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Reconstruction of Phylogenetic Relationships of Korean Chickens Using Mitochondrial D-loop Sequences

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Two hypotheses of monophyletic and multiple origins have been documented for chicken domestication. The maternally inherited D-loop region in mtDNA is widely used for the investigation of relationships between populations and individuals of various animal species. In this study, 854 Korean chicken mtDNA D-loop sequences were investigated. Thirty five nucleotide substitutions were identified from the sequence analyses, and they were classified as twenty eight haplotypes. Phylogenetic analyses revealed five divergent mtDNA clades (A to E) based on geographical distribution. There was no breed specific clade among the Korean chickens. Moreover, the estimation of network profiles was traced using 28 haplotypes and five mtDNA clades. Korean chickens were discriminated based on the nucleotide positions. The clades A, B, and E are distributed universally in Eurasia, and among them, 95.78% Korean chickens were included. On the other hand, C and D clades were represented 2.34 and 1.87% of Korean chickens, respectively. Our mtDNA results indicate that Korean chickens share mtDNA haplotypes with a number of chicken breeds from South China, Japan, Europe, Middle East and Indian subcontinent regions. Therefore, the results suggest that Korean chickens have multiple maternal origins.

Key words: clade, D-loop region, geographical origin, Korean chicken, phylogeny

INTRODUCTION

Korean chicken was first documented approximately 2,000 years ago, and about 20 breeds were present in the Joseon Dynasty (A. D. 1392–1910). However, during the Second World War, many breeds became extinct. In order to conserve native chicken breeds, the Korean government launched a conservation project in 1994, based on the collection of chickens from rural areas, and since then native chickens have been raised by the National Institute of Animal Science, and genetic selection process have been carried out, mainly in order to enhance economic traits and feather colors. As a consequence, five lines of Korean native chicken (KNC: black, red, yellow, gray and white) were described, and along with them, four additional breeds (Rhode Island Red, Cornish, White Leghorn and Ogye) are available for the commercial breeding of native chickens in Korea. Of these, three chicken breeds (RIR, Cornish, and White Leghorn), which were imported during the 1960's and 1970's, have been adapted as pure breeds in Korea. Therefore, the aim of this study is to review all the available Korean chickens, especially focusing on their phylogenetic relationships.

There are two hypotheses of the domestication of chickens within Korea, one is that they are of monophyletic origin and the other is that of multiple origins. Most researchers have reported that domestic chickens originated from the red jungle fowl (*Gallus gallus*) as a sole ancestor (Crawford, 1990; Moiseyeva, 1998). The first molecular genetic study of their mtDNA D-loop

region suggested a monophyletic origin, with a red jungle fowl subspecies as the sole ancestor of all domestic chickens (Fumihito *et al.*, 1996, 1994). However, there were some limitations of that study, based on the small numbers of samples of both domestic and wild subspecies of red jungle fowl from China and India, and the small sample sizes for the analysis (Fumihito *et al.*, 1994). Consequently, analysis of the mtDNA of Chinese native chickens confirmed that they originated in Thailand and its adjacent geographic areas (Niu *et al.*, 2002). Besides, genetic evidence had previously been documented for chicken domestication from multiple progenitors (Nishibori *et al.*, 2005). Also, variability in D-loop region of geographical distributions was suggested as evidence for chicken domestication from multiple origins (Liu *et al.*, 2006). Previous results have indicated that five progenitor subspecies may have contributed to modern chicken domestication in five different regions; *G. g. galus* in Thailand and its adjacent regions, *G. g. spadiceus* in Burma and Yunnan Province of China, *G. g. jabouillei* in Southern China and Vietnam, *G. g. murghi* in India, and *G. g. bankiva* in the Java Islands (Crawford, 1990, 1995; Delacour, 1957; Howard and Moore, 1984). However, there is no clear evidence the origin of modern domesticated chickens.

