



Domestic chicken diversity: Origin, distribution, and adaptation

R. A. Lawal^{*,†}  and O. Hanotte^{*,‡,§}

^{*}Cells, Organisms and Molecular Genetics, School of Life Sciences, University of Nottingham, Nottingham NG7 2RD, UK. [†]The Jackson Laboratory, 600 Main Street, Bar Harbor, ME 04609, USA. [‡]Centre for Tropical Livestock Genetics and Health, The Roslin Institute, Edinburgh EH25 9RG, UK. [§]LiveGene, International Livestock Research Institute (ILRI), P.O. 5689, Addis Ababa, Ethiopia.

Summary

Chicken is the most numerous among the domesticated livestock species. Across cultures, religions, and societies, chicken is widely accepted with little or no taboo compared to other domestic animals. Its adaptability to diverse environmental conditions and demonstrated potential for breeding improvement provide a unique genetic resource for addressing the challenges of food security in a world impacted by climatic change and human population growth. Recent studies, shedding new knowledge on the chicken genomes, have helped reconstruct its past evolutionary history. Here, we review the literature concerning the origin, dispersion, and adaptation of domestic chicken. We highlight the role of human and natural selection in shaping the diversity of the species and provide a few examples of knowledge gaps that may be the focus of future research.

Keywords divergence time, domestication, *Gallus*, junglefowl, Mendelian trait, Migration, Phylogeny

Introduction

The domestic chicken belongs to the genus *Gallus*, which includes four morphologically distinct species (Delacour 1977; McGowan & Kirwan 2020): (i) the Red junglefowl *Gallus gallus* (Linnaeus 1758), which has a geographic distribution spanning continental South and South-East Asia, including Sumatra and Java; (ii) the Grey junglefowl *Gallus sonneratii* (Temminck 1813) found in West and South India; (iii) the Ceylon or Sri Lanka junglefowl *Gallus lafayettii* (Lesson, 1831) endemic to Sri Lanka; and (iv) the Green junglefowl *Gallus varius* (Shaw, 1798) found in Java and neighbouring Indonesian Islands including Bali, Lesser Sundas East to Flores, Sumba, and Alor (see geographic distribution in Fig. 1).

The Red junglefowl is polytypic with five recognised subspecies: (i) *G. g. murghi* (Robinson & Kloss 1920) found in Kashmir, north and north-east India, Nepal, Bhutan, and Bangladesh; (ii) *G. g. spadiceus* (Bonnaterre, 1792) in extreme north-west India (east Arunachal Pradesh, east Assam),

Myanmar, Southwest China (Southwest Yunnan), Thailand, Peninsular Malaysia, and North Sumatra; (iii) *G. g. jabouillei* (Delacour & Kinnear 1928) in South China (south-east Yunnan, Guangxi, and Hainan Island), North Laos, and North Vietnam; (iv) *G. g. gallus* (Linnaeus 1758) in East Thailand, Cambodia, central and south Laos, and central and south Vietnam; and (v) *G. g. bankiva* (Temminck 1813) in East Java. Variations in the plumage colour and length, and the shape of male hackles are distinguishing features across these subspecies. Also, the colour of ear-lappets is red in *G. g. spadiceus* and *G. g. jabouillei* but white in *G. g. murghi* and *G. g. gallus* (Delacour 1977; Madge & McGowan 2002). McGowan & Kirwan (2020) illustrate the five *G. gallus* subspecies with their distinct subtle plumage differences. The current geographic distribution of different Red junglefowl subspecies and the extent of their hybridisation at their geographic zones of contact requires further investigation (Nishida *et al.* 2000). The Red junglefowl populations in the Philippines, Sulawesi, and parts of Lesser Sunda Islands might be feral, following past human-mediated translocation. Also, across Micronesia, Melanesia, Polynesia, Reunion, the Grenadines, and possibly New Zealand and South Africa, several feral populations of the Red junglefowl have been reported (McGowan & Kirwan 2020).

Address for correspondence

R. A. Lawal, The Jackson Laboratory, 600 Main Street, Bar Harbor, ME 04609, USA.

E-mail: lawalakinyanju@yahoo.com

O. Hanotte, Cells, Organisms and Molecular Genetics, School of Life Sciences, University of Nottingham, Nottingham, NG7 2RD, UK.

