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

Xunhe Huang
JiaYing University https://orcid.org/0000-0003-3795-2745
Newton O. Otecko
Kunming Institute of Zoology Chinese Academy of Sciences
Minsheng Peng
Kunming Institute of Zoology Chinese Academy of Sciences
Zhuoxian Weng
JiaYing University
Weina Li
JiaYing University
Jiebo Chen
JiaYing University
Ming Zhong
JiaYing University
Fusheng Zhong
JiaYing University
Sihua Jin
Anhui Agricultural University
Zhaoyu Geng
Anhui Agricultural University
Wei Luo
South China Agricultural University College of Animal Science
Danlin He
South China Agricultural University College of Animal Science
Cheng Ma
Kunming Institute of Zoology Chinese Academy of Sciences
Jianlin Han
Chinese Academy of Agricultural Sciences
Sheila C. Ommeh
Jomo Kenyatta University of Agriculture and Technology
Yaping Zhang

Kunming Institute of Zoology Chinese Academy of Sciences
Xiquan Zhang
South China Agricultural University College of Animal Science
Bingwang Du (dudu903@163.com)

Research article

Keywords: yellow; chicken; genome; BCDO2; breeding; color; genetic diversity

Posted Date: January 22nd, 2020

DOI: https://doi.org/10.21203/rs.2.21585/v1

Version of Record: A version of this preprint was published on April 20th, 2020. See the published version at https://doi.org/10.1186/s12864-020-6736-4.

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 (**Additional file 4: Fig. S4b**). 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% (**Additional file 4: Fig. S5**). 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 (**Additional file 6**). 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 (**Additional file 6**). 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 (**Additional file 7**).

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 (**Additional file 4: Fig. S6b**). 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 [13, 14]. 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 (**Additional file 4: 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 *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. *RYR2* and *RYR3* [45-47]*; IL-18 [48]; FBXO5* [49]; *COL1A2*, *COL4A2*, *COL6A1*; *COL6A2*; *COL4A1*, and *COL23A1* [50]; *GDF8* [51]; *HSPA5* [48]; *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

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) (**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. π-ratio was performed by first calculating the genetic diversity (π) for YFCs and the 24 non-YFCs populations using VCFtools [69] in 50-kb windows with 25-kb stepwise increments, then computing π-ratio ($\pi_{non\text{-}YFCs}/\pi_{YFCs}$). An empirical cutoff of 99^{th} 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 junglefow

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.

Acknowledgements

N.O.O. is grateful for the support from CAS-TWAS President's Fellowship Program for Doctoral Candidates. We are grateful to Guangzhou Genedenovo Biotechnology Co., Ltd for assisting in sequencing and part of bioinformatics analysis.

Funding

This work was supported by Science & Technology Planning Project of Guangdong Province (2016A030303068), Natural Science Foundation of Guangdong (2014A030307018), Provincial and

municipal key construction projects in Jiaying University, and the Bureau of Science and Technology of Yunnan Province. The funding bodies did not involved in the design of the study and collection, analysis, and interpretation of data and in writing the manuscript.

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.

References

1. Huang X-H, Zhang J-F, He D-L, Zhang X-Q, Zhong F-S, Li W-N, Zheng Q-M, Chen J-B, Du B-W: Genetic diversity and population structure of indigenous chicken breeds in South China. Front Agr Sci Eng. 2016;3(2):97-101.
2. Qi J, Li X, Zhang W, Wang H, Zhou G, Xu X: Influence of stewing time on the texture, ultrastructure and in vitro digestibility of meat from the yellow-feathered chicken breed. Anim Sci J. 2018;89(2):474-82.
3. Meng X, Xu T, Du B, Teng X, editors: Chicken art – ancient Chinese wisdom on chicken-raising with an appendix of the Chinese art of calligraphy. Beijing, China Agriculture Press.; 2017.
4. Zheng MQ, Gong GF, Gao HJ, Yao WY, Lv SY, Tian LJ, Wen J: Report of Chinese broiler industry development in 2015. China Poult. 2016;38:67-70.
5. Loog L, Thomas MG, Barnett R, Allen R, Sykes N, Paxinos PD, Lebrasseur O, Dobney K, Peters J, Manica A *et al*: Inferring allele frequency trajectories from ancient DNA indicates that selection on a

chicken gene coincided with changes in medieval husbandry practices. Mol Biol Evol. 2017;34(8):1981-90.