In the mitochondrial genome, the non-coding control (D-loop) region is used for inter-specific population studies (Baker and Marshall, 1997; Moore and Defilippis, 1997) for the advantages of the absence of recombination and rapid nucleotide substitutions compared with genomic DNA sequences (Aquadro and Greenberg, 1983; Cann *et al.*, 1984; Lansman *et al.*, 1983). The investigation of chicken D-loop sequences was previously determined to inspect the origin of breeds or species, and various haplotypes have been reported (Komiyama *et al.*,

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2003, 2004; Liu *et al.*, 2006; Oka *et al.*, 2007). Also, the mtDNA haplotypes of Korean chickens have been determined for the purposes of breed discrimination and determining the origin of domestication (Lee *et al.*, 2007; Hoque *et al.*, 2009, 2011, 2012). The aim of this study is to review the total haplotypes and geographical distribution of all Korean chickens using previously identified mtDNA D-loop sequences. Also, this study should aid our understanding of the origin of Korean chickens, which may help future appropriate conservation breeding programs, and the improvement of the Korean poultry industry.

MATERIALS AND METHODS

Individuals used in this study

A total of 802 sequences from ten chicken breeds/populations and individuals were included in this study. These sequence data were previously published for the genetic discrimination of Korean native chicken populations (Hoque *et al.*, 2009, 2011, 2012). These sequences belong to 67 haplotypes and are deposited in GenBank

under the inclusive accession numbers of KC218503 to KC218569. Also, 52 published sequences (HQ836343 to HQ836363 and DQ629864 to DQ629894) from GenBank were also included in our analysis. A total of 854 individuals from fourteen breeds/populations were examined in this study (Table 1).

Sequence analyses

The chicken mtDNA D-loop nucleotide sequence data were aligned using the ClustalW program (Thompson *et al.*, 1994). Nucleotide replacement export data from mtDNA were carried out in haplotype sequences by using MEGA5 (Tamura *et al.*, 2011). The number of haplotypes, nucleotide variable sites, haplotype diversity and nucleotide diversity (Nei, 1982) were calculated using DnaSP V.5.10 (Rozas *et al.*, 2003). A rectangular Kimura 2-parameter model neighbor-joining (NJ) phylogenetic tree with 1,000 bootstrap replications was constructed for identification of the clades using MEGA5. Also, an outline for median-joining network profiles with positional SNPs for the differentiation of haplotypes was prepared by using NETWORK4610 software (Bandelt *et al.*, 1999).

Table 1. The calculated number of variable sites (S), number of haplotypes (h), haplotype diversity (Hd) and nucleotide diversity (Pi) using mitochondrial D-loop sequence polymorphisms for the Korean chickens

Breed/Population ¹	Sample no.	S ²	H ²	Hd ²	Pi ²
Rhode Island Red (RIR)	140	17	7	0.494	0.0078
Cornish	83	17	11	0.744	0.0113
Korean native chicken black	33	22	11	0.845	0.0138
Korean native chicken red	33	19	6	0.68	0.0124
Korean native chicken yellow	36	22	9	0.716	0.0115
Ogye	32	16	6	0.786	0.0136
White Leghorn	1	0	1	0	0
Korean Longtail A	1	0	1	0	0
Jeju breed	3	7	3	1	0.0105
Hyunin	272	17	6	0.768	0.0083
5 Woorimatdag populations	135	22	7	0.342	0.0046
Parent stock of Woorimatdag (K)	26	0	1	0	0
Hanhyup-3	40	15	5	0.778	0.0068
Parent stock of Hanhyup-3	19	11	5	0.766	0.0049
Total	854				

¹ Rhode Island Red sequences have been published (Hoque *et al.*, 2009, 2011), Cornish sequences have been published (Hoque *et al.*, 2009, 2011), Korean native chicken black sequences have been published (Hoque *et al.*, 2011, 2012, and GenBank Accession no: HQ836346, HQ836347, HQ836350, HQ836356, HQ836359), Korean native chicken red sequences have been published (Hoque *et al.*, 2011, 2012, and GenBank Accession no: HQ836351, HQ836358, HQ836362), Korean native chicken yellow sequences have been published (Hoque *et al.*, 2011, 2012, and GenBank Accession no: HQHQ836343, HQ836348, HQ836349, HQ836355, HQ836357, HQ836360), Ogye sequences have been published (DQ629864 to DQ629894), White Leghorn sequence has been published (HQ836353), Korean Longtail A sequence has been published (HQ836352), Jeju breed sequences have been published (HQ836344, HQ836345, HQ836361), Hyunin sequences have been published (Hoque *et al.*, 2012), 5 Woorimatdag populations: K population (37) sequences have been published (Hoque *et al.*, 2011, 2012) and A (20), B (18), C (20), D (20) and K (20) populations sequences have not published yet, Parent stock of Woorimatdag (K) sequences have been published (Hoque *et al.*, 2011, 2012), Hanhyup-3 sequences have been published (Hoque *et al.*, 2011, 2012), Parent stock of Hanhyup-3 sequences have been published (Hoque *et al.*, 2011, 2012).