E-mail: olivier.hanotte@nottingham.ac.uk

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Phylogeny and divergence between species

A recent genome-wide level evolutionary study shows a sister relationship between the Grey and the Ceylon

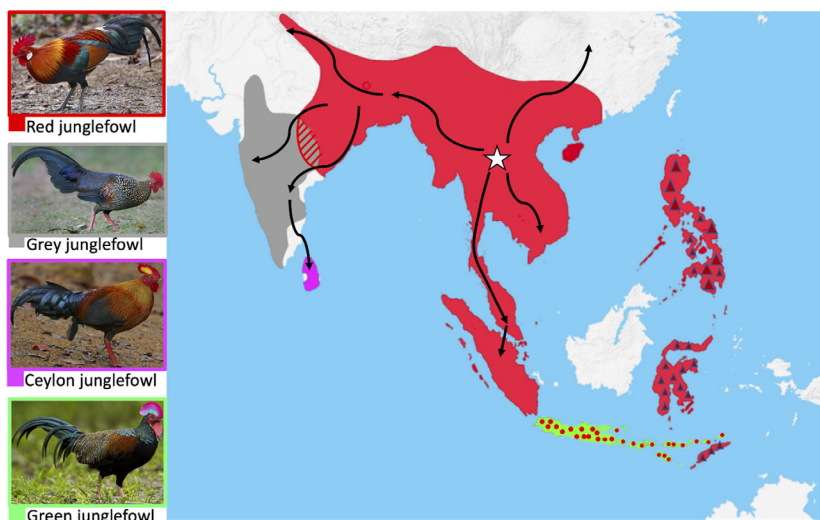


Figure 1 Map showing the geographic distribution of the junglefowls species across Asia, adapted from Lawal *et al.* (2020) (<http://creativecommons.org/licenses/by/4.0>), based on the information from 'Birds of the World' (consulted on 27 April 2021). The sympatric distributions of Red junglefowl with the Grey junglefowl and of Red junglefowl (possibly feral populations) with Green junglefowl are denoted with red stripes and red dots respectively. See main text for the distribution of the five Red junglefowl subspecies. The white star ☆ represents the domestication from *Gallus gallus spadiceus* in South-East Asia (Wang *et al.* 2020). Triangles ▲ denote possible feral Red junglefowl populations (Philippines, Sulawesi, and Timor). The arrows illustrate the dispersion of domestic chicken across Asia. Junglefowl species photo credits: Peter Ericsson (Red junglefowl), Clement Francis (Grey junglefowl), Markus Lilje (Ceylon junglefowl), and Eric Tan (Green junglefowl).

junglefowls, with a common ancestor of ~1.8 mya. It also indicates a common ancestor between the Red junglefowl and these two species of ~2.6 to 2.9 mya and that the Green junglefowl is the oldest *Gallus* lineage with a divergence time of ~4 mya (Lawal *et al.* 2020). This phylogeny, (see also Tiley *et al.* 2020), differs from most of the previous ones inferred from short nuclear genome fragments and mitochondria DNA (mtDNA), which rather support a sister relationship between the Grey and the Red junglefowls (e.g. Eo *et al.* 2009; Li *et al.* 2015) or between the Green and the Red junglefowls (e.g. Jetz *et al.* 2012). It also differs from other alternative topologies including the placement of Red junglefowl at the basal of the *Gallus* tree (Fig. 2). Interestingly, the species relationship of topology T9, also highly supported in Lawal *et al.* (2020), is the one favoured in the recent genome-wide study of Mariadassou *et al.* (2020). The dating of shared ancestry between the species lineages is also uncertain, with more ancient divergence times than those in Lawal *et al.* (2020), reported in other studies (see TimeTree, www.timetree.org).

A genome-wide genetic relationship between different Red junglefowl subspecies has also been reported (Wang *et al.* 2020). Among these five subspecies, *G. g. bankiva* is the most ancient subspecies, with a divergence time of ~0.5 mya. The remaining four subspecies diverged from each other around 50 000–125 000 years ago, with *G. g. murgli* and *G. g. jabouillei* genetically closer to each other than to *G. g. gallus* and *G. g. spadiceus*, and with little genetic differentiation between *G. g. gallus* and *G. g. spadiceus* (Wang *et al.* 2020). It is also possible that

several species or subspecies within the genus *Gallus* are now extinct, with such missing evolutionary links holding the key to our complete understanding of the evolutionary history of the genus *Gallus*.

