Bioscience Evidence 2025, Vol.15, No.5, 209-218
http://bioscipublisher.com/index.php/be

Observation Analysis **Open Access**

Evolutionary Traits in Domestic and Wild Chickens Through Phylogenetic Markers

Qiqi Zhou, Shiqiang Huang
Tropical Animal Medicine Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572000, Hainan, China
Corresponding email: shiqiang.huang@hitar.org

Bioscience Evidence, 2025, Vol.15, No.5 doi: 10.5376/be.2025.15.0021
Received: 18 Jul., 2025
Accepted: 23 Aug., 2025
Published: 08 Sep., 2025

Preferred citation for this article:
Zhou Q.Q., and Huang S.Q., 2025, Evolutionary traits in domestic and wild chickens through phylogenetic markers, Bioscience Evidence, 15(5): 209-218 (doi: 10.5376/be.2025.15.0021)

Abstract This study mainly aims to analyze the evolutionary differences between chickens and wild chickens. We focus on the morphological, physiological, behavioral and genetic changes during the domestication process. Some commonly used tools in research include whole-genome SNPS, mitochondrial DNA and microsatellites, etc. These can help us observe the differentiation and gene exchange between domestic chickens and wild free-range chickens. It was found that domestic chickens exhibited distinct domesticated characteristics in terms of body size, feather color, breeding season, metabolism and response to humans. These changes are closely related to some key genes, such as TSHR, BCO2 and IGF1. In addition, the genes of domestic chickens are also mixed with components from other wild species such as the grey pheasant, making their genetic background more diverse. Phylogenetic analysis also indicates that the domestication and spread of domestic chickens were not accomplished in one go, but rather involved multiple origins and complex gene exchanges, which is why there are significant differences among domestic chicken breeds in different regions. The purpose of this review is to better understand the mechanism and genetic basis of domestic chicken domestication, and also to provide some references for poultry breeding and conservation.

Keywords Domestication of domestic chickens; Phylogenetic markers; Evolutionary traits; Genomic selection; Genetic diversity

1 Introduction

Domestic chickens (*Gallus gallus domesticus*) are among the most widely raised domestic fowls in the world. Its origin and evolution have always been the focus of research in animal genetics and domestic animal domestication. It is generally believed that domestic chickens mainly come from the free-range chickens (*Gallus gallus*) in Southeast Asia. However, recent molecular studies have also found that other wild species such as the grey grouse (*Gallus sonneratii*) and the Ceylon grouse (*G. lafayettii*) also have an impact on the genetic diversity of domestic chickens. This indicates that domestic chickens are not of a single origin but have undergone multiple domestications and complex gene exchanges (Liu et al., 2006; Yw et al., 2012; Lawal et al., 2019; Wang et al., 2020; Zhao et al., 2024). Domestication has brought about significant changes in the body size, behavior and physiology of domestic chickens, and has profoundly altered their genomic structure and genetic diversity (Rubin et al., 2010; Qanbari et al., 2019; Piegu et al., 2020; Wang et al., 2021).

Common phylogenetic markers include mitochondrial DNA (mtDNA), single nucleotide polymorphisms (SNPs), microsatellites (microsatellites), and nuclear DNA. These tools were used to study the evolutionary relationship and domestication history between domestic chickens and their wild relatives. Research on mtDNA has found that domestic chickens have multiple maternal origins, and domestic chicken populations in different regions have their own haplotype distributions (Liu et al., 2006; Yw et al., 2012; Huang et al., 2017; Boudali et al., 2020; Hata et al., 2021). SNPs and microsatellite markers can help analyze gene communication, selection signals and population structure, and also identify genes related to production and adaptation (Rubin et al., 2010; Lawal et al., 2019; Qanbari et al., 2019; Larkina et al., 2021; Wang et al., 2021; Zhao et al., 2024). Sequencing of nuclear DNA has revealed the dynamics of selection, bottleneck effect and genomic recombination during domestication (Sawai et al., 2010; Flink et al., 2014; Li et al., 2017; Liu et al., 2020; Piegu et al., 2020; Wang et al., 2020; Huang et al., 2023; Wu et al., 2023).