6. China National Commission of Animal Genetic Resources: Animal genetic resources in china – poultry. Beijing, China Agriculture Press; 2011.
7. Wang Y, Hui X, Wang H, Kurban T, Hang C, Chen Y, Xing J, Wang J: Association of H-FABP gene polymorphisms with intramuscular fat content in Three-yellow chickens and Hetian-black chickens. J Anim Sci Biotechnol. 2016;7:9.
8. Chiang PD, Yen CT, Mau JL: Non-volatile taste components of various broth cubes. Food Chem. 2007;101(3):932–7.
9. Duan Y, Zheng F, Chen H, Huang M, Xie J, Chen F, Sun B: Analysis of volatiles in Dezhou braised chicken by comprehensive two-dimensional gas chromatography/high resolution-time of flight mass spectrometry. LWT-Food Sci Technol. 2015;60:1235–42.
10. Jaturasitha S, Srikanchai T, Kreuzer M, Wicke M: Differences in carcass and meat characteristics between chicken indigenous to northern Thailand (Black-boned and Thai native) and imported extensive breeds (Bresse and Rhode Island red). Poult Sci. 2008;87(1):160-9.
11. Qu LJ, Li XY, Xu GF, Chen KW, Yang HJ, Zhang LC, Wu GQ, Hou ZC, Xu GY, Yang N: Evaluation of genetic diversity in Chinese indigenous chicken breeds using microsatellite markers. Sci China C Life Sci. 2006;49(4):332–41.
12. Yu YB, Wang JY, Mekki DM, Tang QP, Li HF, Gu R, Ge QL, Zhu WQ, Chen KW: Evaluation of genetic diversity and genetic distance between twelve Chinese indigenous chicken breeds based on microsatellite markers. Int J Poult Sci. 2006;5(6):550–6.
13. Baker M: Structural variation: the genome's hidden architecture. Nat Methods. 2012;9(2):133-7.
14. Alkan C, Coe BP, Eichler EE: Genome structural variation discovery and genotyping. Nat Rev Genet. 2011;12(5):363-76.
15. Wang MS, Huo YX, Li Y, Otecko NO, Su LY, Xu HB, Wu SF, Peng MS, Liu HQ, Zeng L *et al*: Comparative population genomics reveals genetic basis underlying body size of domestic chickens. J Mol Cell Biol. 2016;8(6):542-52.
16. Wang MS, Otecko NO, Wang S, Wu DD, Yang MM, Xu YL, Murphy RW, Peng MS, Zhang YP: An evolutionary genomic perspective on the breeding of dwarf chickens. Mol Biol Evol. 2017;34(12):3081-8.
17. Zhou Z, Li M, Cheng H, Fan W, Yuan Z, Gao Q, Xu Y, Guo Z, Zhang Y, Hu J *et al*: An intercross population study reveals genes associated with body size and plumage color in ducks. Nat Commun. 2018;9(1):2648.
18. Wu Y, Zhang Y, Hou Z, Fan G, Pi J, Sun S, Chen J, Liu H, Du X, Shen J *et al*: Population genomic data reveal genes related to important traits of quail. Gigascience. 2018;7(5).
19. Kidd JM, Cooper GM, Donahue WF, Hayden HS, Sampas N, Graves T, Hansen NF, Teague B, Alkan C, Antonacci F: Mapping and sequencing of structural variation from eight human genomes. Nature. 2008;453(7191):56-64.

20. Paudel Y, Madsen O, Megens H, Frantz LAF, Bosse M, Bastiaansen JWM, Crooijmans RPMA, Groenen MAM: Evolutionary dynamics of copy number variation in pig genomes in the context of adaptation and domestication. BMC Genomics. 2013;14(1):449.
21. Xu SH, He ZW, Zhang Z, Guo ZX, Guo WX, Lyu HM, Li JF, Yang M, Du ZL, Huang YL *et al*: The origin, diversification and adaptation of a major mangrove clade (Rhizophoreae) revealed by whole-genome sequencing. Natl Sci Rev. 2017;4(5):721-34.
22. Zhang X, Wang K, Wang L, Yang Y, Ni Z, Xie X, Shao X, Han J, Wan D, Qiu Q: Genome-wide patterns of copy number variation in the Chinese yak genome. BMC Genomics. 2016;17(1):379.
23. Liu R, Xing S, Wang J, Zheng M, Cui H, Crooijmans R, Li Q, Zhao G, Wen J: A new chicken 55K SNP genotyping array. BMC Genomics. 2019;20(1):410.
24. Ye S, Gao N, Zheng R, Chen Z, Teng J, Yuan X, Zhang H, Chen Z, Zhang X, Li J *et al*: Strategies for obtaining and pruning imputed whole-genome sequence data for genomic prediction. Front Genet. 2019;10:673.
25. Lin S, Lin X, Zhang Z, Jiang M, Rao Y, Nie Q, Zhang X: Copy number variation in SOX6 contributes to chicken muscle development. Genes (Basel). 2018;9(1):42.
26. Yi G, Qu L, Liu J, Yan Y, Xu G, Yang N: Genome-wide patterns of copy number variation in the diversified chicken genomes using next-generation sequencing. BMC Genomics. 2014;15:962.
27. Wright D, Boije H, Meadows JR, Bed'hom B, Gourichon D, Vieaud A, Tixier-Boichard M, Rubin CJ, Imsland F, Hallbook F *et al*: Copy number variation in intron 1 of SOX5 causes the Pea-comb phenotype in chickens. PLoS Genet. 2009;5(6):e1000512.
28. Dorshorst B, Molin AM, Rubin CJ, Johansson AM, Stromstedt L, Pham MH, Chen CF, Hallbook F, Ashwell C, Andersson L: A complex genomic rearrangement involving the endothelin 3 locus causes dermal hyperpigmentation in the chicken. PLoS Genet. 2011;7(12):e1002412.
29. Elferink MG, Vallee AA, Jungerius AP, Crooijmans RP, Groenen MA: Partial duplication of the PRLR and SPEF2 genes at the late feathering locus in chicken. BMC Genomics. 2008;9:391.
30. Hsieh T: Origin and migrations of the Hakkas. The Chinese Social & Political Sci Rev (Beijing). 1929;13:202-27.
31. Chen J, Zheng H, Bei JX, Sun L, Jia WH, Li T, Zhang F, Seielstad M, Zeng YX, Zhang X *et al*: Genetic structure of the Han Chinese population revealed by genome-wide SNP variation. Am J Hum Genet. 2009;85(6):775-85.
32. Nazari-Ghadikolaei A, Mehrabani-Yeganeh H, Miarei-Aashtiani SR, Staiger EA, Rashidi A, Huson HJ: Genome-Wide Association Studies Identify Candidate Genes for Coat Color and Mohair Traits in the Iranian Markhoz Goat. Front Genet. 2018;9:105.
33. Hoekstra HE: Genetics, development and evolution of adaptive pigmentation in vertebrates. Heredity (Edinb). 2006;97(3):222-34.
34. Alshanbari F, Castaneda C, Juras R, Hillhouse A, Mendoza MN, Gutierrez GA, Ponce de Leon FA, Raudsepp T: Comparative FISH-Mapping of MC1R, ASIP, and TYRP1 in new and old world camelids

