statistics for all chickens sequenced in this study.

Additional file 4: Fig. S1: Constitution of clean sequencing reads of all 110 chicken genomes produced in this study. Fig. S2: Summary of the average sequencing coverage of all 110 chicken genomes generated in this study. Fig. S3: Circos plot depicting the genomic variants landscape in each chromosome. Fig. S4: Annotation of the clean genomic SNPs of all 110 chickens sequenced in this study. Fig. S5: Transition-transversion analysis of the clean SNPs of all 110 chicken genomes sequenced in this study. Fig. S6: Annotation of the clean InDels of all 110 chicken genomes sequenced in this study. Fig. S7: Summary of the structural variations (SVs) and copy number variations (CNVs) in all 110 chicken genomes generated in this study.

Additional file 5: Base information statistics before and after quality filtering of all chicken genomes sequenced in this study.
Additional file 6: Individual transitional and transversional SNP statistics of all chickens sequenced in this study.

Additional file 7: Annotation of the hybrid status of SNPs in each chicken genome sequenced in this study.

Figures

Figure 1

Population genomic analysis of the YFCs. a. Pictorial representation of the male and female chickens of each of the 10 YFC breeds and HB chicken population. The photos for WH were taken by X.H. and the rest were retrieved from Ref 6. b. Principal component analysis (PCA) of all 110 chickens sequenced in this study. YFCs’ clustering patterns are highlighted by dotted red (northern cluster), black (central cluster), and blue (southern cluster) circles. c. Sampling map showing the
geographical locations of all chicken breeds/populations. The newly described chicken breeds are noted by their respective populations IDs, while red cycles indicate chicken populations retrieved from previous studies [15, 65]. The dotted horizontal lines demarcate the three population clusters. d-e. ADMIXTURE analysis for K=2, K=3, and K=4. The lowest cross validation error is observed when K=2.
Population genomic analysis of YFCs in the context of other Chinese indigenous chickens. a. PCA showing the evolutionary relationships among YFCs, other Chinese indigenous chickens, red junglefowl (RJF), and green junglefowl (GVF). b. Neighbor joining tree including all chickens and RJF (root). The tree was viewed and edited using FigTree software (v1.4.3). c-d. ADMIXTURE analysis for K=2 up to K=5. The lowest cross validation error is observed when K=2.
Candidate positively selected genes (PSGs). a. PSGs in the top 1% windows of LSL and π-ratio genome selection tests. The identities of annotated genes overlapping in both tests are shown. b. Summary of the functional enrichment analysis of the 28 overlapping PSGs. Only terms with adjusted P values less than 0.05 are shown.
Figure 4

Genome-wide distributions of selection signals. a. $\pi$-ratio contrasting Yellow-feathered chickens (YFC) against chicken with non-yellow (black) phenotypes, denoted as Others. b. Locus-specific branch length (LSBL) analysis contrasting YFC against non-yellow chicken with red junglefowl (RJF) outgroup. The horizontal dotted lines represent the top 1% cut-off.
Genomic diversity and BCDO2 gene structure of YFCs and other chickens.

Haplotype pattern analysis of the yellow skin gene, BCDO2 (GGA24: 6,110,301-6,130,965 reverse strand) across different populations separated by white gaps.

Red color denotes reference alleles while blue indicates alternative alleles. Initials represent chicken breeds/population names as defined in the methods. The three YFC clusters are indicated by red, black, and blue boxes representing
northern, central, and southern clusters, respectively.

Supplementary Files

This is a list of supplementary files associated with the primary manuscript. Click to
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