This study compiles the new progress in the research on the evolution of domestic chickens and pheasants in recent years. The key points include: systematic relationships of the genus Gallus and evidence of multi-source domestication of domestic chickens; The roles of mtDNA, SNPs, microsatellites and nuclear DNA in the study of evolution and trait differentiation; The main findings of domestic chickens and pheasants in terms of genetic diversity, selection signals, gene exchange and adaptive evolution. At the same time, the application of these tools in the genetic improvement and protection of poultry was also prospected. Through these analyses, this study hopes to provide assistance in understanding the evolutionary mechanisms and genetic basis of domestic chickens, and also offer references for the protection and utilization of poultry resources.

2 Evolutionary Context of Chickens

2.1 Origin and diversification of junglefowls (*Gallus gallus, G. sonneratii, G. lafayettii, G. varius*)

There are four wild chicken species in the genus Gallus: the red jungard (*Gallus gallus*), the gray jungard (*G. sonneratii*), the Ceylon jungard (*G. lafayettii*), and the green jungard (*G. varius*). Studies show that the red pheasant is the main ancestor of domestic chickens. However, grey, Ceylon and green pups have also contributed to the genetic diversity of domestic chickens (Sawai et al., 2010; Lawal et al., 2019; Wang et al., 2020; Zhao et al., 2024). Phylogenetic analysis revealed that the grey Grouse is more closely related to the Ceylon grouse. Together, they form a sister group and are also closely related to the red Grouse, while the green Grouse was the first to differentiate (Lawal et al., 2019). In terms of distribution, the red grouse is mainly found in South and Southeast Asia, the grey grouse in southern and western India, the Ceylon grouse only in Sri Lanka, and the green grouse in Java and surrounding islands of Indonesia (Zhao et al., 2024). There is gene exchange among these species, especially gene infiltration between the grey pheasant and domestic chickens, which has an impact on the appearance and adaptability of domestic chickens (Lawal et al., 2019; Zhao et al., 2024).

2.2 Timeline of domestication (~8 000 years ago in Southeast Asia)

Both archaeological and molecular studies have shown that the domestication of domestic chickens began approximately 8,000 years ago during the Neolithic Age, mainly in Southeast Asia and Southwest China (Yw et al., 2012; Lorenzo et al., 2015; Lawal et al., 2019; Wang et al., 2020; Hata et al., 2021). The earliest domestication center was in the distribution area of the spadiceus subspecies of the red pheasant, which is today's southwestern China, northern Thailand and Myanmar. After that, humans brought domestic chickens to Southeast Asia, South Asia and other places . Archaeological sites and ancient DNA analysis support the claim that domestic chickens were independently domesticated in many places in Southeast Asia, and also indicate that domestic chickens were used for religion, rituals and food very early.

2.3 Phylogeographic insights into chicken domestication and migration

Phylogenetic and distribution studies have shown that the domestication and spread process of domestic chickens is very complex. Mitochondrial DNA and whole-genome analysis revealed that there was a mixture of maternal lines and genomes among multiple subspecies of domestic chickens and red pheasants, and domestic chickens in different regions also had their own haplotypes and gene penetration patterns (Yw et al., 2012; Lorenzo et al., 2015; Lawal et al., 2019; Wang et al., 2020; Hata et al., 2021). The study also found fragments of grey Grouse, Ceylon Grouse and green Grouse in the genomes of domestic chickens, among which the genes of grey Grouse are directly related to the yellow skin of domestic chickens (Lawal et al., 2019; Zhao et al., 2024). The migration routes of domestic chickens are closely related to human activities. Archaeological evidence shows that about 2 250 years ago, domestic chickens crossed the Wallace Line with human migration and entered Indonesia and Pacific islands (Meijer et al., 2022). In East Asia, South Asia and the Pacific region, domestic chickens have gradually developed many different local breeds.

