

Phylogenomic Insights into the Origin and Dispersal of Domesticated Chickens

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Abstract The origin, domestication process and genetic diversity of domesticated chickens have always been important contents in the study of animal genetics and the evolution of poultry. Based on the latest achievements in phylogenetic genomics in recent years, this study sorted out the multiple independent domestication processes of domesticated chickens, the gene exchange between wild junglefowl and domesticated chickens, and the paths by which they spread from their native habitats to the world, and explored the genetic reasons for domesticated chickens to adapt to different environments and form local breeds. This study also analyzed the relationship between the geographical distribution of domesticated chickens and human migration, and expounded some representative diffusion cases in the Pacific and African regions. This study aims to provide a theoretical basis for understanding the evolutionary history and genetic structure of domesticated chickens, and also to offer a scientific basis for the protection of local chicken breeds and future breeding strategies.

Keywords Domesticated chickens; Phylogenomics; Genomic introgression; Genetic diversity; Phylogeography

1 Introduction

Domesticated chickens are widely raised in many countries and regions and are the most numerous domestic animals. It can adapt to various environments, is rarely restricted by culture or religion, has a strong reproductive capacity, and is also rich in genetic resources. It plays a significant role in addressing food security issues brought about by climate change and population growth (Lawal et al., 2020; Wang et al., 2021; Lin and Chen, 2024). In human society, domesticated chickens are not only an important source of meat and eggs, but are also often raised as recreational animals, religious symbols or ornamental birds. Lawal and Hanotte (2021) hold that domesticated chickens are popular in various social contexts due to their high cultural acceptance and few taboos. They are also important experimental animals in genetic research and are often used in the study of phenotypic evolution, environmental adaptation, and domestication processes.

Wang et al. (2021) gained a more accurate understanding of the evolutionary process of domesticated chickens through large-scale genomic sequencing and mitochondrial DNA analysis, helping researchers clarify the origin of domesticated chickens, genetic diversity, and how they gradually adapted to the environment during the domestication process. Quan et al. (2020) and Hata et al. (2021) found that domesticated chickens have undergone multiple independent domestication processes in South Asia, Southwest China and Southeast Asia. The genomes of domesticated chickens have become more abundant as genes from different junglefowl species continuously flow into the gene pool of domesticated chickens (Lawal et al., 2019; Lawal et al., 2020; Wang et al., 2020). During the process of domestication and variety differentiation, some gene loci related to functions such as metabolism and reproduction played important roles, and some unfavorable variations were gradually eliminated.

This study introduces the origin of domesticated chickens, analyzes how they gradually spread to various parts of the world, assesses the impact of the domestication process on the genetic diversity, environmental adaptability, and accumulation of harmful mutations of domesticated chickens, and focuses on exploring the genetic causes of domesticated chickens in domestication, environmental adaptation, and appearance changes. This study aims to provide a scientific basis for the protection of genetic resources of local chicken breeds through phylogenetic analysis and genetic diversity research, and help determine which breeds need priority protection.

2 Evolutionary Background of the *Gallus* Genus

2.1 Taxonomy of wild junglefowl species

The genus *Gallus* mainly includes four species: Red junglefowl (*G. Gallus*), Green junglefowl (*G. varius*), Grey junglefowl (*G. sonneratii*), and Ceylon junglefowl (*G. lafayettii*) (Figure 1) (Mariadassou et al., 2020; Tiley et al., 2020). The Green junglefowl was the first to differentiate from other species. The Grey junglefowl is most closely related to the Ceylon junglefowl. They are a pair of “sister species”, and this branch forms a relative “sister group” with the Red junglefowl (Lawal et al., 2019; Lawal et al., 2020).