and association analysis with coat color phenotypes in the dromedary (*Camelus dromedarius*). Front Genet. 2019;10:340.

35. Nakamura K, Tozaki T, Kakoi H, Owada S, Takasu M: Variation in the MC1R, ASIP, and MATP genes responsible for coat color in Kiso horse as determined by SNaPshot genotyping. J Vet Med Sci. 2019;81(1):100-2.
36. Shang S, Yu Y, Zhao Y, Dang W, Zhang J, Qin X, Irwin DM, Wang Q, Liu F, Wang Z *et al*: Synergy between MC1R and ASIP for coat color in horses (*Equus caballus*). J Anim Sci. 2019;97(4):1578-85.
37. Yang CW, Ran JS, Yu CL, Qiu MH, Zhang ZR, Du HR, Li QY, Xiong X, Song XY, Xia B *et al*: Polymorphism in MC1R, TYR and ASIP genes in different colored feather chickens. 3 Biotech. 2019;9(5):203.
38. Zhang J, Liu F, Cao J, Liu X: Skin transcriptome profiles associated with skin color in chickens. PLoS One. 2015;10(6):e0127301.
39. Nadeau NJ, Minvielle F, Ito S, Inoue-Murayama M, Gourichon D, Follett SA, Burke T, Mundy NI: Characterization of Japanese quail yellow as a genomic deletion upstream of the avian homolog of the mammalian ASIP (agouti) gene. Genetics. 2008;178(2):777-86.
40. Lamason RL, Mohideen MA, Mest JR, Wong AC, Norton HL, Aros MC, Jurynec MJ, Mao X, Humphreville VR, Humbert JE *et al*: SLC24A5, a putative cation exchanger, affects pigmentation in zebrafish and humans. Science. 2005;310(5755):1782-6.
41. Eck PK, Corpe C, Levine MA: Temporo-spacial microanatomical distribution of the murine sodium-dependent ascorbic acid transporters Slc23a1 and Slc23a2 in the kidney throughout development. Biochem & Cell Biol. 2017;95(3):421-7.
42. Ayyappan S, Philip S, Bharathy N, Ramesh V, Kumar CN, Swathi S, Kumar AA: Antioxidant status in neonatal jaundice before and after phototherapy. J Pharm Bioallied Sci. 2015;7(Suppl 1):S16-21.
43. Fan X, Reneker LW, Obrenovich ME, Strauch C, Cheng R, Jarvis SM, Ortwerth BJ, Monnier VM: Vitamin C mediates chemical aging of lens crystallins by the Maillard reaction in a humanized mouse model. Proc Natl Acad Sci U S A. 2006;103(45):16912-7.
44. Gao YS, Jia XX, Tang XJ, Fan YF, Lu JX, Huang SH, Tang MJ: The genetic diversity of chicken breeds from Jiangxi, assessed with *BCDO2* and the complete mitochondrial DNA D-loop region. Plos One. 2017;12(3).
45. Droval AA, Binneck E, Marin SR, Paiao FG, Oba A, Nepomuceno AL, Shimokomaki M: A new single nucleotide polymorphism in the ryanodine gene of chicken skeletal muscle. Genet Mol Res. 2012;11(2):821-9.
46. Paiao FG, Ferracin LM, Pedrao M, Kato T, Shimokomaki M: Skeletal muscle calcium channel ryanodine and the development of pale, soft, and exudative meat in poultry. Genet Mol Res. 2013;12(3):3017-27.
47. Strasburg GM, Chiang W: Pale, soft, exudative turkey--The role of ryanodine receptor variation in meat quality. Poult Sci. 2009;88(7):1497-505.