3 Phylogenetic Markers and Methodological Advances

3.1 Mitochondrial DNA (mtDNA) markers

Mitochondrial DNA is commonly used in the origin studies of domestic chickens and pheasants, with the D-loop region and COI gene being the most common. Because it is inherited only through the maternal line and changes rapidly, it is very suitable for systematic analysis. Research has found that domestic chickens have multiple maternal origins and independently formed haplotypes in different parts of Asia. This indicates that domestic chickens have been independently domesticated many times in South Asia and Southeast Asia. After whole genome sequencing, haplogroups could be further classified and complex mixtures between domestic chicken and red pheasant lineages were observed (Liu et al., 2006; Yw et al., 2012; Hata et al., 2021) (Figure 1). In the research of local breeds, mtDNA is also often used to trace the origin and genetic diversity of domestic chickens (Huang et al., 2017; Boudali et al., 2020; Liu et al., 2020).

3.2 Nuclear DNA markers

Nuclear DNA markers can provide more information, including population structure, breed differences and trait changes. Studies of microsatellites and SNPS have shown that both domestic chickens and pheasants have high genetic diversity and complex population structures (Hata et al., 2021; Larkina et al., 2021). Some gene loci, such as NCAPG-LCORL, BCO2 and TSHR, are closely related to the production traits and appearance differences of poultry, and therefore are very important in molecular breeding and systems research (Rubin et al., 2010; Qanbari et al., 2019; Larkina et al., 2021). Nuclear DNA data also revealed that there was gene infiltration and hybridization between domestic chickens and various pheasants, which enriched the genetic background of domestic chickens (Sawai et al., 2010; Lawal et al., 2019; Wang et al., 2020; Zhao et al., 2024).

3.3 Whole-genome sequencing (WGS)

Whole-genome sequencing technology has enabled more detailed research on the evolution of domestic chickens and pheasants. WGS can detect tens of millions of SNPS and structural variations, and can also systematically identify selection signals, gene rearrangements and functional gene changes (Rubin et al., 2010; Qanbari et al., 2019; Wang et al., 2020; Wang et al., 2021). By analyzing a large number of samples worldwide, researchers have found that domestic chickens have multiple origins, complex gene exchanges, have also experienced domestication bottlenecks, and have an impact on genetic burden. WGS also identified gene regions related to growth, immunity and reproduction, providing new evidence for poultry breeding and conservation (Wu et al., 2023).

4 Evolutionary Traits Shaped by Domestication

4.1 Morphological traits

Compared with wild free-range chickens, domestic chickens have more significant differences in appearance, mainly reflected in their body size, feather color and skull structure. Research has found that the skull changes of domestic chickens are more obvious than those of wild purebred chickens, especially in the areas where the neural crest originates, such as the protrusion of the skull of the crown-top chicken. This indicates that manual selection has a significant impact on appearance and functionality (Stange et al., 2018; Nunez-Leon et al., 2021). In addition, domestic chickens vary greatly in size, weight and feather color. Different breeds often correspond to different uses, such as laying eggs, producing meat or for ornamental purposes (Li et al., 2019; Larkina et al., 2021; Wang et al., 2021).

4.2 Physiological traits

Domestic chickens differ from wild free-range chickens in terms of metabolism, reproduction and adaptation. The most typical example is the selection of the TSHR gene, which affects metabolic and reproductive rhythms. Domestic chickens generally no longer have strict seasonal breeding like wild breeds (Rubin et al., 2010; Lawal and Hanotte, 2021). In addition, domestic chickens also show different abilities in terms of growth rate, egg production, high-altitude tolerance and heat tolerance, which are closely related to some genetic variations (such as IGF2BP1, LEPR) (Li et al., 2019; Qanbari et al., 2019; Wang et al., 2021).

4.3 Behavioral traits

Domestication has brought about significant changes in the behavior of domestic chickens. Domestic chickens are generally less afraid of humans, have lower aggression and are more sociable, all of which are regarded as manifestations of "domestication syndrome" (Belteky et al., 2018; Mehlhorn and Caspers, 2021). Experimental studies have found that as long as low fear is selected for five consecutive generations, it will lead to differences in behavior and hypothalamic DNA methylation, suggesting that behavioral evolution may be closely related to epigenetics (Belteky et al., 2018). Furthermore, the foraging, breeding and social interaction patterns of domestic chickens have also changed due to artificial selection (Li et al., 2019; Mehlhorn and Caspers, 2021).