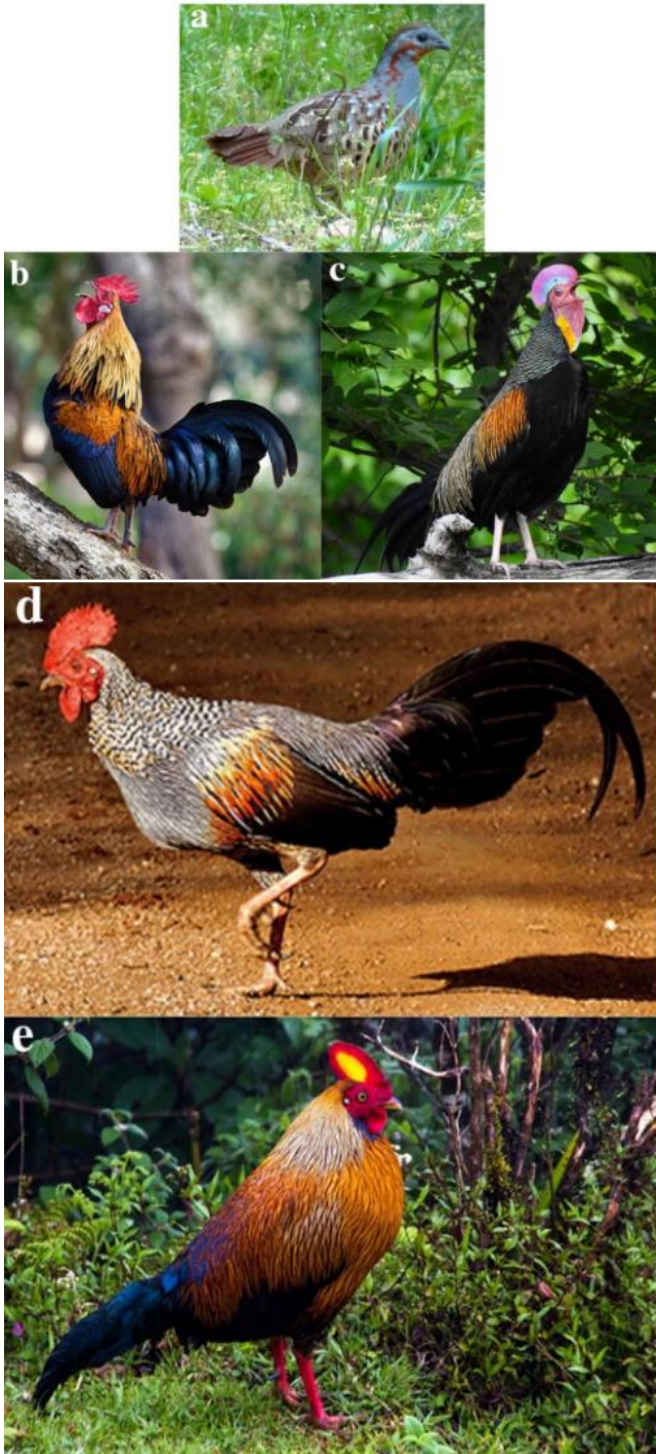


Figure 1 Appearance of each focal species (Adopted from Tiley et al., 2020)

Image caption: a *Bambusicola thoracicus*. b *Gallus gallus*. c *G. varius*. d *G. sonneratii*. e *G. lafayettii*. For *Gallus*, only males are shown; *Bambusicola* is sexually monomorphic (Adopted from Tiley et al., 2020)

2.2 Genomic relationships within the genus

Lawal et al. (2019) and Tiley et al. (2020) found that among these species, the Green junglefowl was the first to differentiate, followed by the Grey junglefowl and the Ceylon junglefowl, and finally the Red junglefowl. The red junglefowl is the main ancestor of domesticated chickens. However, due to the occurrence of gene flow and incomplete lineage differentiation in history, the evolutionary relationships within the genus have become more complex (Lawal et al., 2020; Mariadassou et al., 2020).

2.3 Genome-wide introgression events

The studies of Lawal et al. (2019) and Lawal et al. (2020) found that there was relatively frequent two-way gene exchange between domesticated chickens and Grey junglefowl, less gene infiltration with Ceylon junglefowl, and almost no exchange with Green junglefowl. These gene exchanges mainly occur in regions related to development, immune function and gene expression. Wu et al. 's research in 2020 suggested that the genetic flow between wild junglefowl and domesticated chickens has been ongoing, both in the past and at present. Mariadassou et al. 's 2020 research found that in some wild Red junglefowl populations, varying degrees of domesticated chickens gene infiltration have been detected, and it indicates that researchers should pay attention to sample screening when conducting systems genomics studies to avoid selecting individuals that have recently hybridized with Gray junglefowl, which could interfere with the research results.