² S=number of variable sites, H=number of haplotype, Hd=haplotype diversity, Pi=nucleotide diversity.

RESULTS AND DISCUSSION

Genetic diversity

A total of 854 mtDNA D-loop sequences were used to calculate the number of variable sites (S), number of haplotypes (H), haplotype diversity (Hd) and nucleotide diversity (Pi) among the chicken populations (Table 1). D-loop sequences of 140 individuals in RIR breed obtained 17 variable sites about 7 haplotypes, for which Hd and Pi values of 0.494 and 0.0078, respectively, were calculated. The Cornish chicken breed was estimated as: S (17), H (11), Hd (0.744) and Pi (0.0113), respectively,

based on 83 individuals. 32 Ogye sequences were collected from the GenBank database, obtaining 16 variable sites with 6 haplotypes which measured Hd (0.786) and Pi (0.0136). Previously, it has been reported that four haplotypes were found in the Korean Ogye chicken (Lee *et al.*, 2007). Only one sequence was found in the GenBank database for the Korean White Leghorn breed. 33 sequences of KNC black were considered for the determination of S (22), H (11), Hd (0.845) and Pi (0.0138). Also, 33 sequences were observed in KNC red, for which S (19), H (6), Hd (0.68) and Pi (0.0124) were calculated. 36 sequences of KNC yellow were analyzed to obtain 22

Table 2. The identified haplotypes and clades with mitochondrial D-loop sequence polymorphisms among the Korean chickens

Nucleotide substitution of D-loop region																																		
Haplotype (Sample no.)	1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 3 3 3 4																																Breed/Population (Sample no.) ¹	Clade
	1 6 7 9 9 1 1 1 2 2 2 3 4 4 4 4 5 6 6 8 9 0 1 1 1 3 4 5 5 6 6 7 9 9 4																																	
	2 7 7 8 9 0 2 7 0 2 5 9 2 3 5 6 6 1 5 1 1 6 0 3 5 0 2 2 5 3 7 0 1 9 3																																	
H_1 (3)	G T A C C C G C T A C A G C C C C T C A A T T C C C A C T C T T C G T																																PHf (3)	
H_2 (66)	A -																																	

¹ R=Rhode Island Red; H=Cornish; WL=White Leghorn; O=Ogye; KB=Korean black, KR=Korean red; KY=Korean yellow; JB=Jeju breed, KLtA=Korean Longtail A; Hn=Hyunin; A=Woorimatdag A; B=Woorimatdag B; C=Woorimatdag C; D=Woorimatdag D; K=Woorimatdag K; PK=Parent stock of Woorimatdag K; Hf= Hanhyup-3; PHf= Parent stock of Hanhyup-3.

variable sites with 9 haplotypes, for which Hd (0.716) and Pi (0.0115) were calculated. Analysis of 272 mtDNA D-loop sequence data from the Hyunin population from single flock revealed six haplotypes, comprised of seventeen nucleotide substitutions. All of the six mtDNA haplotypes for the Hyunin chicken population were discovered from chickens with ten different plumage colors. Based on statistical analysis, the identified Hd and Pi were 0.768 and 0.0083, respectively, in Hyunin chickens. Three individuals from Jeju native chickens were identified, with S, H, Hd and Pi determined to be 7, 3, 1 and 0.0105, respectively.

