doi:10.1017/S0043933915000318

The role of mitochondrial DNA to determine the origin of domestic chicken

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Mitochondrial DNA (mtDNA) is has recently lost relevance especially when utilised to study species that are characterised with a history of several migrations. Nonetheless, mtDNA can still represents a useful additional tool in the study of molecular genetic diversity. The reason for the adoption of mtDNA is that it is easy to amplify because it appears in multiple copies in the cells and the mitochondrial gene content is strongly conserved across generations. Thousands of published studies have reached conclusions about population history, patterns of gene flow, genetic structure, and species limits, on the basis of mtDNA sequence variation. MtDNA has been used to study phylo-geographic structure of avian species, and to identify the number of maternal lineages and their geographic origins. Most studies of chicken mtDNA rely on sequences of partial control region but recent researches used the complete mtDNA genome to reconstruct the history of animal domestication. The first genetic study on mtDNA suggests that the Indochinese Red Junglefowl subspecies *Gallus gallus gallus* is the primary ancestor of the domestic chicken (*Gallus gallus domesticus*). Other studies showed that at least three subspecies of *Gallus gallus* were enrolled in the origin of domestic chicken breeds, and that there may be at least two domestication centres: one in Southeast Asia and one in the Indian subcontinent. The authors suggested nine highly divergent clades (named clade A-I) related to geographical distribution in a wide range of domestic chickens and Red Junglefowls across Eurasian regions. Understanding when chickens were transported out of domestication centres and the directions in which they were moved provides information about prehistoric human migration, trade routes and cultural diffusion. MtDNA has been used to infer regions of domestication and to identify the number of maternal lineages and their geographic origins in macroevolution studies.

Keywords: molecular markers; maternal lineage; phylogeographic structure; animal domestication

World's Poultry Science Journal, Vol. 71, June 2015
Received for publication July 28, 2014
Accepted for publication February 6, 2015

Introduction

The chicken has a long history of anthropomorphic usage in Southeast and East Asia, where it has been bred for entertainment and show (Macdonald and Blench, 2000). The origin and domestication of chickens has been of interest to people since at least Roman times (Storey *et al.*, 2012). Based on archaeological and historical evidence the domestication of the fowl is thought to have occurred in multiple, independent centres. Archaeological research has identified centres of chicken domestication in India and China; both within the natural range of wild Junglefowl (Crawford, 1990).

Chickens were likely domesticated from wild Red Junglefowl, though some have suggested possible genetic contributions from other Junglefowl species (Eriksson *et al.*, 2008; Nishibori *et al.*, 2005). Darwin (1896) was the first to propose that all domestic fowls descended directly from one common ancestor; the *Gallus Bankiva*, or wild Junglefowl breed that originated in Eastern and Southern Asia. He came to this conclusion based on comparisons of morphology and progeny produced from crosses between various species of Gallus. The genus Gallus consists of four species, Red Junglefowl, Grey Junglefowl (*Gallus sonnerati*), Green Junglefowl (*Gallus varius*), and Ceylon Junglefowl (*Gallus lafayetii*) (Delacour, 1977; Sibley and Ahlquist, 1990; Johnsgard, 1999). Based on the morphological differences and geographical distributions, the Red Junglefowl is further subdivided into five subspecies, *Gallus gallus gallus* (Red Junglefowl gal), *Gallus gallus spadicus* (Red Junglefowl spa), *Gallus gallus banchiva* (Red Junglefowl ban), *Gallus gallus jabouillei* (Red Junglefowl jab), and *Gallus gallus murgi* (Red Junglefowl mur) (Johnsgard, 1999). Zoologists at the time of Darwin had reservations on giving consensus to the opinion that all our domestic chicken breeds owe their origin to the genus *Gallus Bankiva*; nonetheless it was acknowledged that a great majority of breeds known at the time are its descendants. With the advent of molecular biology techniques, DNA sequence-based phylogenetic analyses have been conducted. The most extensive of these DNA-based analyses examined the D-Loop region mitochondrial, and provided support for Darwin's conclusion that the chicken was established through domestication of Red Junglefowl (Fumihito *et al.*, 1996). This conclusion was supported by other studies using microsatellites DNA (Hillel *et al.*, 2003) and a large number of D-loop sequences (Liu *et al.*, 2006). Recently, the analysis of the entire mtDNA genome has demonstrated that domestic chickens and wild Junglefowl may have substantial gene flow and genetic admixture following the domestication. In other case, some domestic chickens might have become feral with their descendants living as wild fowl (Miao *et al.*, 2013). The various investigative techniques described above, do not substitute each other, but rather come together as different tools that complement each other in their specific specialisations to unravel the riddle of the history of domestication.