3 Identifying the Wild Ancestor(s) of Domestic Chickens

3.1 Nuclear vs. mitochondrial genome evidence

The whole-genome analysis results of Wang et al. in 2020 unanimously agreed that the Red junglefowl (*Gallus gallus*) was the main wild ancestor of domesticated chickens, and the subspecies *Gallus gallus spadiceus* made the greatest contribution to the genes of domesticated chickens. Lawal et al. 's research in 2019 and 2020 also found that the genomes of domesticated chickens were mixed with genes from other junglefowl species. The infiltration was most obvious in the Gray junglefowl, while it was less common in the Ceylon junglefowl and the Green junglefowl. The mitochondrial DNA research conducted by Hata et al. in 2021 also supported that the Red junglefowl was the maternal ancestor of domesticated chickens, but many different haplotypes were also discovered. These findings suggest that domesticated chickens may have multiple maternal origins and even had independent domestication processes in different regions. Hybridization events have also led to more new changes in the mitochondrial genes of domesticated chickens.

3.2 Geographic origin inference

A large number of genomic studies have found that domesticated chickens originated from a subspecies of the red junglefowl mainly distributed in Southwest China, Northern Thailand and Myanmar - *G. g. spadiceus*. After being domesticated, domesticated chickens began to spread to Southeast Asia and South Asia. Wang et al. (2020) and Hata et al. (2021) found that throughout the process, domesticated chickens interbred with local Red junglefowl subspecies and other junglefowl species, resulting in some modern chicken breeds having multiple different genetic sources. Hata et al. 's genetic research in 2021 indicates that some regions in Southeast Asia may have independently undergone domestication of domesticated chickens, as certain specific haplogroups only emerged in these areas.

3.3 Candidate domestication traits and selection signals

Domesticated chickens and wild junglefowl can be distinguished by some genotype markers. Wu et al. 's research in 2023 found that many selected genes are related to development, reproduction and vision. Yellow skin and the *TSHR* gene are two important characteristics of domesticated chickens, but these characteristics have only begun to emerge widely in the last 500 years, suggesting that they may not have been present since early domestication but were strongly selected and bred by people later. The research of Lawal et al. (2019) and Lawal et al. (2020) indicates that some gene regions introduced from other junglefowl species also contain genes related to gene expression, development and immunity, which make the diversity and adaptability of domesticated chickens stronger.

4 Dating Domestication: Phylogenomic Timelines

4.1 Molecular clock calibration

When researchers study the domestication time of chickens, they usually estimate it using a “molecular clock”, which is calibrated by observing the mutation rates of nuclear DNA and mitochondrial DNA. In some chicken flocks in Pakistan, Khan et al. (2020) measured the mutation rate to be approximately 3.6×10^{-6} per site per year, and they used Bayesian phylogenetic analysis to estimate the domestication time. The obtained domestication time may vary greatly due to the use of different genetic markers or calibration points, which indicates that to obtain more accurate results, it is best to analyze with multiple genetic loci and more stable samples.

4.2 Estimating divergence from *G. gallus* wild populations

Researchers have found through phylogenetic analysis of nuclear DNA that domestic chickens diverged from the Red junglefowl (*Gallus gallus*) approximately 58 000 years ago (\pm 16 000 years), which is much earlier than the domestication time of domesticated chickens discovered through archaeology, which is about 10 000 years ago. Khan et al. (2020) believe that this time difference might be due to the continuous genetic exchange between domesticated chickens and Red junglefowl, or because their ancestors originally had many genetic differences. Studies on mitochondrial DNA have shown that domesticated chickens and Red junglefowl, especially the subspecies *G. g. gallus* and *G. g. spadiceus*, have a very close maternal relationship. Moreover, in some areas, the differentiation time of domesticated chicken populations can be traced back approximately 7 000 years ago. Hata et al. also found in their genetic research in 2021 that some areas in East Asia and Southeast Asia might have domesticated domesticated chickens independently. The fact that some haplogroups only occur in specific regions also indicates the local evolution characteristics of these areas.