Domestication and dispersal across the globe

The scientific naming of the domestic chicken as *Gallus gallus domesticus*, rather than *Gallus domesticus*, follows the substantial morphological and behavioural evidence supporting the Red junglefowl *G. gallus* as the primary ancestor of the domestic form (Darwin 1859). Charles Darwin refers to Blyth when stating "...that all breeds of poultry have proceeded from the common wild Indian fowl (*Gallus bankiva*)" (Darwin 1859). While further discussing chicken's origin in his book on 'The Variation of Animals and Plants under Domestication' (Darwin 1868), he concluded, "...that not only the Game-breed but that all our breeds are probably the descendants of the Malayan or Indian variety of *G. bankiva*". The species name *G. bankiva* for the Red junglefowl was subsequently replaced with *G. gallus*, following the priority's rules for species nomenclature.

The process of chicken domestication probably followed a commensal route (Larson & Burger 2013), with the wild birds foraging in areas close to human settlements. The primary reason for its domestication remains unclear. In the absence of evidence for domestication for meat or egg consumption (Lawler 2014), early farmers probably preferred them for aesthetic, socio-cultural, and/or recreational purposes. Genome-wide studies support domestication

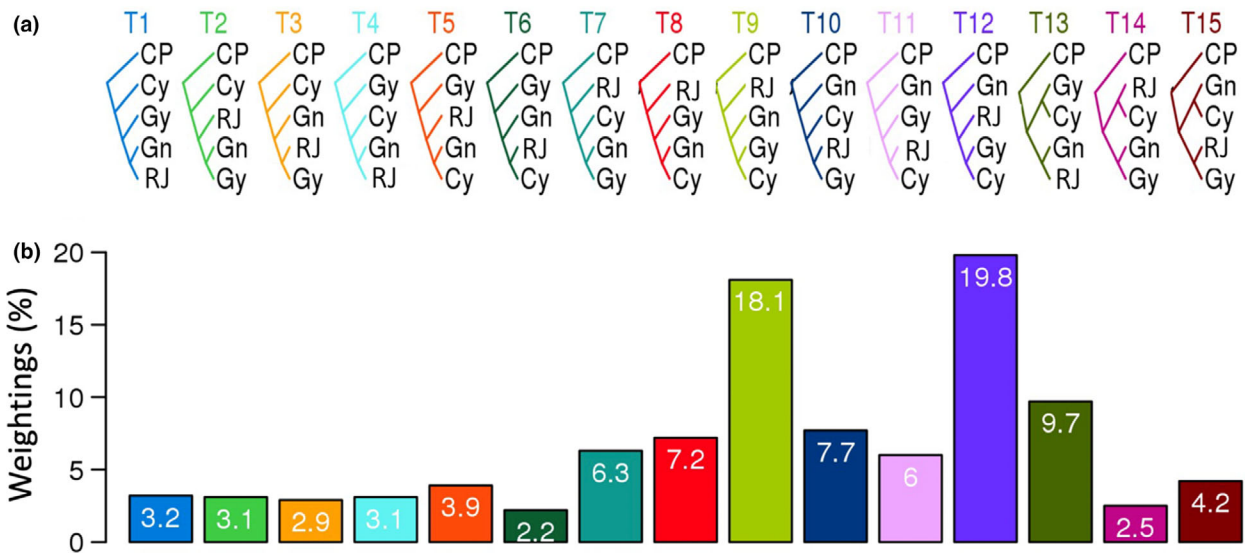


Figure 2 Topologies weighting (Martin & Van Belleghem 2017) for the relationships within the genus *Gallus*, adapted from Lawal *et al.* (2020). (a) The 15 possible topologies (T1–T15) from five taxa [Red junglefowl (RJ), Grey junglefowl (Gy), Ceylon junglefowl (Cy), Green junglefowl (Gn), and common pheasant (CP)]. (b) Average weightings (%) for each of the 15 topologies indicated in each bar.

during the Neolithic time ~8000 years ago (confidence interval: 7014–8768) (Lawal *et al.* 2020) or ~9500 ± 3300 years ago (Wang *et al.* 2020).

Identification of geographic centre(s) of origin(s) for domestic chicken is challenging. Differentiating the bones of domestic chicken from those of the wild *Gallus* or other Phasianidae species is difficult. Several wild species of Phasianidae live sympatrically across Asia and across the present-day geographic distribution of the Red junglefowl (Delacour 1977; Madge & McGowan 2002). A study examining osteological material and ancient mtDNA proposed the domestication of the chicken in the North China plains around 10 000 years ago (Xiang *et al.* 2014). However, this has now been disputed by several studies challenging the species identification of the bones, the genetic information provided, and in light of the climate in north China at the time, which may not have been suitable for the wild Red junglefowl (Peng *et al.* 2015; Peters *et al.* 2015; Xiang *et al.* 2015). Also, the earliest farmers of Northwest China probably exploited grain-fed pheasant *Phasianus colchicus* and not chicken (Barton *et al.* 2020).