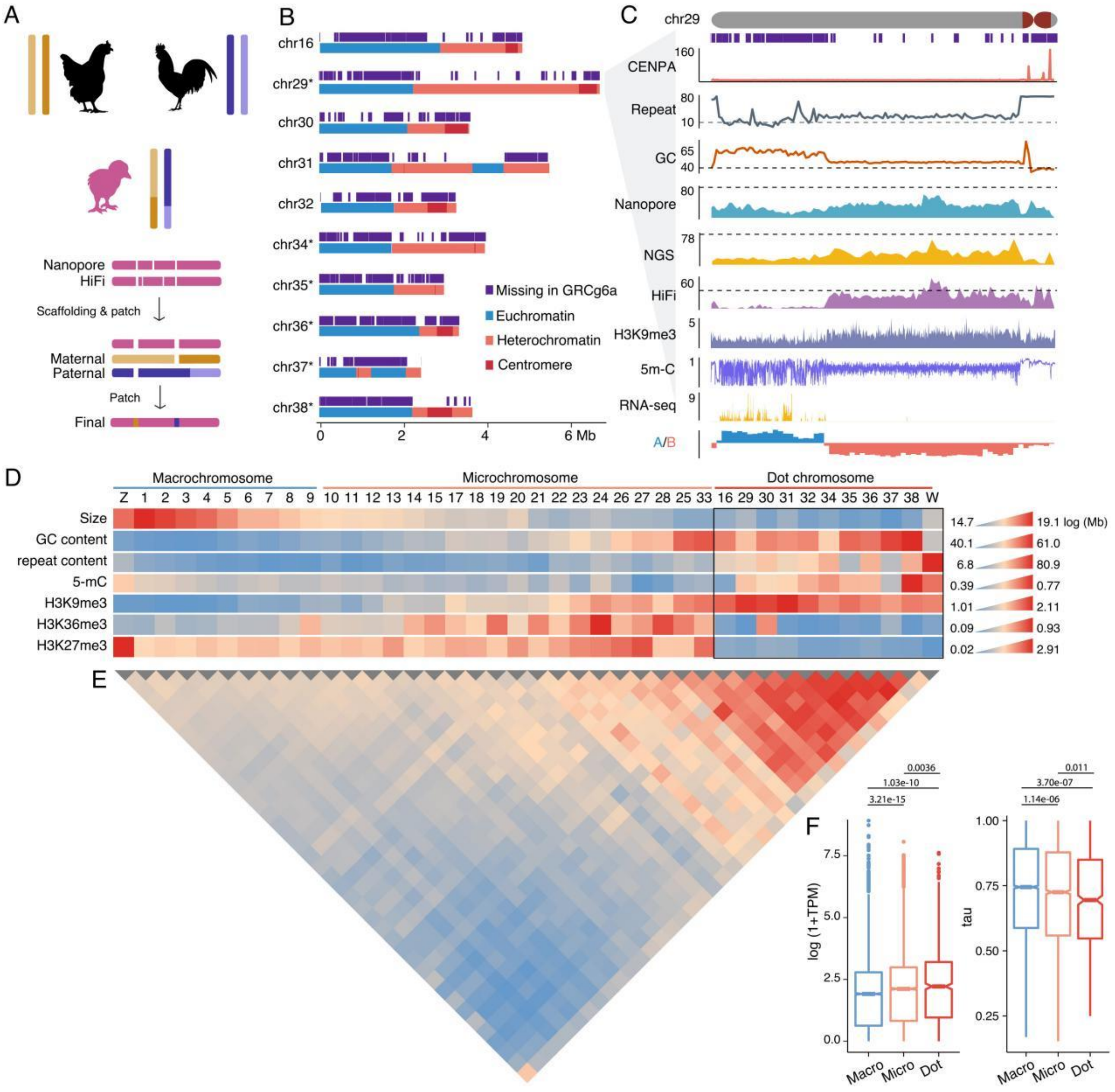

Figure 1 A complete chicken genome with 10 dot chromosomes. (A) A trio-based genome assembly pipeline. Rounded rectangles represent contigs. Paternal and maternal contigs were used to fill gaps in the primary contigs. (B) The dot chromosomes are in general composed of a euchromatic part and a heterochromatic part. The asterisks denote newly assembled chromosome models. (C) A zoom-in view for chr29, showing CENP-A and H3K9me3 binding, coverage of Nanopore ultralong, HiFi, NGS (BGISEQ-500, dashed lines indicate genomic average), gene expression (RNA-seq read counts in 1 kb windows), 5-mC levels, and A/B compartments. (D) The heatmap shows the chromosomal sizes (log-transformed), GC content, repeat content, chromosome-wide 5-mC levels, and ChIP/input ratios for H3K9me3, H3K36me3, and H3K27me3. (E) Interchromosomal interaction frequency measured using Hi-C data. (F) Dot chromosomes have a lower Tau value, i.e., lower level of tissue specificity but a higher expression level. P values were calculated using the Wilcoxon signed-rank tests (Adopted from Huang et al., 2023)

4.4 Genetic underpinnings

The domestication of domestic chickens has been accompanied by significant changes in the genome, including selection, mutation, deletion and the addition of exogenous genes. Genome-wide studies have found that domestic chickens and wild free-range chickens have significant differences in many gene loci, such as BCO2, TSHR, IGF1 and CORIN. These genes are related to morphology, pigment, metabolism, reproduction and behavior (Rubin et al., 2010; Qanbari et al., 2019; Wang et al., 2021; Zhao et al., 2024). Meanwhile, there are more harmful mutations in the genome of domestic chickens, which is in line with the "domestication cost" hypothesis, that is, when favorable traits are obtained through artificial selection, unfavorable variations will also accumulate (Mehlhorn and Caspers, 2021; Wang et al., 2021). Furthermore, changes in gene structure (such as deletions and duplications) and the introduction of exogenous genes (such as the BCO2 gene of the gray pheasant) have also increased the genetic diversity of domestic chickens (Lawal et al., 2019; Piegu et al., 2020; Zhao et al., 2024).

5 Case Study: Using Phylogenetic Markers to Trace Domestic and Wild Lineages