Korean longtail A (GenBank accession no. HQ836352) chicken was found only to contain one sequence for participation in our analyses. Two commercial Korean native chicken populations (Woorimatdag and Hanhyup) have recently been developed by crossing Korean native chickens with other commercial chicken breeds, in order to increase the meat content. Based on the continued crossing of chicken populations, five distinct Woorimatdag (A, B, C, D and K) chicken populations have been developed in Korea. A total of 135 individuals from five distinct Woorimatdag populations obtained 22 variable sites with 7 haplotypes for which we calculated Hd and Pi of 0.342 and 0.0046, respectively. Besides, 26 individuals of parent stock of Woorimardag K were obtained for just one haplotype. Hanhyup-3 commercial chicken population

obtained 40 sequences to calculate S, H, Hd and Pi values of 15, 5, 0.778 and 0.0068, respectively. Also, 19 sequences of parent stock of Hanhyup-3 obtained 11 variable sites with 5 haplotypes for which Hd and Pi values of 0.766 and 0.0049, respectively, were calculated. Comparatively, KNC black conveyed the highest value for Hd and Pi (0.845 and 0.0138, respectively). However, a high value of Hd (0.964) was also documented in Laiwa black Chinese native chickens (Liu *et al.*, 2010).

Phylogeny of the haplotypes and network profiles

Hence, analyses of 854 mtDNA D-loop sequences in Korean chickens from fourteen populations identified 35 nucleotide variations, which were classified into 28 haplotypes (Table 2). Previous studies identified nine highly divergent mtDNA clades (A–I) from 169 haplotypes, using the red jungle fowls and domestic chickens (Liu *et al.*, 2006). This study identified 28 haplotypes, and clades using 44 sequences were constructed for phylogenetic analyses of Korean chickens (Figure 1). While, four clades (F, G, H and I) are absent of haplotypes in Korean chickens, the phylogenetic analyses revealed five highly divergent mtDNA clades (A–E). Phylogenetic analysis revealed that Korean chickens were domesticated from continental chickens breed. Among these 28 haplotypes, H_1 to H_9, H_10 to H_11, H_12 to H_13, H_14 to H_23, and H_24 to H_28 belonged to clades E, C, D, A, and B,

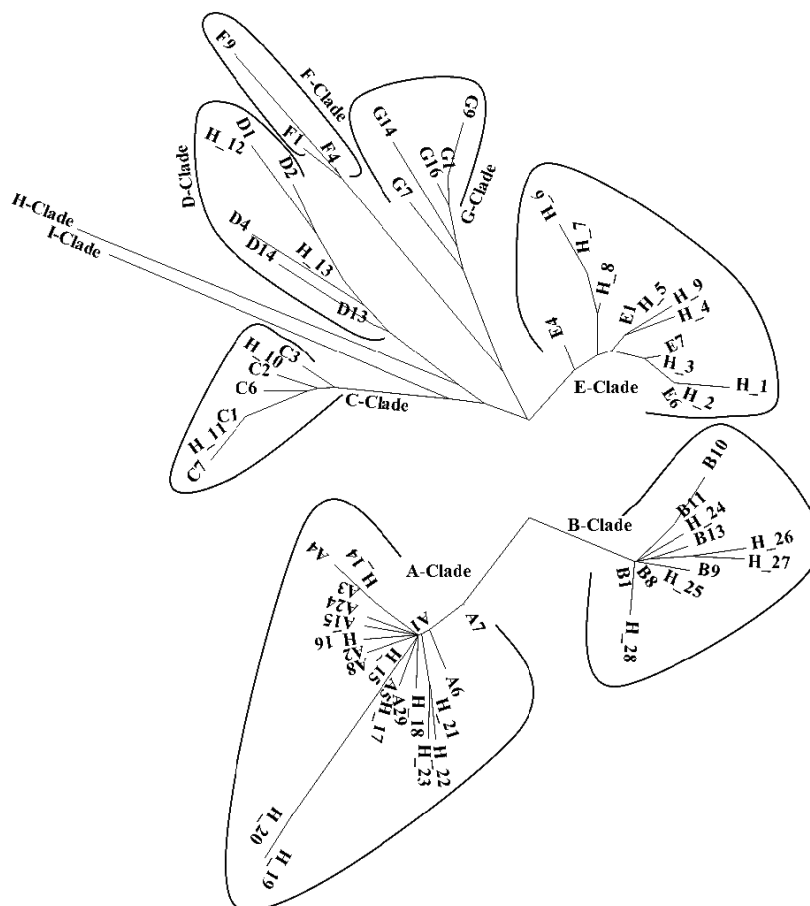


Fig. 1. The construction of phylogenetic analyses to identify the clades using 28 haplotypes and reported haplotypes by Liu *et al.* (2006).