48. Li X, Kim SW, Do KT, Ha YK, Lee YM, Yoon SH, Kim HB, Kim JJ, Choi BH, Kim KS: Analyses of porcine public SNPs in coding-gene regions by re-sequencing and phenotypic association studies. Mol Biol Rep. 2011;38(6):3805-20.
49. Edea Z, Hong JK, Jung JH, Kim DW, Kim YM, Kim ES, Shin SS, Jung YC, Kim KS: Detecting selection signatures between Duroc and Duroc synthetic pig populations using high-density SNP chip. Anim Genet. 2017;48(4):473-7.
50. Sun Y, Zhao G, Liu R, Zheng M, Hu Y, Wu D, Zhang L, Li P, Wen J: The identification of 14 new genes for meat quality traits in chicken using a genome-wide association study. BMC Genomics. 2013;14:458.
51. Tu PA, Lo LL, Chen YC, Hsu CC, Shiau JW, Lin EC, Lin RS, Wang PH: Polymorphisms in the promoter region of myostatin gene are associated with carcass traits in pigs. J Anim Breed Genet. 2014;131(2):116-22.
52. Wang H, Zhang L, Cao J, Wu M, Ma X, Liu Z, Liu R, Zhao F, Wei C, Du L: Genome-Wide Specific Selection in Three Domestic Sheep Breeds. PLoS One. 2015;10(6):e0128688.
53. Warren WC, Hillier LW, Tomlinson C, Minx P, Kremitzki M, Graves T, Markovic C, Bouk N, Pruitt KD, Thibaud-Nissen F *et al*: A new chicken genome assembly provides insight into avian genome structure. G3 (Bethesda). 2017;7(1):109-17.
54. Li H: Toward better understanding of artifacts in variant calling from high-coverage samples. Bioinformatics. 2014;30(20):2843-51.
55. Li H, Durbin R: Fast and accurate short read alignment with Burrows-Wheeler transform. Bioinformatics. 2009;25(14):1754-60.
56. McKenna A, Hanna M, Banks E, Sivachenko A, Cibulskis K, Kernytsky A, Garimella K, Altshuler D, Gabriel S, Daly M *et al*: The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. Genome Res. 2010;20(9):1297-303.
57. Quinlan AR: BEDTools: The Swiss-Army Tool for Genome Feature Analysis. Curr Protoc Bioinformatics. 2014;47:11 2 1-34.
58. Wang K, Li M, Hakonarson H: ANNOVAR: functional annotation of genetic variants from high-throughput sequencing data. Nucleic Acids Res. 2010;38(16):e164.
59. Chen K, Wallis JW, McLellan MD, Larson DE, Kalicki JM, Pohl CS, McGrath SD, Wendl MC, Zhang Q, Locke DP *et al*: BreakDancer: an algorithm for high-resolution mapping of genomic structural variation. Nat Methods. 2009;6(9):677-81.
60. Fan X, Abbott TE, Larson D, Chen K: BreakDancer: Identification of genomic structural variation from paired-end read mapping. Curr Protoc Bioinformatics. 2014;45:15.6.1-.6.1.
61. Abyzov A, Urban AE, Snyder M, Gerstein M: CNVnator: an approach to discover, genotype, and characterize typical and atypical CNVs from family and population genome sequencing. Genome Res. 2011;21(6):974-84.
62. Yang J, Lee SH, Goddard ME, Visscher PM: GCTA: A tool for genome-wide complex trait analysis. Am J Hum Genet. 2011;88(1):76-82.

63. Alexander DH, Novembre J, Lange K: Fast model-based estimation of ancestry in unrelated individuals. Genome Res. 2009;19(9):1655-64.
64. Chang CC, Chow CC, Tellier LC, Vattikuti S, Purcell SM, Lee JJ: Second-generation PLINK: rising to the challenge of larger and richer datasets. Gigascience. 2015;4:7.
65. Li D, Che T, Chen B, Tian S, Zhou X, Zhang G, Li M, Gaur U, Li Y, Luo M *et al*: Genomic data for 78 chickens from 14 populations. Gigascience. 2017;6(6):1-5.
66. Simonsen M, Mailund T, Pedersen CNS: Rapid Neighbor-Joining. In: Proceedings of the Eighth International Workshop on Algorithms in Bioinformatics: 15-19 September 2008 (Crandall KA and Lagergren J, eds.). Karlsruhe: Springer Berlin Heidelberg; 2008.
67. Shriver MD, Kennedy GC, Parra EJ, Lawson HA, Sonpar V, Huang J, Akey JM, Jones KW: The genomic distribution of population substructure in four populations using 8,525 autosomal SNPs. Hum Genomics. 2004;1(4):274-86.
68. Akey JM, Zhang G, Zhang K, Jin L, Shriver MD: Interrogating a high-density SNP map for signatures of natural selection. Genome Res. 2002;12(12):1805-14.
69. Danecek P, Auton A, Abecasis G, Albers CA, Banks E, DePristo MA, Handsaker RE, Lunter G, Marth GT, Sherry ST *et al*: The variant call format and VCFtools. Bioinformatics. 2011;27(15):2156-8.
70. McLaren W, Gil L, Hunt SE, Riat HS, Ritchie GR, Thormann A, Flicek P, Cunningham F: The Ensembl Variant Effect Predictor. Genome Biol. 2016;17(1):122.
71. Raudvere U, Kolberg L, Kuzmin I, Arak T, Adler P, Peterson H, Vilo J: g:Profiler: a web server for functional enrichment analysis and conversions of gene lists (2019 update). Nucleic Acids Res. 2019;47(W1):W191-W8.
72. Eriksson J, Larson G, Gunnarsson U, Bed'hom B, Tixier-Boichard M, Stromstedt L, Wright D, Jungerius A, Vereijken A, Randi E *et al*: Identification of the yellow skin gene reveals a hybrid origin of the domestic chicken. PLoS Genet. 2008;4(2):e1000010.
73. Browning SR, Browning BL: Rapid and accurate haplotype phasing and missing-data inference for whole-genome association studies by use of localized haplotype clustering. Am J Hum Genet. 2007;81(5):1084-97.