Equally challenging is the interpretation of genetic information. Here, it is worth remembering that: (i) the present genetic diversity of modern domestic chicken may represent only a subset of its past diversity, with the recent movements and dispersions of domestic chicken having erased the genetic signatures of more ancient ones; (ii) introgression between the wild Red junglefowl and domestic chicken might have blurred the ancestral diversity of the Red junglefowl population (e.g. Berthouly *et al.* 2009, Wu *et al.* 2020); and (iii), as mentioned above, hybridisation is likely among the Red junglefowl subspecies following their

overlapping geographic distribution, e.g. between the *G. g. gallus*, *G. g. spadiceus* and *G. g. jabouillei* in Southeast Asia (Delacour 1977).

Early studies to determine the centre(s) of chicken domestication were based on mitochondrial DNA (mtDNA) analysis, including those supporting a single geographic origin (from *G. g. gallus* in Thailand) (Fumihito *et al.* 1994; Fumihito *et al.* 1996) or multiple domestication centres (e.g., Indian subcontinent and Southeast Asia) (Liu *et al.* 2006; Kanginakudru *et al.* 2008; Miao *et al.* 2013). They all excluded the maternal contribution of *G. g. bankiva* to domestic chicken ancestry. Recently, an autosomal genome-wide investigation involving 863 domestic chicken and the five wild Red junglefowl subspecies shows strong support for *G. g. spadiceus*, native to southwestern China, northern Thailand, and Myanmar, as the main ancestral subspecies of modern Asian domestic chickens. Subsequently, chicken dispersed across Southeast and South Asia (Fig. 1), where they interbred locally with other Red junglefowl subspecies (Wang *et al.* 2020). Whether this domestication scenario applied to all domestic chickens across the world remains to be investigated, with, for example, only a few European and no African domestic chickens included in the study. Ancient DNA analysis may further clarify the past evolutionary history of the species (Frantz *et al.* 2020).

From its centre(s) of domestication in Asia, chicken colonised the world through human migrations, terrestrial, and maritime trading routes. Perry-Gal *et al.* (2015) proposed three phases of domestic chicken dispersion towards Europe: (i) domestication of Red junglefowl within its natural range; (ii) dispersion of domesticated chickens

towards West Asia; and (iii) introduction of domestic chicken in Europe following the intensification of its use as domestic poultry for food production. Chicken husbandry was common on the Indian subcontinent, a postulated centre of domestication, by the 3rd millennium BC (Fuller 2006). The earliest chicken remains in the Near East are found in Iran (3900 BC), Turkey and Syria (2400–2000 BC), and Jordan (1200 BC). In Egypt, the domestic chicken may have been introduced by 1120 BC or earlier (Redding 2015). During this period, chickens were probably not used intensively in the household for egg and/or meat consumption, but rather as an exotic animal for cockfighting and for displaying in the royal zoological gardens (Perry-Gal *et al.* 2015). In north and west Europe, chicken bones, present at a low proportion in archaeological sites around the Mediterranean Basin (Spain, southern France, and Greece), are dated to the late 9th and 8th century BC (Perry-Gal *et al.* 2015). In Britain, the earliest confirmed osteological record of chicken is dated between cal 770 and 390 BC (Kitch 2006).

In Africa, domestic chicken entered the continent following terrestrial (*via* Egypt) and maritime, along the Red Sea coast and the Horn of Africa, routes (Woldekiros & D'Andrea 2016). While Egypt provides the earliest iconographic evidence of domestic chicken (Mwacharo *et al.* 2013), the oldest African chicken bones, dated to cal 820–595 BC (indirect/charcoal AMS cal 921–801 BC), are found in Ethiopia at the Mezber site (Tigray region) (Woldekiros & D'Andrea 2016). Their association to domestic food waste in the early rural settlement at Mezber, and their presence in later Aksumite urban contexts, show that chickens might have been relatively common. Chickens were a significant component of the Iron Age economy in West Africa by the sixth century AD. In East Africa, chickens were well established by 800 AD (Mwacharo *et al.* 2013).