4.3 Ancient DNA contributions

Scientists have discovered some chicken bones dating back about 10 000 years in northern China and extracted mitochondrial DNA from them, indicating that there were already Jungian animals in this area at that time. This also supports that northern China was one of the regions where domesticated chickens were early domesticated. Ancient DNA analysis also found that early domesticated chickens contributed to the gene pool of modern domesticated chickens. The research conducted by Wu et al. in 2023 indicates that the genome of modern domesticated chickens not only contains components of the Red junglefowl (*Gallus gallus*), but also some genes of the Gray junglefowl (*Gallus sonneratii*). By comparing ancient and modern genomes, scientists have also found that due to long-term gene exchange with domesticated chickens, the original “wild-type” genome of the wild Red junglefowl is gradually decreasing. Some of the genes selected during the domestication process are mainly related to development, reproduction, vision and other functions.

5 Dispersal Patterns Revealed by Genomic Signatures

5.1 Tracing chicken expansion across Asia and Africa

The genetic research and mitochondrial DNA analysis conducted by Osman et al. in 2016 and by Yonezawa et al. in 2024 revealed that African domesticated chickens have two main sources. One transmission route started from South Asia, passed through West Asia and Egypt, and spread to North Africa and Central Africa. Another route was to enter East Africa through the Indian Ocean, possibly brought there by Austronesian merchants from the Pacific Ocean and Southeast Asia. Researchers have discovered a variety of different mitochondrial haplogroups in African domesticated chickens, which indicates that domesticated chickens have not been introduced only once but have been brought to Africa multiple times, taking more than one route.

5.2 Distinguishing European, Indian, and Southeast Asian lineages

The domesticated chicken breeds in Europe have obvious genetic differences from those in Asia and Africa. Their population differences are greater and their genetic diversity is lower. This might be because these chickens have undergone long-term intensive selection and isolation breeding. Domesticated chickens in India have some unique genetic markers, suggesting that their domestication might have occurred independently. The ancestors of these chickens might have included the local Red junglefowl (*Gallus gallus murghi*) and some other wild subspecies, which also supports the view that “there are multiple domestic chicken domestication centers in Asia”. Godinez et

al. 's research in 2022 suggests that the genetic diversity of domesticated chickens in Southeast Asia is very rich, and their maternal genetic lineages are also rather unique. For instance, some V-shaped haplogroups differentiate very early, while other lineages spread to island regions later. The domesticated chickens in Africa have genetic overlaps with some breeds in Eastern Europe and the Mediterranean region, indicating that they once had genetic exchanges in history, reflecting the impact brought about by human migration.

5.3 Founder effects and bottlenecks in new regions

After domesticated chickens spread from their wild ancestors, genetic diversity gradually declined as the distance increased. This change was caused by the “priming effect” and the “genetic bottleneck”. The first batch of chickens to go out took away some genes, and the genes of their offspring were fewer than those of the original ones. Malomane et al. (2021) found that the genetic diversity of European domesticated chickens decreased, while the differences among different groups increased, indicating that the early introduction and subsequent artificial selection had a significant impact on them. Osman et al. 's research in 2016 and Yonezawa et al. 's research in 2024 suggest that in Africa, the gene flow of chickens occurs on a small scale, with little communication between regions. This has enabled native African chickens to form their own unique evolutionary lineages and genetic structures.