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

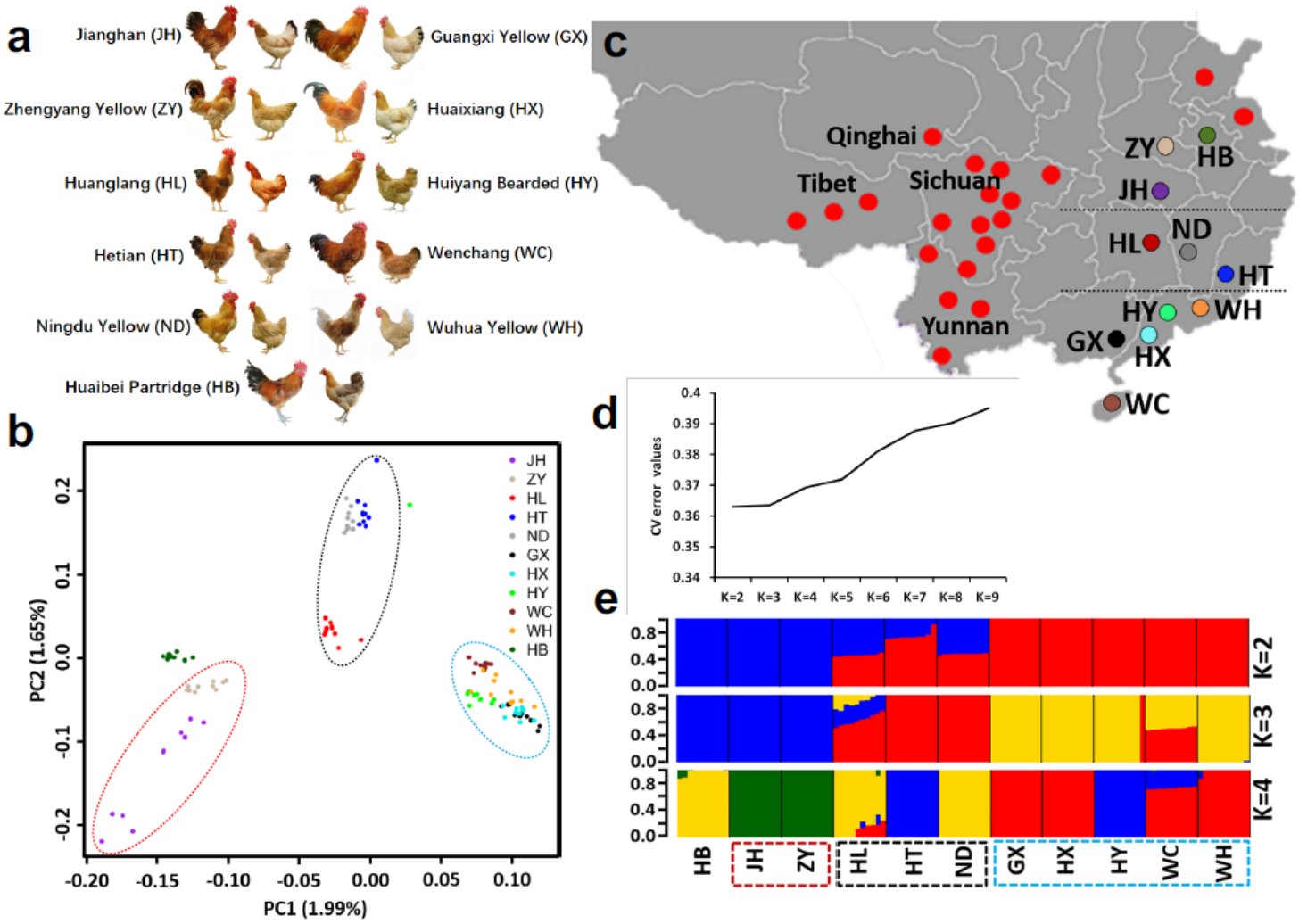


Figure 1

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.