5.1 Example: analysis of mtDNA haplotypes showing multiple domestication centers in Southeast Asia and South China

Mitochondrial DNA (mtDNA) is often used as a maternal genetic marker to study the origin of domestic chickens. Many large-scale studies have found that domestic chickens and red pheasants (*Gallus gallus*) have multiple haplotype clusters (A-I) that are quite different. These haplotypes exist independently in Southeast Asia, South China and the Indian subcontinent, etc., suggesting that domestic chickens may have domestication centers in these places. For instance, domestic chickens and red pheasants in Thailand, Yunnan and Vietnam exhibit rich haplotype differences, some of which exist only in specific regions, indicating multiple domestication and complex diffusion processes (Liu et al., 2006; Yw et al., 2012; Hata et al., 2021; Kanakachari et al., 2023) (Figure 2).

5.2 Highlight how SNPs revealed introgression from wild *Gallus sonneratii* into South Asian domestic chickens

Genome-wide SNP analysis revealed that domestic chickens in South Asia carry a considerable number of gene fragments from the grey grouse (*Gallus sonneratii*). These fragments indicate the presence of bidirectional gene infiltration (Lawal et al., 2019; Zhao et al., 2024). The infiltrated regions not only include the known BCO2 genes, but also genes related to growth and immunity, such as IGFBP2, TKT, TIMP3, HSPB2 and CRYAB. This indicates that the grey pheasant has a significant impact on the genetic diversity and adaptability of domestic chickens.

5.3 Demonstrate functional impact: e.g., yellow skin allele traced back to *G. sonneratii* via phylogenetic analysis

Phylogenetic analysis shows that the yellow skin of domestic chickens can be traced back to the gray grouse. Research has found that the BCO2 gene alleles of domestic chickens and gray pheasants are very similar, and BCO2 fragments from gray pheasants can be detected in many domestic chicken breeds. This indicates that yellow skin was introduced into domestic chickens through gene infiltration and was subsequently strongly selected (Zhao et al., 2024; Wu et al., 2023). This result reveals the genetic basis of the phenotypic diversity of domestic chickens and also indicates that functional gene flow is of great significance in domestication.