Analysis of modern domestic chicken genetic diversity provides some further insight into the history of dispersion of the species. In North and West Africa, mtDNA analysis indicates the predominant presence of a single haplogroup that probably originated from the Indian subcontinent (e.g. Adebambo *et al.* 2010; Hassaballah *et al.* 2015; Al-Jumaili *et al.* 2020; Boudali *et al.* 2020). Chicken dispersion in North Africa may have followed the terrestrial and the Mediterranean sea trading routes (Al-Jumaili *et al.* 2020). North–south trans-Saharan trading routes and movements along the Sahelian belt probably brought the domestic chicken to West Africa in pre-European times (Adebambo *et al.* 2010; Hassaballah *et al.* 2015).

MtDNA also supports at least two main origins of domestic chicken in the eastern part of the African continent (Mwacharo *et al.* 2013). The first wave may have followed maritime and terrestrial routes, which probably started on the Indian subcontinent. The second wave (around the mid-first millennium AD) saw the arrival

of chicken in the eastern African coast through maritime trading routes which may have brought chicken genetic diversity originally from Southeast and East Asia (Muchadeyi *et al.* 2008; Mwacharo *et al.* 2011; Lyimo *et al.* 2013; Prendergast *et al.* 2017). MtDNA diversity of indigenous chickens from Madagascar supports a maternal origin from the eastern part of the African continent rather than through direct maritime contact between Madagascar and the Indian subcontinent and/or the Indonesian Islands (Razafindraibe *et al.* 2008; Herrera *et al.* 2017). The Malagasy term for the chicken is borrowed from the Bantu languages of the eastern African coast (Blench 2010).

Eastward of the Red junglefowl geographic distribution, domestic chicken dispersed to the north, south, and east. In central and northern China, *Gallus*-type bones were initially reported widespread at Neolithic sites by the sixth/fifth millennium BC (West & Zhou 1988). However, a recent re-examination of the avian bones at these sites could only identify chicken bones at two sites, Xianwanggang (Henan Province) and Zhoujiazhuang (Shanxi Province), which are dated back to 3000–700 BC and 2300–1900 BC respectively (Eda *et al.* 2016). Domestic chickens are first documented in the Korean Peninsula ~2000 years ago (Hoque *et al.* 2013). Japanese native chickens have multiple origins. They were initially introduced *via* the Korean Peninsula during the Yayoi Era (300 BC to 300 AD), then from the Chinese Tang Dynasty during the Heian Era (794–1192), and from Thailand during the Edo Era (1603–1867) (Oka *et al.* 2007).

Across the Pacific Islands, ancient and modern mtDNA studies support a domestic chicken dispersion towards east, up to Easter Island, following the Polynesian and Melanesian expansions (Dancause *et al.* 2011; Storey *et al.* 2012). However, it remains unclear if chicken subsequently reached the southern American continent at a pre-Columbian time. A pre-Columbian Polynesian introduction of chickens to America was initially supported by radiocarbon dating and ancient DNA sequence information of a chicken bone from the archaeological site of El Arenal-1 on the Arauco Peninsula (Chile) (Storey *et al.* 2007; Storey *et al.* 2008). However, the evidence is now deemed inconclusive having been based on a single bone, non-diagnostic DNA sequence information, and in the absence of local isotopic standards to assess the relationships between diet and isotopic signatures (Gongora *et al.* 2008). A recent mtDNA analysis involving native chicken from six South American countries did not find any evidence for a maternal genetic relationship between the South American chicken and their counterparts in the Pacific Islands, including Easter Island (Herrera *et al.* 2020). This study rather supports a European or Asian origin for the modern native chicken of the South American continent (Herrera *et al.* 2020). Additional ancient DNA samples may further clarify the issue of the origin of South American chicken.

Phenotypic diversity and its genetic control

There are three major groups of domestic chicken: the commercial lines/strains; the indigenous village chicken; and the fancy chicken breeds. Commercial chickens are classified, based on their productivity traits, as broilers, egg-layers, or dual-purpose (egg and meat) (Crawford 1990). The indigenous village chickens are referred to as local, native, or non-descript or, in relation to their agro-ecologies, as ecotypes (Desta *et al.* 2013). Fancy chicken breeds are referred to as traditional or standard breeds (Scrivener 2006; Scrivener 2009).

The Red junglefowl shows a strong sexual dimorphism, with uniformity in plumage and morphology within both sexes. Only subtle morphological and plumage differentiation distinguish different subspecies (Delacour 1977; McGowan & Kirwan 2020). However, the process of domestication, which relaxed the constraints from natural selection on the morphology, plumage colour, and pattern of domestic birds and human preferences for new phenotypes led to allelic fixation within breeds defining their phenotypic standards (Scrivener 2006; Scrivener 2009). Today, the indigenous village chicken populations often display a vast array of phenotypes with differences in plumage colour and pattern, size, comb shape, earlobe colour, and skin colour among adult birds (e.g. Dessie *et al.* 2011; Desta *et al.* 2013; Bett *et al.* 2014).