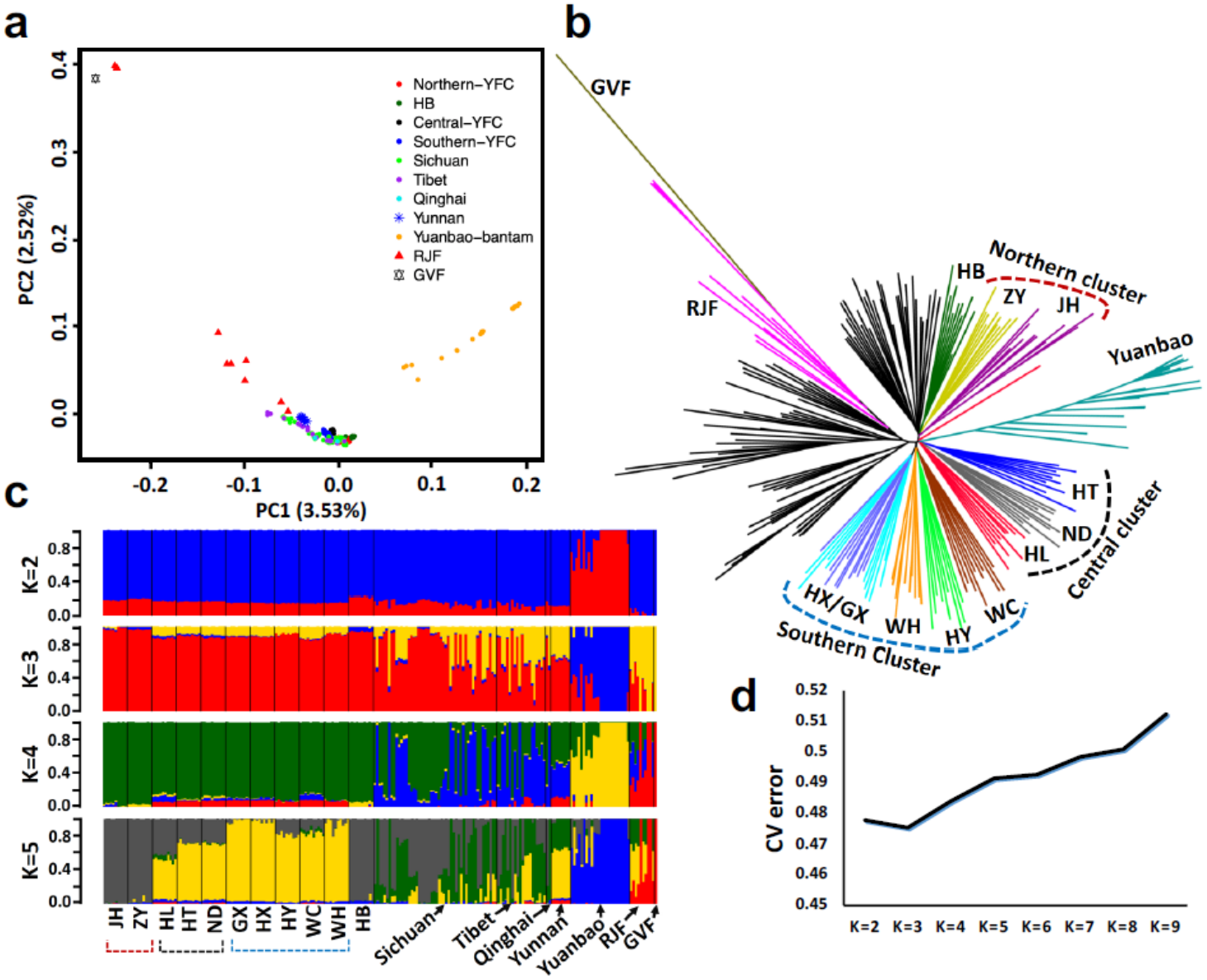
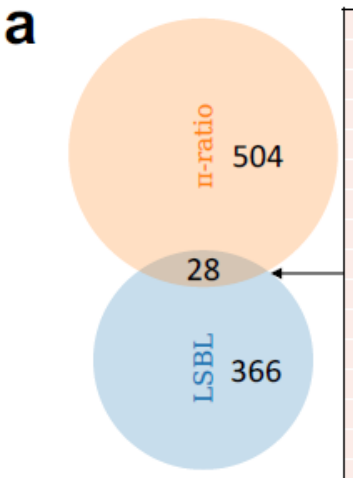


Figure 2

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.



Gene ID	Symbol	Name
ENSGALG00000035266	ANOS1	Anosmin-1
ENSGALG00000030603	ANTXR1	anthrax toxin receptor 1
ENSGALG00000000606	ARL8A	ADP ribosylation factor like GTPase 8A
ENSGALG00000000616	ELF3	E74 like ETS transcription factor 3
ENSGALG00000014331	FKBP4	FK506 binding protein 4
ENSGALG00000036391	GFPT1	glutamine--fructose-6-phosphate transaminase 1
ENSGALG00000000607	GPR37L1	G protein-coupled receptor 37 like 1
ENSGALG00000040834	LGR4	leucine rich repeat containing G protein-coupled receptor 4
ENSGALG00000030200	NFU1	NFU1 iron-sulfur cluster scaffold
ENSGALG00000036093	PTPN7	protein tyrosine phosphatase, non-receptor type 7
ENSGALG00000033696	RALY	RALY heterogeneous nuclear ribonucleoprotein
ENSGALG00000010812	RYR2	ryanodine receptor 2
ENSGALG00000009705	RYR3	ryanodine receptor 3
ENSGALG00000000195	SVCT2	solute carrier family 23 member 2
ENSGALG00000009207	TRIM2	tripartite motif containing 2