5.4 Comparative insight: how gene flow shaped adaptive traits like feather pattern and skin pigmentation

Gene flow and hybridization have played a key role in the domestication and evolution of domestic chickens. In addition to yellow skin, traits such as feather patterns and skin pigmentation are also influenced by the infiltration of wild species genes. Genome-wide comparisons and selective scans have revealed significant differences between domestic chickens and wild purebred chickens in many genes related to development, immunity, reproduction and vision. These variations are directly related to the appearance diversity and environmental adaptation of domestic chickens (Rubin et al., 2010; Lawal et al., 2019; Wu et al., 2023). Therefore, gene flow not only increases the genetic resources of domestic chickens but also helps them adapt to different ecological environments.

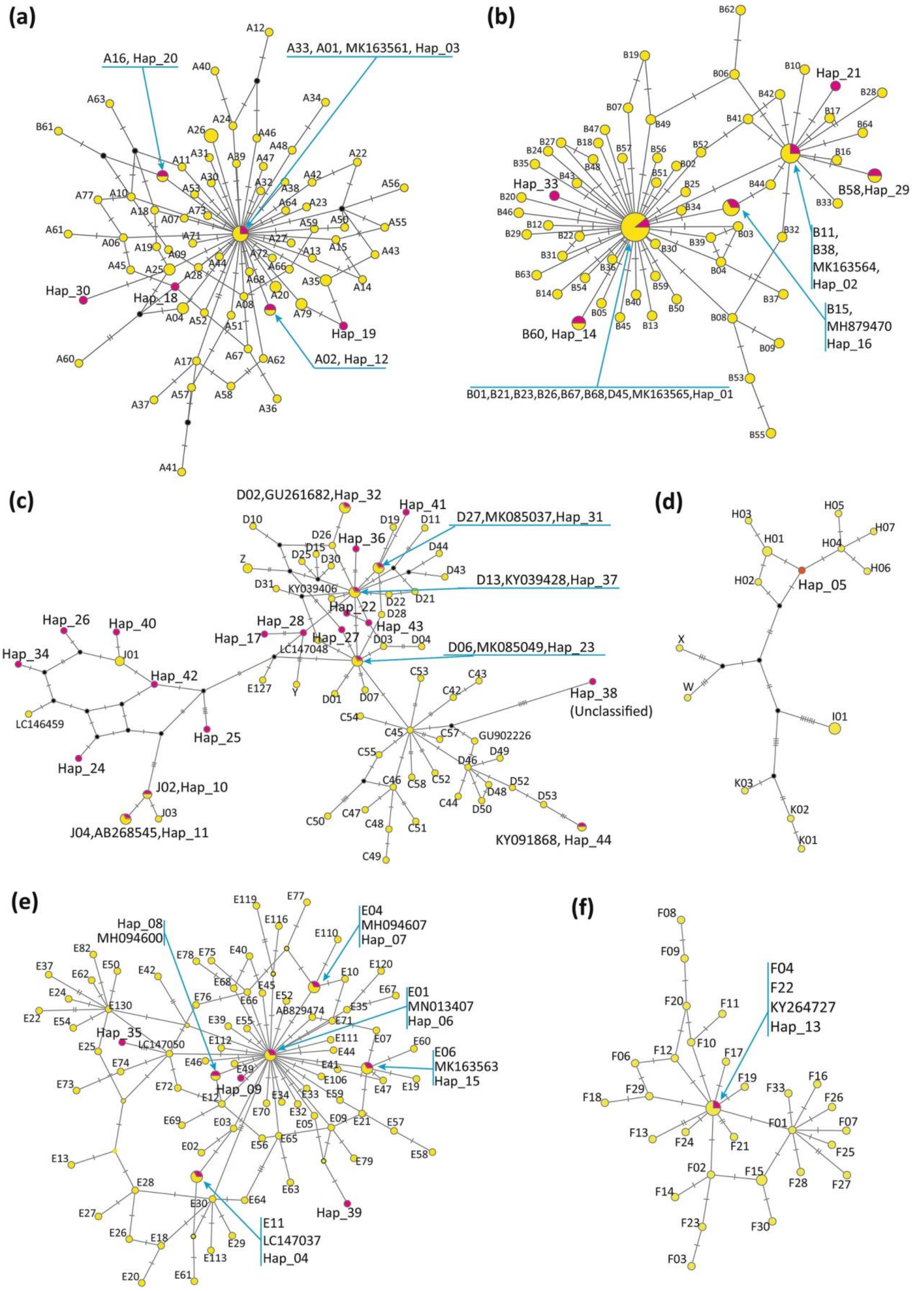

Figure 2 Locations of mtDNA D-loop haplotypes of Thai red junglefowl and indigenous chicken populations in the global chicken population network. (a) Haplogroup A. (b) Haplogroup B. (c) Haplogroups CD, Y, Z, J, and an unclassified haplotype, Hap_38. (d) Haplogroups H, I, K, X, and W. (e) Haplogroup E. (f) Haplogroup F. Haplotypes that were found in the present study and representative haplotypes reported by Miao et al.5 are shown by magenta and yellow circles, respectively. Black nodes are the inferred intermediate haplotypes. The number of bars on the lines, which link haplotypes, represent the number of nucleotide substitutions that occurred between the haplotypes for comparison (Adopted from Hata et al., 2021)

6 Implications for Evolutionary Biology and Agriculture

6.1 Broader lessons on animal domestication processes

The domestication and breed changes of domestic chickens are important examples for studying the mechanisms of animal domestication. Genomic and mitochondrial DNA studies have shown that domestic chickens mainly come from red pheasants (*Gallus gallus*). However, during the domestication and diffusion process, the grey grouse, the Ceylon grouse and the green grouse, etc. also participated in gene exchange, forming a history of multiple origins and multiple hybridization (Liu et al., 2006; Yw et al., 2012; Lawal et al., 2019; Wang et al., 2020; Zhao et al., 2024). These results indicate that animal domestication is not a process of a single ancestor, but involves multiple gene flows and independent domestication in different regions (Hata et al., 2021). Meanwhile, selective sweeping and rapid differentiation of trait related genes emerged in domestic chickens during domestication, demonstrating the combined effect of artificial selection and natural selection (Rubin et al., 2010; Qanbari et al., 2019; Wang et al., 2021).

6.2 Conservation strategies for wild junglefowls