Understanding when chickens were transported out of domestication centres and the directions in which they drifted provides information about prehistoric human migration patterns, trade routes and cultural diffusion (Thomson *et al.*, 2014). Possible interactions may be reconstructed by mapping the presence of chickens in archaeological assemblages (Storey *et al.*, 2008) using historical evidence (Peters, 1913; Crawford, 1984) also thought the mtDNA application (Liu *et al.*, 2006, Miao *et al.*, 2013).

Mitochondrial DNA is a useful marker to trace back the origin of livestock species and has been widely used to reconstruct domestication patterns (Groeneveld *et al.*, 2010). Microsatellites (SSR) and mitochondrial DNA (mtDNA) sequences have already proved to be useful for assessing genetic variability, while single nucleotide polymorphisms (SNPs) are becoming more and more popular due to their very density and availability of high throughput genotyping techniques. A combination of SSR and

mtDNA markers is a complementary approach that combines the highly polymorphic microsatellites whose high mutation rates allow for small scale resolution of more recent demographic event with mtDNA which shed light on phylogeographic events dating back further in time (Feulner *et al.*, 2004). Microsatellites have been used to asses genetic diversity of a number of native chicken population in Africa (Leroy *et al.*, 2012; Goraga *et al.*, 2012; Eltanany *et al.*, 2011), Europe (Ceccobelli *et al.*, 2013; Wilkinson *et al.*, 2012; Zanetti *et al.*, 2011; Bodzsar *et al.*, 2009) and Asia (Pham *et al.*, 2013; Cuc *et al.*, 2010; Berthouly *et al.*, 2009; Ngo Thim *et al.*, 2006). The first chicken genome sequence draft was completed in 2004 (International Chicken Consortium, 2004); its availability offers new opportunities in the evaluation of chicken genetic diversity using SNPs (Gholami *et al.*, 2014; Granevitze *et al.*, 2014; Siwek *et al.*, 2013; Groenen *et al.*, 2009; Muir *et al.*, 2008). The inheritance of mtDNA differs from that of nuclear DNA in that it has a direct lineage to the ancestral mother. The reason for this maternal inheritance pattern is that when an egg is fertilised, the cells of the resulting embryo contain the mtDNA and cytoplasm of the egg, not of the sperm. As the embryo continues to develop all of the cells contain the cytoplasm and mtDNA of the ancestral mother. The reason for the popular adoption of mtDNA markers is that it is found in great abundance in cell cytoplasm and hence easily amplified (Galtier *et al.*, 2009). Furthermore, across a wide range of animal species, the mitochondrial gene content is strongly conserved, has little duplication, has no intron, and has very short intergenic regions (Gissi *et al.*, 2008). The mtDNA also has specific biological properties, *i.e.* its direct link to its ancestral maternal inheritance and its involvement in metabolic functions that make it an appropriate marker of molecular biodiversity. Lastly, it is worth noting that mtDNA is of little use in investigating recent loss of genetic variation and any individual-level events such as identity, individual dispersal, and mating systems. Males will carry the mtDNA of their dam, but their offspring will carry the mtDNA of their own mother, and not of their father. Thus, only daughters will pass the mtDNA on to future generations.

Numerous published studies have reached conclusions about population history, patterns of gene flow, genetic structure, and species limits, on the basis of mtDNA sequence variation (Zink and Barrowclough, 2008). MtDNA has been used to study phylo-geographic structure of avian species (Ceccobelli *et al.*, 2013), to infer regions of domestication and to identify the number of maternal lineages and their geographic origins (FAO, 2007). The huge abundance of mtDNA makes it an excellent candidate for archaeological studies that are often old or degraded samples.

Evolution of mt-DNA studies in chicken

A large amount of research has focused on reconstructing the matrilineal history of domestic chickens using mtDNA sequence data. Chicken mtDNA sequence polymorphisms have been investigated to address the questions of maternal origin and subsequent domestication events (Silva *et al.*, 2008). It is widely accepted that within and between populations genetic diversity is essential for effective management practices and to develop sustainable conservation strategies. Most studies of chicken mtDNA rely on sequences of partial control region (Muchadeyi *et al.*, 2008; Razafindraibe *et al.*, 2008) but recent researches used the complete mtDNA genome to reconstruct the history of animal domestication, such as in cattle (Achilli *et al.*, 2008; 2009; Bonfiglio *et al.*, 2010), pigs (Wu *et al.*, 2007), chicken (Miao *et al.*, 2013) and sheep (Lancioni *et al.*, 2013). As already alluded two different hypotheses are discernible about the origin of domestic chickens. Initially, it was suggested that one sub-species of Red Junglefowl (*Gallus*