6 Local Adaptation and Genetic Differentiation

6.1 Signatures of selection in different environments

Genomic research has found that domesticated chickens exhibit strong selection signals in the process of adapting to different environments and meeting human breeding goals. These selections mainly focus on genes of some economic traits, such as the color of feathers and skin, growth rate, etc., as well as local traits like high-altitude adaptation. Tibetan chickens have demonstrated genetic adaptations related to energy metabolism and body shape maintenance, which help them survive in high-altitude environments. These adaptations are usually due to the influence of “selective sweeping” on certain gene regions. In the same year, that is, in 2019, Li et al. and Qanbari et al. found that the genes affecting color included *BCO2*, *TSHR*, *ALXI*, *KITLG*, and the genes related to yield included *LEPR*, *MEGF10*, *SPEF2*, etc. Li et al. (2019) found that the genetic diversity on sex chromosomes was lower than that on autosomes and the selection signal was stronger, indicating that sex chromosomes played a certain role in the adaptation and domestication of domesticated chickens.

6.2 Regional breed formation and differentiation

The formation of regional chicken breeds is influenced by human selection and breeding as well as the natural environment. Over a hundred chicken breeds with significant differences in appearance and traits have emerged worldwide. The differences among various chicken breeds are related to their geographical origins, breeding histories, and breeding purposes. Guo et al. 's research in 2021 found that modern broiler breeds in both Asia and the West are genetically influenced by large Asian chicken breeds. Phylogenetic and population structure analyses also revealed that there were obvious gene clustering phenomena among chicken breeds in different regions, and there was also gene exchange among different breeds. Nie et al. (2019) and Dementieva et al. (2024) hold that geographical isolation and environmental adaptation together have promoted the genetic differentiation of chicken breeds in Eurasia.

6.3 Admixture and hybrid vigor

Lawal et al. 's research in 2019 and Wang et al. 's research in 2020 demonstrated that the genomic achievements of modern commercial chicken breeds are like a Mosaic, with a mixture of genes from multiple Red junglefowl subspecies and other junglefowl species. In China, hybridization between local chickens and commercial chickens is very common, and there is also genetic exchange between fighting chickens and local chickens. Ren et al. (2023) hold that these hybridizations enhance genetic diversity and may also bring about “heterosis”, making the next generation stronger. Nie et al. (2019) and Guo et al. (2021) found that most of these hybridization were achieved through trade and population migration, bringing about new genetic variations that enabled chickens to survive and produce better in different environments. Wattanadilokcahtkun et al. 's research in 2023 found that the Lao Pa Koi fighting chicken in Thailand has a relatively high genetic diversity, with the characteristics of both Red junglefowl and domesticated chickens in its genes, showing obvious hybrid vigor.

7 Case Study: The Phylogeography of Pacific Chickens

7.1 Background and research objectives

The systematic geographical study of the Pacific domesticated chickens aims to clarify the origin, genetic diversity and transmission routes of domesticated chickens in Southeast Asia and the Pacific region, understand the domestication history of domesticated chickens, identify which are unique genetic lineages, and also study how human migration affects the spread of domesticated chickens on Pacific islands. The research aims to reconstruct the population history of domesticated chickens, identify different maternal lineages, and link the diffusion process of domesticated chickens with the migration history of humans in places such as Oceania (Godinez et al., 2021; Godinez et al., 2022).

7.2 Genomic findings from island populations

Genomic analysis, especially mitochondrial DNA (mtDNA) research, has found that domesticated chickens on Pacific Islands have a high degree of genetic diversity and some unique gene types. Studies show that the chickens on these islands have many specific haplotypes related to geographical location, mainly belonging to the two haplogroups of type D and type E. In Vanuatu and Guam, the D-type haplogroup is the most common, while the E-type is relatively rare. These findings indicate that some ancient lineages of Pacific domesticated chickens have been preserved on the islands and have not been greatly affected by the introduction of modern global domesticated chickens (Figure 2) (Godinez et al., 2021; Godinez et al., 2022).