Moreover, the estimation of network profiles was traced using 28 haplotypes inside five mtDNA clades, which were discriminated by nucleotide positions of

Breed and population distribution in the clade

A total of fourteen chicken breeds/populations were distributed in the identified five clades (Table 3). The geographical distribution clades of Korean chickens A, B, C, D and E contained 584 (68.38%), 56 (6.56%), 20 (2.34%), 16 (1.87%), and 178 (20.84%) individuals, respectively. However, clades A, B, and E were most widely distributed in Eurasia, whereas 95.78% of sampled Korean chickens fall into these clades. Accordingly, Korean chickens were domesticated from A (68.38%) and B (6.56%) clades from South China and Japanese chickens, whereas the E (20.84%) clade is from the regions of Europe, the Middle East and the Indian subcontinent. In the clades, C (2.34%) and D (1.87%) were distributed from Japanese, Indian, and Indonesian regions. Most Korean chickens were involved in A clade, except Korean Ogye and Jeju breeds. Also, KNC (black, red and yellow) and commercial Woorimatdag chickens were found in the D clade. However, breed specific clades were not determined in our studies. Our mtDNA results indicated that the Korean chickens have same mtDNA haplotypes as chicken breeds from South China, Japan, Europe, the Middle East and the Indian subcontinent.

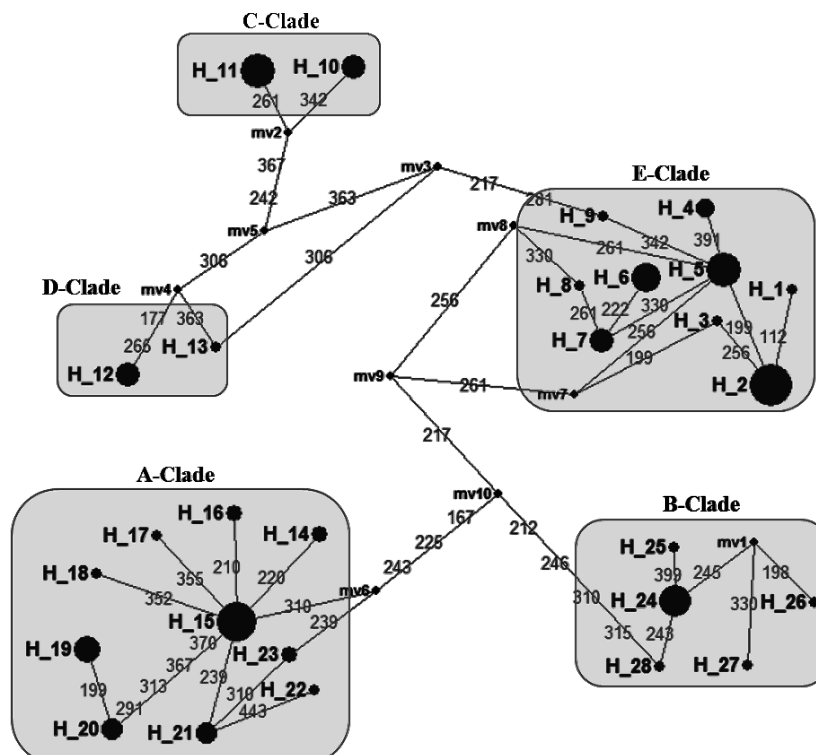


Fig. 2. Network profiles of the 28 haplotypes among the Korean chickens. The links are labeled by the nucleotide positions. The order of the mutations on the branch is arbitrary. The median vectors (mv) are nucleotide junctions.

