

Monophyletic origin and unique dispersal patterns of domestic fowls

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ABSTRACT With the aim of elucidating in greater detail the genealogical origin of the present domestic fowls of the world, we have determined mtDNA sequences of the D-loop regions for a total of 21 birds, of which 12 samples belong to red junglefowl (*Gallus gallus*) comprising three subspecies (six *Gallus gallus gallus*, three *Gallus gallus spadiceus*, and three *Gallus gallus bankiva*) and nine represent diverse domestic breeds (*Gallus gallus domesticus*). We also sequenced four green junglefowl (*Gallus varius*), two Lafayette's junglefowl (*Gallus lafayettei*), and one grey junglefowl (*Gallus sonneratii*). We then constructed a phylogenetic tree for these birds by the use of nucleotide sequences, choosing the Japanese quail (*Coturnix coturnix japonica*) as an outgroup. We found that a continental population of *G. g. gallus* was the real matriarchic origin of all the domestic poultries examined in this study. It is also of particular interest that there were no discernible differences among *G. gallus* subspecies; *G. g. bankiva* was a notable exception. This was because *G. g. spadiceus* and a continental population of *G. g. gallus* formed a single cluster in the phylogenetic tree. *G. g. bankiva*, on the other hand, was a distinct entity, thus deserving its subspecies status. It implies that a continental population of *G. g. gallus* sufficed as the monophyletic ancestor of all domestic breeds. We also discussed a possible significance of the initial dispersal pattern of the present domestic fowls, using the phylogenetic tree.

There is a little doubt that the successive domestication of various wild animals contributed greatly to the sustenance and cultural developments of mankind. In particular, the domestication of chickens seems to have a long history. Indeed, the earliest sign of domestication of the chicken has been pushed back to nearly 8000 years ago because remains of domesticated chickens were evident in 16 neolithic sites along the Huang He (Yellow River) in Northeast China, some of which were dated to be at least 7500 years (1).

The domestication of chickens has also been observed at the well-known Mohenjo-Doro site in the Indus Valley in Pakistan (2). Moreover, earlier signs of domestication of the chicken were found in unlikely places far distant from the habitat of junglefowls, e.g., Ukraine and Spain (1). Thus, whether or not the domestication of junglefowls occurred only once in a fixed site or occurred repeatedly in different locations has remained an open question. In fact, various population studies using isozyme polymorphism suggested the multiple and independent sites of domestication (3).

In an earlier paper (4), we studied the noncoding region of the mitochondrial DNA of various gallinaceous birds with regard to its restriction fragment length polymorphism and its sequences of the first 400 bases. We then showed that whereas

the 7.0% sequence divergence was seen between *Gallus gallus bankiva* inhabiting Indonesian island of Java and two other subspecies of *Gallus gallus*, both inhabitants of Thailand (*Gallus gallus gallus* and *Gallus gallus spadiceus*), a mere 0.5–3.0% difference separated the three domestic breeds of the chicken of divergent geographical origins from the two *G. g. gallus* of Thailand. Thus, we indicated a strong possibility that a single domestication event has taken place in Thailand and its immediate surroundings (4). Inasmuch as the sequence divergence between two individuals of *G. g. gallus* from Thailand was 1.25%, we concluded that this subspecies alone had been sufficient to yield all the diverse breeds of domestic chicken (4). However, because this conclusion has been drawn from a limited number of *G. gallus* subspecies and domestic fowls, it was felt that the validity of the above conclusion should be verified by a more expanded survey.

With the aim of elucidating in greater detail the genealogical origin of the present domestic fowls in the world, we have determined mtDNA sequences of the D-loop regions for a total of 21 birds that belong to three subspecies of *G. gallus* (six *G. g. gallus*, three *G. g. spadiceus*, and three *G. g. bankiva*) and nine domestic breeds and/or races (*Gallus gallus domesticus*) such as white leghorn. We also sequenced the same regions of mtDNA for all other *Gallus* species (four *Gallus varius*, two *Gallus lafayettei*, and one *Gallus sonneratii*). Using these sequence data, a phylogenetic tree was constructed that indeed verified the previous conclusion that the genealogical origin of the domestic fowls is monophyletic descending from a continental population of *G. g. gallus*. We shall also discuss a possible significance of the initial dispersal pattern of the present domestic fowls using the phylogenetic tree.