gallus gallus) was the main progenitor of all domestic chickens and the centre of domestication event was in Southeast Asia (Fumihito *et al.*, 1996). Later on, other studies revealed that chickens have also been domesticated from multiple geographic centres of origin in South and Southeast Asia, (Kanginakudru *et al.*, 2008; Oka *et al.*, 2007). Furthermore, interspecies introgressions have also occurred from the related Grey Junglefowl (*Gallus sonnerati*) and possibly from Ceylon Junglefowl (*Gallus lafayeti*) during the domestication process (Eriksson *et al.*, 2008).

The first genetic study on mtDNA suggest that the Indochinese Red Junglefowl subspecies *Gallus gallus gallus* is the primary maternal ancestor of the domestic chicken (*Gallus gallus domesticus)* (Fumihito *et al.*,1994). Liu *et al.* (2006) showed that at least three subspecies of *Gallus gallus* were enrolled in the origin of domestic chicken breeds, but also that there may be at least two domestication centres: one in Southeast Asia and one in the Indian subcontinent. The authors suggested nine highly divergent clades (named clade A-I) related to geographical distribution in a wide range of domestic chickens and Red Junglefowls across Eurasian regions. The study, involved 834 mtDNA sequences from domestic chickens and 66 mtDNA sequences from four Red Junglefowl subspecies (mainly *Gallus gallus spadiceus, Gallus gallus gallus, Gallus gallus jabouillei* and *Gallus gallus bankiva*), and identified a total of 169 different haplotypes clustered in nine highly divergent clades, named A to I, seven of them including both wild and domestic individuals. Clade E was the most ubiquitous, dominating in Europe, Middle East and India. Clades A and E were mainly distributed in South China and Japan; C clade was found in chickens from Japan and Southeast China, while F and G clades were only found in the northern part of Southeast China. Clade D could be associated to the distribution of game birds, used for cockfighting. Clade D was the most frequent in Red Junglefowl. Clade H was found only in Red Junglefowl and clade I was mainly present in Vietnam. Similarly, Oka *et al.* (2007) identified seven clades (named clade A-G) in Japanese chickens of which four clades A, B, C and E are identical to Liu's clades E, A, D and B, respectively. Additional data confirmed that domestication had occurred independently in different locations of Asia including India (Kanginakudru *et al.*, 2008). A later study concluded that clade D was also the second most frequent clade in India, after clade E. Furthermore, Eriksson *et al.* (2008) highlighted the hybrid origin of the domestic chicken, due to ancestral hybridisation involving the Grey Junglefowl (*Gallus sonneratii*). Three studies have made an attempt to address the origin of African village chickens through the analysis of partial mtDNA D-Loop sequences. Muchadeyi *et al.* (2008) observed two distinct haplogroups in Zimbabwe village chickens which they postulated came from Southeast Asia and the Indian subcontinent. Similarly, Razafindraibe *et al.* (2008) observed two haplougroups in Madagascar village chicken and speculated that one was of Indonesian and the other of African continental origin or an introgression from commercial lines. At the opposite a single haplogroup thought to be of Indian origin was observed in Nigeria village chickens by Adebambo *et al.* (2010), while no information is yet available for the East African region. Survey its genetic diversity and trace the history of domestication Miao *et al.* (2013) investigated a total of 4938 mitochondrial DNA fragments including 2843 previously published and 2095 *de novo* units from 2044 domestic chickens and 51 Red Junglefowl (*Gallus gallus*). Common haplogroups A-G were shared by domestic chickens and Red Junglefowl. Rare haplougroups H-I and W-Z were specific to domestic chickens and Red Junglefowl, respectively.

The result revealed new complexities of history in chicken's domestication because the phylogeny lineages from the Red Junglefowl were mingled with those of the domestic chickens.

Conclusions

In conclusion, mtDNA studies provide a valuable preliminary description of the population structure and demographic history, but nuclear markers (such as microsatellite and SNPs) would provide valuable additional information to complete the analysis. Several mtDNA studies demonstrated that domestic chicken is closely related to Red Junglefowl, although genetic contributions from other Junglefowls is evident. Furthermore, the chicken mitochondrial genome provides an opportunity to study their human-mediated dispersal out of domestication centres. Future archaeological investigations and multidisciplinary research, including genetic studies, are required to unravel more details.

Acknowledgments

The authors wish to thank the referee for the valuable comments to the manuscript and the constructive suggestions.

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