Table 3. Breed and population distribution in clades of Korean chickens

Breed/Population	A-Clade	B-Clade	C-Clade	D-Clade	E-Clade	Total
Rhode Island Red (RIR)	98 (70)	8 (5.71)	1 (0.71)	–	33 (23.57)	140
Cornish	27 (32.53)	38 (45.78)	–	–	18 (21.69)	83
Korean native chicken black	7 (21.21)	–	4 (12.12)	5 (15.15)	17 (51.52)	33
Korean native chicken red	25 (75.76)	–	3 (9.09)	3 (9.09)	2 (6.06)	33
Korean native chicken yellow	22 (61.11)	–	–	1 (2.78)	13 (36.11)	36
Ogye	–	6 (18.75)	9 (28.13)	–	17 (53.12)	32
White Leghorn	1 (100)	–	–	–	–	1
Korean Long tail A	1 (100)	–	–	–	–	1
Jeju	–	–	1 (33.33)	–	2 (66.67)	3
Hyunin	242 (88.98)	3 (1.1)	–	–	27 (9.92)	272
5 Woorimatdag populations	125 (92.59)	1 (0.74)	–	7 (5.19)	2 (1.48)	135
Parent stock of Woorimatdag (K)	26 (100)	–	–	–	–	26
Hanhyup-3	8 (20)	–	2 (5)	–	30 (75)	40
Parent stock of Hanhyup-3	2 (10.53)	–	–	–	17 (89.47)	19
Total	584 (68.38)	56 (6.56)	20 (2.34)	16 (1.87)	178 (20.84)	854

Also, the results suggest that Korean chickens have multiple maternal origins and that domestications may have occurred in Eurasia and Southeast Asia.

In conclusion, Korean chickens were domesticated from a number of migrations of chicken breeds, and were adopted in Korea as pure breeds, which support the theory of multiple origins in Eurasia and Southeast Asia regions. Our results have identified haplotypes and clades based on geographical distribution, which will help the conservation of future breeding plans, and will improve Korean chickens.