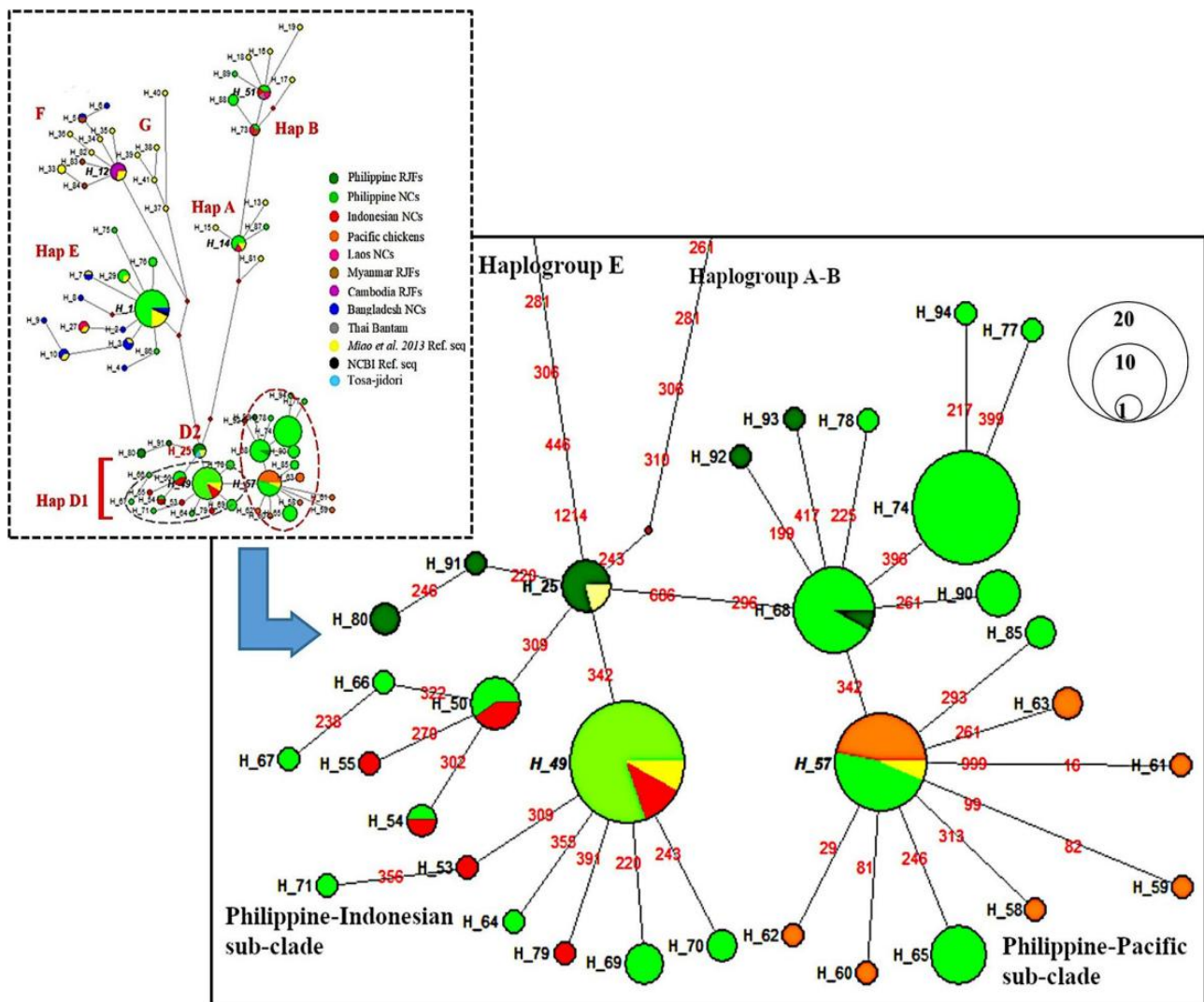


Figure 2 Median-joining network of the complete mtDNA D-loop region (1 232 bp) depicting relationship of Philippine chickens, Indonesian chickens, and Pacific chickens. The area of each circle is proportional to the frequency of the corresponding haplotypes. The length of branch connecting to other haplotypes correspond to mutational positions (Adopted from Godinez et al., 2021)

The research has discovered a new and highly differentiated maternal lineage - the V-type haplogroup. Godinez et al. 's analysis in 2022 revealed that these island chicken flocks separated from the mainland domesticated chickens approximately 2 100 years ago, and the entire process occurred after the earlier spread of the mainland domesticated chickens in Southeast Asia. Godinez et al. 's research in 2021 found that the Philippines is regarded as an important source of diversity for Pacific domesticated chickens. This is because the Philippines not only has a rich variety of haplotypes but also has obvious genetic ties with many chicken flocks on Pacific islands, supporting the view that “Pacific domesticated chickens originated in the Philippines”. The study of ancient DNA has more clearly confirmed that some unique Pacific haplotypes still exist at higher frequencies in multiple islands, indicating that the genetic lineage of early Polynesian domesticated chickens has continued to this day.