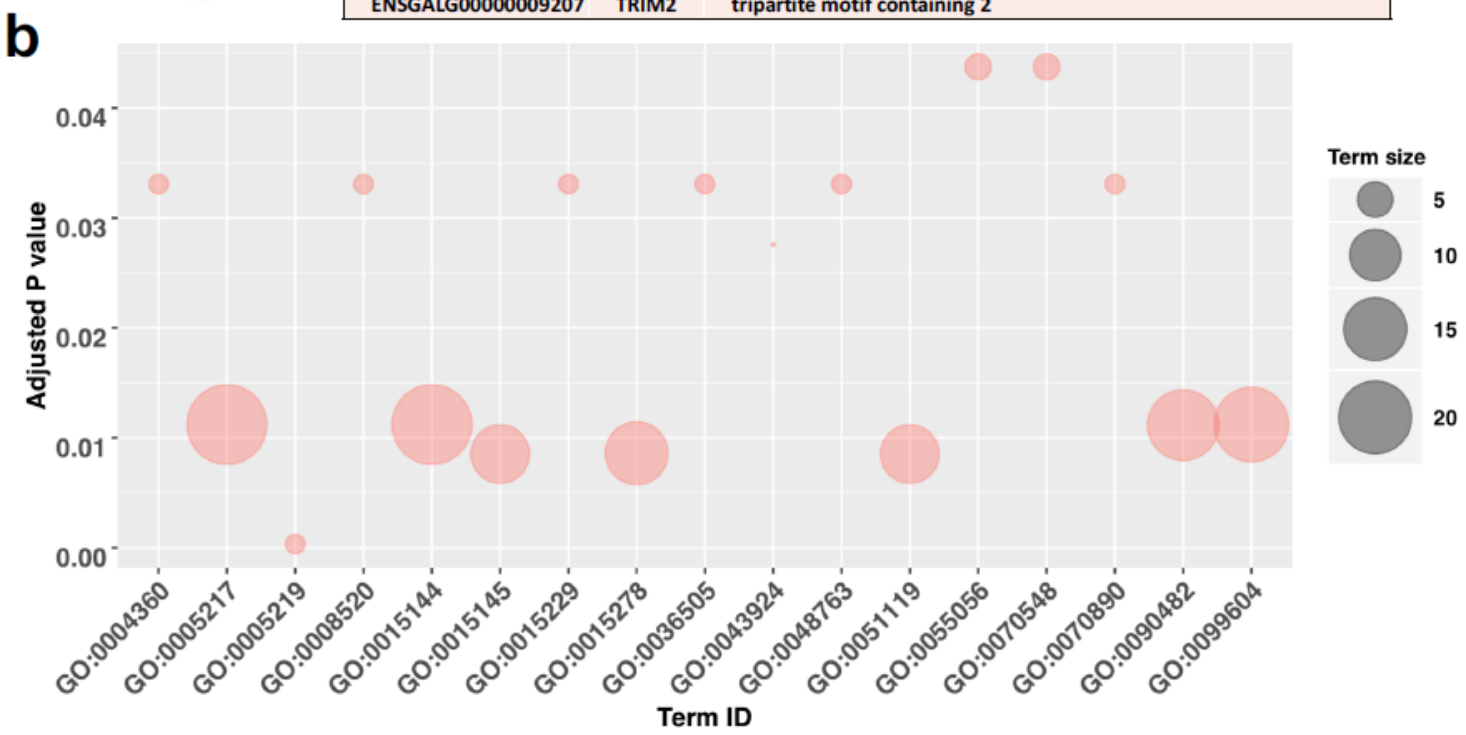


Figure 3

Candidate positively selected genes (PSGs). a. PSGs in the top 1% windows of LSBL 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.