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REFERENCES

- Aquadro, C. F. and B. D. Greenberg 1983 Human mitochondrial DNA variation and evolution: Analysis of nucleotide sequences from seven individuals. *Genetics*, **103**: 287–312
- Baker, A. J. and H. D. Marshall 1997 Mitochondrial control region sequences as tools for understanding evolution. In: *Avian molecular evolution and systematic*, Mindell D. P. ed. Academic press, (San Diego) pp. 51–82
- Bandelt, H. J., P. Forster and A. Rohl 1999 Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.*, **16**: 37–48
- Cann, R. L., W. M. Brown and A. C. Wilson 1984 Polymorphic sites and the mechanism of evolution in human mitochondrial DNA. *Genetics*, **106**: 479–499
- Crawford, R. D. 1990 Origin and history of poultry species. Poultry genetic resources: evolution, diversity, and conservation. In: *Poultry Breeding and Genetics*, Crawford R. D. ed. Elsevier, (Amsterdam) pp. 1–59
- Crawford, R. D. 1995 Origin, history, and distribution of commercial poultry. In: *Poultry Production*, Hunton P. ed. Elsevier, (Amsterdam) pp. 1–20
- Delacour, J. 1957 *The Pheasants of the World*, 2nd ed. Spue Publications, Surrey, Hindhead
- Fumihito, A., T. Miyake, S. Sumi, M. Takada, S. Ohno and N. Kondo 1994 One subspecies of the red jungle fowl (*Gallus gallus gallus*) suffices as the matriarchic ancestor of all domestic breeds. *Proc. Natl. Acad. Sci. U. S. A.*, **91**: 12505–12509
- Fumihito, A., T. Miyake, M. Takada, R. Shingu, T. Endo, T. Gojobori, N. Kondo and S. Ohno 1996 Monophyletic origin and unique dispersal patterns of domestic fowls. *Proc. Natl. Acad. Sci. U. S. A.* **93**: 6792–6795.
- Hoque, M. R., N. R. Choi, H. Sultana, B. S. Kang, K. N. Heo, S. K. Hong, C. Jo and J. H. Lee 2012 Phylogenetic analysis of a privately-owned Korean native chicken population using mtDNA D-loop variations. *Asian-Aust. J. Anim. Sci.*, (In press)
- Hoque, M. R., K. C. Jung, B. K. Park, K. D. Choi and J. H. Lee 2009 Genetic Variability of mtDNA D-loop Region in Korean Native Chickens. *Korean J. Poult. Sci.* **37**(4): 323–328
- Hoque, M. R., S. H. Lee, K. C. Jung, B. S. Kang, M. N. Park, H. K. Lim, K. D. Choi and J. H. Lee 2011 Discrimination of Korean Native Chicken Populations Using SNPs from mtDNA and MHC Polymorphisms. *Asian-Aust. J. Anim. Sci.*, **24**(12): 1637–1643
- Howard, R. and A. Moore 1984 *A Complete Checklist of Birds of the World*, revised ed. Macmillan (London)
- Komiyama, T., K. Ikeo and T. Gojobori 2003 Where is the origin of the Japanese gamecock? *Gene*, **317**: 195–202
- Komiyama, T., K. Ikeo and T. Gojobori 2004 The evolutionary origin of long-crowing chicken: its evolutionary relationship with fighting cocks disclosed by the mtDNA sequence analysis. *Gene*, **333**: 91–99
- Lansman, R. A., J. C. Avise and M. D. Huettel 1983 Critical experimental test of the possibility of 'paternal leakage' of mitochondrial DNA. *Proc. Natl. Acad. Sci. U. S. A.*, **80**: 1969–1971
- Lee, Y. J., M. S. A. Bhuiyan, H. J. Chung, W. Y. Jung, K. D. Choi, B. G. Jang, W. K. Paek, J. T. Jeon, C. S. Park and J. H. Lee 2007 Mitochondrial DNA diversity of Korean Ogo chicken. *Asian-Aust. J. Anim. Sci.* **20**(4): 477–481
- Liu, W. Y. and C. J. Zhao 2010 Comprehensive genetic analysis with mitochondrial DNA data reveals the population evolution relationships between Chinese Gamecocks and their neighboring native chicken breeds. *Asian J. Anim. Vet. Adv.*, **5**(6): 388–401
- Liu, Y. P., G. S. Wu, Y. G. Yao, Y. W. Miao, G. Luikart, M. Baig, A. B. Pereira, Z. L. Ding, M. G. Palanichamy and Y. P. Zhang 2006 Multiple maternal origins of chickens: Out of the Asian jungles.

- Mol. Phylogenet. Evol.*, **38**: 12–19
- Moiseyeva, I. G. 1998 Ancient evidence for the origin and distribution of domestic fowl. In: Proceedings of the 10th European Conference, The Poultry Industry Towards the 21st Century (Jerusalem). **1**(21–28): 244–245
- Moore, W. S. and V. R. DeFilippis 1997 The window of taxonomic resolution for phylogenies based on mitochondrial cytochrome b. In: Avian molecular evolution and systematic, Mindell D. P. ed. Academic press (San Diego) pp. 84–119
- Nei, M. 1982 Evolution of human races at the gene level. *Prog. Clin. Biol. Res.*, 167–181
- Nishibori, M., T. Shimogiri, T. Hayashi and H. Yasue 2005 Molecular evidence for hybridization of species in the genus *Gallus* except for *Gallus varius*. *Anim. Genet.* **36**(5): 367–375
- Niu, D., Y. Fu, J. Luo, H. Ruan, X. P. Yu, G. Chen and Y. P. Zhang 2002 The origin and genetic diversity of Chinese native chicken breeds. *Biochemi. Genet.*, **40**(5–6): 163–174
- Oka, T., Y. Ino, K. Nomura, S. Kawashima, T. Kuwayama, H. Hanada, T. Amano, M. Takada, N. Takahata, Y. Hayashi and F. Akishinomiya 2007 Analysis of mtDNA sequences shows Japanese native chickens have multiple origins. *Anim. Genet.*, **38**: 287–293
- Rozas, J., J. C. Sanchez-DelBarrio and X. Messeguer 2003 DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, **19**: 2496–2497
- Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei and S. Kumar 2011 MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.*, **10**: 1093
- Thompson, J. D., D. G. Higgins, T. J. Gibson and W. Clustal 1994 Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Res.*, **22**: 4673–4680