7.3 Broader implications for human migration studies

Godinez et al. 's research in 2021 found that the distribution of some specific haplogroups of domesticated chickens was highly consistent with the routes and times of human settlement, indicating that symbiotic animals such as domesticated chickens can be used as alternative indicators for tracking prehistoric human migrations. The genetic connection between Pacific domesticated chickens and the Philippines and Southeast Asian islands also supports the hypothesis that “humans and poultry migrated from west to east together”. Researchers did not find haplotypes of Pacific domesticated chickens in South American archaeological samples from before Columbus’ arrival, which challenges the claim that “Polynesians had early contact with South America” and also gives us a clearer understanding of the interaction history across the Pacific. The research conducted by Godinez et al. in 2021 and 2022 indicates that the systematic geographical study of the Pacific domesticated chickens not only reveals the domestication and spread history of domestic fowls but also provides a scientific basis for a more comprehensive understanding of how humans migrated, settled, and influenced the entire Pacific region.

8 Challenges and Future Prospects

8.1 Current research limitations and challenges

The research by Hibbins and Hahn in 2021 and by Bjornson et al. In 2024 indicates that “conflict signals” often occur in systems genome studies, making it difficult to reconstruct the evolutionary history of species. Most of these conflicts are caused by phenomena such as incomplete lineage separation, gene recombination, hybridization, and gene infiltration. Bravo et al. (2019) and Guo et al. (2022) hold that the existing analytical methods are still unable to handle these complex evolutionary processes well, and the traditional “evolutionary tree” model is also not applicable to those groups whose evolutionary processes are more like a “network structure”. McKain et al. (2018) and Young and Gillung (2019) found that how to correctly determine which genes are directly homologous, how to select appropriate models, how to design sequencing schemes, and how to deal with large and complex data are common problems encountered in research. These challenges are not easy for both beginners and experienced researchers. McKain et al. (2018) and Bravo et al. (2019) hold that there are also problems in the integration and reuse of many genomic data at present. From sample collection, data analysis to the final release, the entire process still lacks a unified platform or network system to be connected, which affects the research efficiency.

8.2 Future directions for research development

Bjornson et al. (2024) demonstrated in their research that it is necessary to develop and apply some new methods, so as to better consider common but complex evolutionary processes such as hybridization, gene infiltration and horizontal gene transfer. This is helpful for breaking the limitations of the traditional “binary tree” model and understanding the real relationships between species more accurately. Guo et al. (2022) hold that conducting whole-genome sequencing is also very important, which enables researchers to select gene markers for analysis more flexibly and accurately in their studies and improve the overall quality of systems genome research. McKain et al. (2018) and Bravo et al. (2019) proposed that establishing an integrated platform covering specimen collection, data analysis and paper publication could also greatly simplify the scientific research process and promote cooperation among researchers. The research by Hibbins and Hahn in 2021 and that by Bjornson et al. in 2024 indicates that theoretical frameworks such as the multispecies coalescent model still need continuous improvement, and new analytical tools need to be developed to address the technical challenges encountered.

8.3 Strategic significance and future vision of phylogenomics research

Rodelsperger et al. (2019) and Guo et al. (2022) hold that systems genomics is of great significance in revealing deep evolutionary relationships and the origin of biodiversity. Its research achievements have significant impacts on ecology, agriculture and medicine, providing important assistance for a better understanding of the relationships among species and how they evolve. The research by McKain et al. in 2018 and by Bravo et al. in 2019 indicates that a more integrated, collaborative and methodistic research system should be established in the future to address the complex issues in the history of life evolution.

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Conflict of Interest Disclosure

The author affirms 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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