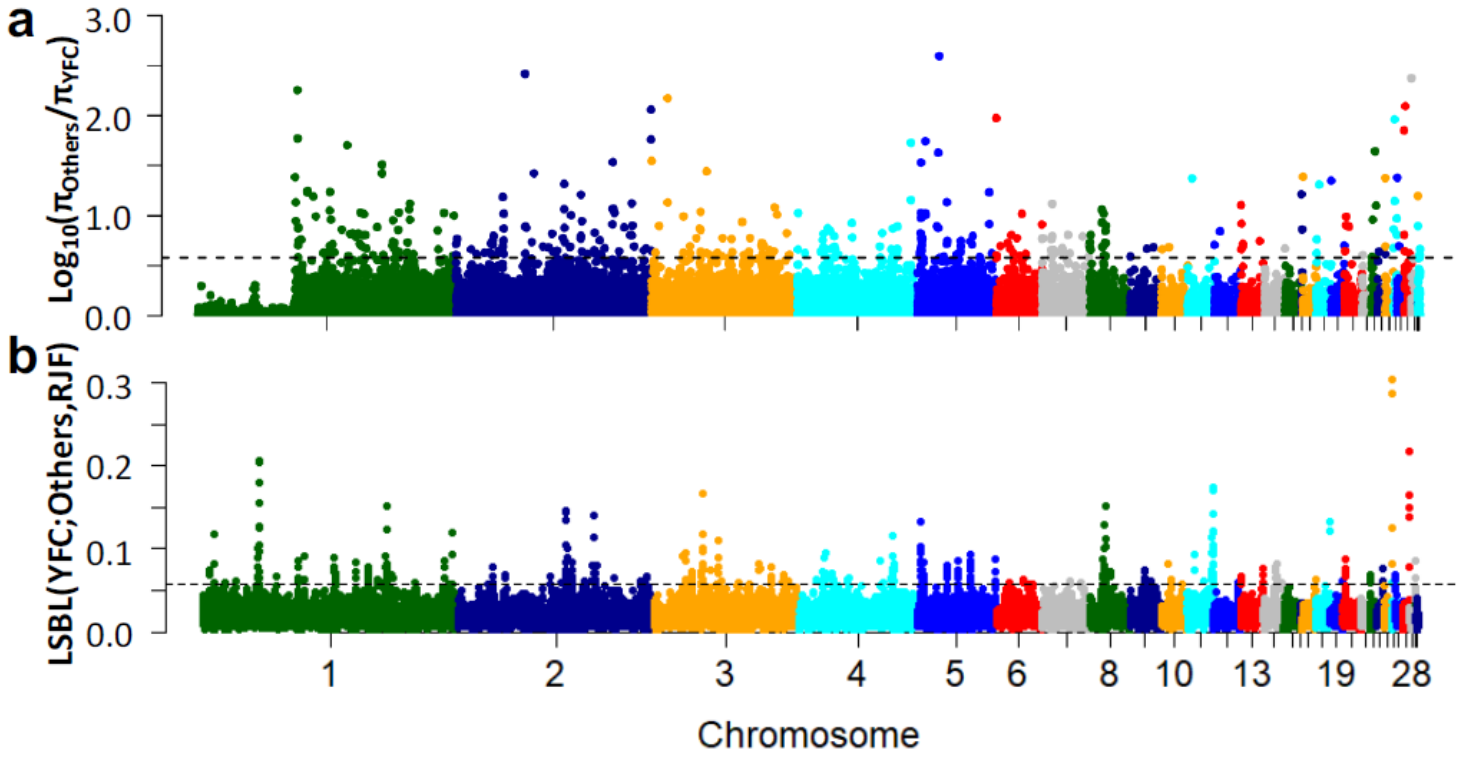


Figure 4

Genome-wide distributions of selection signals. a. π-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.

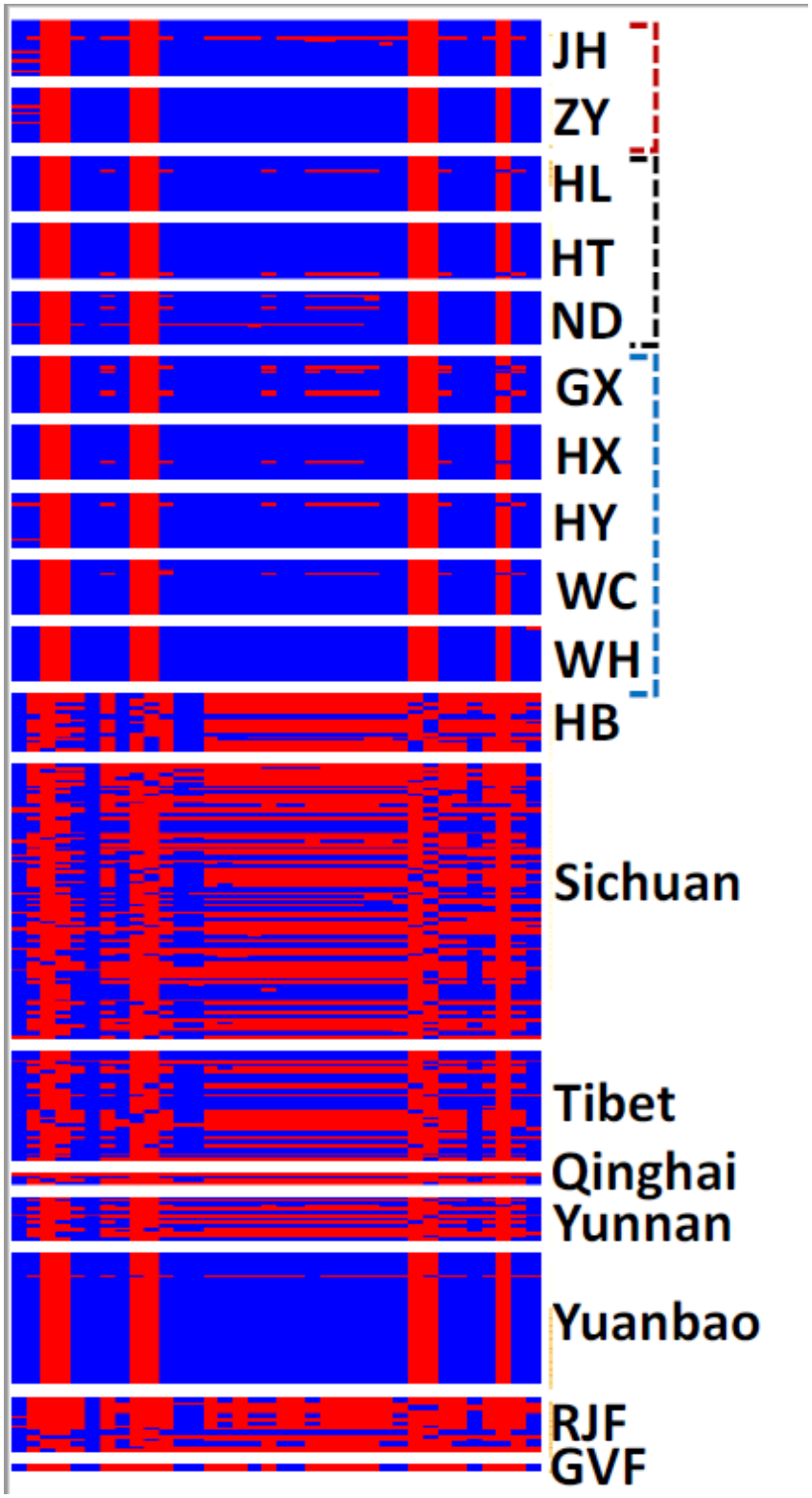


Figure 5

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 this preprint. Click to download.

- Additionalfile7.xlsx
- Additionalfile5.xlsx
- Additionalfile6.xlsx
- Additionalfile4.docx
- Additionalfile3.xlsx
- Additionalfile1.xlsx
- Additionalfile2.xlsx