Wild free-range chickens are the ancestors of domestic chickens and retain rich genetic diversity, making them an important resource. However, the genetic exchange between modern domestic chickens and wild purebred chickens has caused some wild groups to lose their original genotypes. Studies have found that in some wild populations, the proportion of gene infiltration in domestic chickens is as high as 20%-50%, posing a threat to their genetic integrity (Lawal et al., 2019; Wu et al., 2023; Zhao et al., 2024). Conservation strategies include: strengthening genetic surveillance, giving priority to protecting populations with less gene infiltration, using molecular markers (such as mtDNA, SNPs) to track wild-type genes, and reducing genetic pollution (Bondoc and Santiago, 2013; Hata et al., 2021; Wu et al., 2023). The genetic diversity of wild free-range chickens is also of great significance for future poultry breeding and adaptation improvement (Lawal et al., 2019; Wu et al., 2023).

6.3 Application of phylogenetic markers in breeding programs (disease resistance, climate adaptation)

Phylogenetic markers (such as SNPS, mtDNA and functional genes) have been widely applied in chicken breeding at home. Through genome-wide screening and molecular marker-assisted selection (MAS), researchers can identify gene regions related to production traits, disease resistance, and climate adaptation, such as BCO2, TSHR, IGF1, and LEPR (Rubin et al., 2010; Qanbari et al., 2019; Larkina et al., 2021). These markers can not only increase yield but also play a role in disease resistance and environmental tolerance improvement. For example, the heat shock protein gene helps domestic chickens adapt to high temperatures (Zhao et al., 2024). Meanwhile, by combining linkage disequilibrium (LD) and population structure analysis, tag selection can also be optimized to reduce costs and improve efficiency.

7 Future Directions

7.1 Integration of multi-omics (genomics, transcriptomics, epigenomics)

Future research will need to combine different types of data, such as genomes, transcriptomes and epigenomes. Only in this way can we have a more comprehensive understanding of the genetic regulation methods of domestic chickens and pheasants during evolution. Nowadays, genomic sequencing has identified many selection signals related to domestication and trait differences (Rubin et al., 2010; Qanbari et al., 2019; Wang et al., 2021; Wen et al., 2025). However, if one only looks at one type of data, it is difficult to explain how complex traits are formed. Combining multiple omics can simultaneously study the effects of gene variation, gene expression and epigenetic modifications. For instance, studies have revealed similar evolution of behavioral traits by comparing brain transcriptome and genomic signals (Hou et al., 2020). In the future, this multi-omics analysis should continue to be promoted to identify key regulatory networks and important genes, providing more theoretical support for poultry breeding and adaptability research.