Increasingly, the genetic controls of morphological and plumage diversity of domestic chicken are being unravelled. Commercial chicken productivity traits (e.g. egg number, growth rate, feed conversion ratio) are under the genetic control of many quantitative trait loci (Hu *et al.* 2019). Many examples of phenotypic diversity controlled by loci with major effects are now known and reported at the Online Mendelian Inheritance in Animals database (<https://omia.org/>, accessed on 12 February 2021). These include plumage colour (e.g. white, lavender, chocolate, silver, Henny feathering), feather colour pattern (mottling, barred), feather structure (frizzle, silkie, naked neck), comb morphology (rose, pea, duplex), size (dwarfism), skin colour (yellow, black, green), feather growing (muffs and beard, ear-tuff, crest), and eggshell colouration (blue). Causative polymorphisms for these Mendelian traits include missense and nonsense mutations (stop/gain), insertion/deletion, duplication, inversion, copy-number variant, alternative splicing, and complex rearrangement involving several distinct polymorphisms. For example, the genetic control of autosomal dwarfism is linked to a loss-of-function variant in the transmembrane protein gene, *TMEM363*, leading to approximately 30% growth reduction (Wu *et al.* 2018). The genetic control and molecular mechanism of blue egg colouration, an autosomal dominant phenotype of some South American (e.g. Araucana) and Asian (e.g. Dongxiang, Lushi) breeds, has

now been identified (Wang *et al.* 2013; Wragg *et al.* 2013). An endogenous avian retroviral (EAV-HP) insertion is responsible for the phenotype with the over-expression of a solute carrier (*SLCO1B3*) involved in the transport of bile salts (biliverdin). The over-expression in the shell gland and oviduct is under the control of the retrovirus promoter (Wang *et al.* 2013; Wragg *et al.* 2013). Interestingly, this retroviral insertion occurred independently on the South American and Asian continents (Wragg *et al.* 2013). This example highlights the genetic contribution of retroviral insertions in the phenotypic diversity of domestic chicken. The rooster's comb morphology is providing several examples of the role of structural variants in shaping the chicken phenotypic diversity (Headon 2015). An approximately 30-fold expansion of a tandem duplication found near a non-coding sequence of the *SOX5* transcription factor is responsible for the pea-comb phenotype (Wright *et al.* 2009). The rose-comb is the result of a large chromosomal inversion spanning a 7.4 Mb region of chromosome 7, leading to *MNR2* expression (Imsland *et al.* 2012). The duplex-comb involves a 20 kb tandem duplication within an intron of *CMC1* (Dorshorst *et al.* 2015).

Finally, while the Red junglefowl is the main ancestral contributor to chicken genetic diversity, we now know that post-domestication events involving crosses with other junglefowl species took place (Eriksson *et al.* 2008; Lawal *et al.* 2020). Lawal *et al.* (2020) were the first to show introgression from the four junglefowl species into the domestic chicken gene pool. The absence of mtDNA of Grey junglefowl, Ceylon junglefowl, and Green junglefowl into domestic chicken supports a male-mediated introgression process at the F1 generation (Lawal *et al.* 2020). All these studies so far support a relatively small contribution of these introgression events into the genetic diversity of modern domestic chicken. Nevertheless, domestic chickens across the world may have been differently affected by such introgression episodes (Lawal *et al.* 2020), which probably correlated with the geographic distribution of the four *Gallus* species and the dispersion routes of domestic chickens.

The yellow skin phenotype remains the most compelling example of a phenotype linked to a *Gallus* species introgression into the domestic chicken (Eriksson *et al.* 2008). It is under the genetic control of a recessive regulatory mutation inhibiting the expression of *BCDO2* (β -carotene dioxygenase) in the skin. It probably originates from the Grey junglefowl (Eriksson *et al.* 2008). The diversity of domestic chicken feather colour and pattern is extremely large, and the four species within the genus *Gallus* are recognised easily through their distinct plumages and morphologies. Therefore, it is tempting to hypothesise that some domestic chicken phenotypes may have originated from similar introgression episodes.