7.2 Advances in ancient DNA for tracing early domestication events

The development of ancient DNA technology has brought new ideas to the study of the early domestication and gene flow of domestic chickens. By analyzing the DNA of ancient chicken bones at archaeological sites, it was found that some trait genes of modern domestic chickens (such as TSHR and BCO2) were not fixed very early, but were strongly selected in modern times (Flink et al., 2014). In addition, by combining ancient DNA with the whole genome, the processes of multiple origins, interspecific hybridization and gene infiltration in domestic chickens can be observed more clearly (Flink et al., 2014; Lawal et al., 2019; Wang et al., 2020; Zhao et al., 2024). In the future, with the advancement of sequencing and DNA extraction methods, ancient DNA research can more accurately reconstruct the history of domestication, diffusion and trait evolution of domestic chickens.

7.3 Role of CRISPR and functional genomics in validating phylogenetic inferences

Gene editing technologies such as CRISPR have provided new tools for verifying candidate genes in phylogenetic research. Genomics has identified many genes related to domestication and traits, but the specific functions of these genes still need to be experimentally confirmed (Rubin et al., 2010; Qanbari et al., 2019; Wang et al., 2021; Wen et al., 2025). By using CRISPR knockout or knock-in technology, the impact of a certain gene variation on phenotypes can be directly tested, and the relationship between genes and traits can be verified. At the same time, by integrating functional genomics methods, such as single-cell transcriptomics and epigenetic editing, a deeper understanding of the roles of key genes in different tissues and developmental stages can be achieved. This will make phylogenetic inference more accurate and more biologically significant (Hou et al., 2020).

8 Concluding Remarks

Domestic chickens (*Gallus gallus domesticus*) have undergone significant genetic and appearance changes during the domestication process. Compared with wild free-range chickens (such as red free-range chickens), domestic chickens differ greatly in growth rate, body size, egg production, skin color, behavior and reproductive cycle. These changes are mainly driven by artificial selection, environmental adaptation and gene exchange. For instance, the BCO2 gene and the TSHR gene are strongly selected in domestic chickens. The former is related to skin pigmentation, while the latter is associated with the breeding season. In addition, different domestic chicken breeds also show significant differences in body size, egg production and usage. Some mainly lay eggs, some produce meat, and some are ornamental breeds.

Phylogenetic markers (such as whole-genome SNPS, mitochondrial DNA and microsatellites, etc.) are important tools for studying the evolution of domestic chickens and pheasants. Through these molecular markers, researchers can track whether domestic chickens have multiple origins, identify selected gene regions, recognize genes related to traits, and also reconstruct the lineage relationship between domestic chickens and pheasants. For instance, mitochondrial DNA and whole-genome data reveal that domestic chickens come from the distribution areas of multiple red pheasant subspecies and have also engaged in gene exchange with other pheasants during their spread. Phylogenetic markers have also helped to identify functional regions in the domestic chicken genome that have been retained due to domestication and artificial selection.

A lot of evidence indicates that hybridization and gene infiltration have played an important role in the evolution of domestic chickens. Domestic chickens not only have a close genetic relationship with red purebred chickens, but also have undergone multiple gene exchanges with gray purebred chickens, Ceylon purebred chickens, green purebred chickens, etc. These gene flows increase the genetic diversity of domestic chickens and also affect important traits such as skin color, growth rate and immunity. For instance, the genetic infiltration of the grey pheasant has brought about the yellow skin of domestic chickens, while other fragments are related to growth and environmental adaptation. Meanwhile, the gene exchange between modern domestic chickens and wild purebred chickens has also led to the loss of some wild genotypes. Therefore, it is very important to protect the genetic diversity of wild purebred chickens.

Acknowledgments

We would like to express our gratitude to the two anonymous peer researchers for their constructive suggestions on our manuscript.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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