Chicken genome diversity

The chicken karyotype includes 78 chromosomes ($2n$) (Pollock & Fechheimer 1976), which are conventionally classified as macrochromosomes (MACs) and microchromosomes (MICs), depending on their lengths. Being larger than 40 Mb in size, chromosomes 1–5 are generally considered MACs, chromosomes 6–12 are classified as ‘intermediate’ and the remainder being MICs. The female chicken is the heterogametic (ZW) sex, while the male is the homogametic (ZZ) sex. The chicken genome assembly was first reported in 2004 (Hillier *et al.* 2004). It was the first avian and livestock species whose genome sequence was assembled, and it served as a reference genome for the exploration of other bird genomes (Schmid *et al.* 2000, 2005, 2015). The *de novo* genome assembly was derived from a single female individual from an inbred strain (line UCDO01) of Red junglefowl. Over the last 15 years, four different versions of the chicken genome assembly of improved quality were released. The latest is GRCg6a, released on 27 March 2018. GRCg6a has a total sequence length of around 1.07 Gigabase encompassing 16 878 coding genes with 39 288 gene transcripts along with 7166 non-coding genes (https://www.ensembl.org/Gallus_gallus/Info/Annotation, accessed on 12 February 2021). It includes a total of 524 scaffolds with 68 genome gaps and 1402 contigs representing all the MACs, most of the MICs and the sex chromosomes (see the global statistics at https://www.ncbi.nlm.nih.gov/assembly/GCF_000002315.5/). Since then, hundreds of shot-read whole-genome sequences from different local and commercial chicken breeds have been made publicly available and accessible in the Sequence Read Archive (<https://www.ncbi.nlm.nih.gov/sra>), European Nucleotide Archive (<https://www.ebi.ac.uk/ena/browser/home>), and DNA Data Bank of Japan sequence reads archive (<https://www.ddbj.nig.ac.jp/dra/index-e.html>). Also, *de novo* genome assemblies for a broiler and a layer chicken are now available through NCBI, accession numbers GCA_016699485.1 and GCA_016700215.1 respectively.

Millions of polymorphic variants have also been reported in domestic chickens and wild relatives. Approximately 17 million SNPs, corresponding to ~16 SNPs/kb and including ~13% novel variants, were identified in 27 geographically diverse indigenous village chickens (Lawal *et al.* 2018). When combined with the genomes of the four *Gallus* species and an outgroup (common pheasant *Phasianus colchicus*), it yields a total of 91 million variants from 87 genomes (Lawal *et al.* 2020). Similarly, Qanbari *et al.* (2019) uncovered more than 21 million SNPs, including 34% novel variants, in 127 chicken genomes, including Red junglefowl and populations of commercial broilers and layers. Around 33 million non-redundant SNPs have also been reported from 863 genomes (167 wild junglefowl and 696 domestic chicken) (Wang *et al.* 2020).

A total of 12 783 QTL representing 430 different traits have now been documented (<https://www.animalgenome.org/cgi-bin/QTLdb/GG/index>, accessed on 12 February 2021). The Online Mendelian Inheritance in Animals database (<https://omia.org/>, accessed on 2 March 2021) includes 223 chicken Mendelian traits, 51 known causal genetic variants, and 53 traits of relevance as models for human diseases.

The selection process for adaptive, production preferred human phenotypes and breeding management practices has shaped the genetic makeup and diversity of chicken populations. Muir *et al.* (2008) were the first to assess the genetic diversity of several inbred lines of chicken ($n = 2580$) using a commercial SNP genotyping array. They showed that more than 50% of the ancestral genetic diversity was lost in the commercial lines compared to the experimental lines and standard breeds. The most extensive study so far compared the diversity of 3235 individuals from 162 populations (32 countries from Africa, South America, Asia, and Europe) and 12 commercial purebred lines (four white egg layers, four brown egg layers, and four broilers), as well as two populations of Red junglefowl (*G. g. gallus* and *G. g. spadiceus*) using a genotyping array encompassing 580K SNPs (Malomane *et al.* 2019). All these studies indicate that the process of artificial selection leads to a significant loss of chicken genetic diversity. In particular, Malomane *et al.* (2019) show that many of the fancy breeds have reduced within-population genetic diversity and that the genetic diversity is low in the highly selected commercial layer lines. This study clusters the brown egg-layers and broiler chickens separately from the white egg-layers, with the latter grouped with the European breeds. Finally, Asian domestic chickens are grouped with the wild Red junglefowl populations rather than the European breeds (see figure 1 in Malomane *et al.* 2019). Whole-genome sequence analyses support these observations with, for example, high genetic diversity in several indigenous domestic chicken populations and Red junglefowl (Lawal *et al.* 2018), higher diversity in Red junglefowl compared to egg-layer and broilers lines, and more diversity in broiler than layer lines (Qanbari *et al.* 2019).

Chicken adaptive traits

The domestic chicken has the largest geographic distribution among the domesticated species and a long history of adaptation to extreme habitats. Accordingly, its domestication and dispersion processes were accompanied by human and natural selection pressures which enhanced its adaptability to human societies and the environments.

One of the first genes to be reported under selection during chicken domestication is the thyroid stimulating hormone receptor (*TSHR*) locus (Rubin *et al.* 2010). The selection signature at this gene was initially linked to the improvement of domestic chicken productivity, possibly an

increase in egg production (Rubin *et al.* 2010; Loog *et al.* 2017), with possible pleiotropic effects, including in behavioural and environmental adaptive traits, considering the importance of the gene in hormonal pathways (Falahshahroudi *et al.* 2021). Signatures of selection at the *TSHR* locus have been detected in several populations of indigenous village chicken living in different agro-ecologies (Lawal 2018; Lawal *et al.* 2018).

In the high-altitude Tibetan plateau, the domestic chicken faces extreme hypoxia conditions, low-temperature, and ultraviolet radiation (Wang *et al.* 2015; Zhang *et al.* 2016). By comparing four highland and four lowland chicken populations, Zhang *et al.* (2016) show that genes under positive selection in the highland populations are specifically linked to cardiovascular and respiratory system development, DNA repair, response to radiation, inflammation, and immune response. These biological responses could be expected for organisms adapted to these environmental conditions.

Domestic chicken can also survive food and water scarcity and have developed resistance to parasitic infection (Bettridge *et al.* 2018; Ibeagha-Awemu *et al.* 2019). Evidence also shows a strong selection to hot climates in the Middle East, Africa, and Asia (Lawal *et al.* 2018; Walugembe *et al.* 2018). A recent study using 245 whole-genome sequences of Ethiopian indigenous village chicken from 25 geographically diverse populations under 34 different agro-ecological and climatic variables also found genomic regions under positive selections associated with altitude-induced stresses, water scarcity, and the challenge of scavenging feeding behaviour (Gheyas *et al.* 2021). This study uses an integrative approach combining ecological niche modelling and genome association analysis with environmental variables. It represents the most comprehensive study so far on chicken environmental adaptation.

While the above describes adaptation mainly specific to domestic chicken populations, there is evidence of shared adaptive evolution with the ancestral wild Red junglefowl, including, for instance, cockfighting behavioural ability and the rooster's aggressiveness (Guo *et al.* 2016; Lawal *et al.* 2018; Luo *et al.* 2020). It may also be argued that some of the domestic chicken adaptations to high temperatures may have their origin in the tropical Red Junglefowl.

Perspectives

The advent of genomics in poultry is rapidly changing our knowledge of the origin, diversity, and history of domestic chicken. More investigations to unravel the distribution of domestic chicken diversity, its adaptation to its local environment is expected. However, understanding the evolution of domestic chicken across time will be likely to remain challenging with a paucity of poultry zoo-archaeological materials. A combination of modern and ancient genetic studies, historical documents,

archaeological investigations, and inferences about the importance of chicken husbandry across human societies may provide some insights. The large phenotypic diversity of chicken, the allelic fixation in some fancy breeds, and the segregation in other populations, including in the indigenous village chicken flocks, have elevated the species as a model organism for studying the genetic control of avian Mendelian traits. Further breakthroughs may be expected through comparative genomics studies as the number of new chicken whole-genome sequences increase.

Potential questions for future investigations

The indigenous village chicken, scavenging under the extensive and semi-intensive production systems across the African and Asian continents, provides an opportunity to understand the mechanisms of adaptation to local environments. One area of interest is the understanding of how climate change may generate new adaptive responses across chicken populations. To what extent does adaptation to the local environment shape the observed morphology, physiology, behaviour, and productivity in chicken populations? These interesting questions require insight from both genetics and epigenetic mechanisms. Furthermore, domestic chickens are found across different agro-ecological conditions, and thus, may harbour different infectious pathogens and parasites. What are the genetic and non-genetic strategies underlying tolerance and resistance to diseases and parasites in the domestic chicken? What are the roles and importance of the chicken gut microbiome in relation to chicken adaptation to local environments, and more broadly, to its physiological phenotypes? These questions will attract the attention of researchers in the coming years.

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Conflict of interest

The authors declare no conflict of interest.

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