MATERIALS AND METHODS

The species that we examined in the present study are listed in Table 1. Three subspecies of *G. gallus* were represented by six specimens from *G. g. gallus*, three from *G. g. spadiceus*, and three from *G. g. bankiva*. Nine specimens were from diverse domesticated breeds. Moreover, we examined three other species of junglefowls of the genus *Gallus*: four specimens of *G. varius*, two of *G. lafayettei*, and one of *G. sonneratii*.

Blood samples were obtained from live birds without harming them; DNA was then extracted. Amplified copies of the mitochondrial control region were obtained by PCR reaction using two primers previously described (4, 6). The DNA sequencing procedure was as described (4, 6).

The nucleotide sequences obtained were aligned with each other (see Fig. 1), and the number of nucleotide substitutions were estimated by the six-parameter method (7). A phylogenetic tree was constructed by the neighbor-joining method

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Data deposition: The sequences reported in this paper have been deposited in the GenBank data base (accession nos. D82897–D82925).
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Table 1. List of the specimens and their localities

Species/Subspecies/Races	Localities
<i>G. g. bankiva</i> 15	Singaraja, Bali, Indonesia
<i>G. g. bankiva</i> 18	West Jawa, Indonesia
<i>G. g. bankiva</i> 19	Lampung, East Sumatra, Indonesia
<i>G. g. gallus</i> 8,10	Department of Forestry, Thailand
<i>G. g. gallus</i> 11	Tama Zoological Garden, Tokyo, Japan
<i>G. g. gallus</i> 39,41,58	Palembang, South Sumatra, Indonesia
<i>G. g. spadiceus</i> 3,4,5	Department of Forestry, Thailand
<i>G. lafayettei</i> 1,2	Dehiwela Zoo, Dehiwela, Sri Lanka
<i>G. sonneratii</i>	India
<i>G. varius</i> 2,6	Singaraja, Bali, Indonesia
<i>G. varius</i> 32	Madura, Indonesia
<i>G. varius</i> 50	Banyuwangi, East Jawa, Indonesia
<i>G. g. domesticus</i> (Ayam Cemani 1)	Surabaya Zoo, Surabaya, East Jawa, Indonesia
<i>G. g. domesticus</i> (Ayam Kokok Balenggek 63,71)	Solok, West Sumatra, Indonesia
<i>G. g. domesticus</i> (Ayam Pelung 76)	Bogor, Jawa, Indonesia
<i>G. g. domesticus</i> (Barred Plymouth Rock 1)	The Domestic Fowl Trust, Worcestershire, U.K.
<i>G. g. domesticus</i> (Nagoya)	Hiroshima Animal Husbandry Experimental Station, Hiroshima, Japan
<i>G. g. domesticus</i> (Thai Bantam 8)	Thailand
<i>G. g. domesticus</i> (White Leghorn 1)	Ref. 5
<i>G. g. domesticus</i> (White Leghorn 2)	Hiroshima Animal Husbandry Experimental Station, Hiroshima, Japan
<i>Coturnix coturnix japonica</i>	Hiroshima, Japan

using the substitution numbers estimated (8). The statistical significance was evaluated by the bootstrapping method (9).

RESULTS AND DISCUSSION

Evolutionary Relationships Among Four Species in the Genus *Gallus*. The genus *Gallus* is composed of four species: *G. gallus*, *G. varius*, *G. lafayettei*, and *G. sonneratii*. Their phylogenetic relationship shown in Fig. 1 was consistent with our previous report (6) in which the dendrogram was constructed by the use of only one specimen from each species. At the first glance, *G. varius* appears to be the most divergent of the four species. However, the bootstrap value that sets this species apart is only 34.7%. Accordingly, it is likely that *G. varius*, *G. gallus*, *G. sonneratii*, and *G. lafayettei* branched out from the common stem almost simultaneously in the evolutionary time scale. Taking into account the phylogenetic tree in fig. 2 in our previous report (6) together with the present results, we speculate that the split should have occurred shortly thereafter in *Gallus* of Indian subcontinent to yield a mainland species (*G. sonneratii*) and an island species (*G. lafayettei*).

In our first paper of this series (4), we found that a 60-bp-long unit containing the nearly invariant tetradecamer, AACTATGAATGGTT, in its center of the D-loop region is duplicated only in members of the genus *Gallus* and not in other phasianine birds. Furthermore, greater than two copies of this unit were found in three of the four *Gallus* species. In the case of *G. varius*, whereas two copies were found in two individuals, three and four copies were found in the remaining two. All specimens of *G. lafayettei* as well as *G. sonneratii* had three copies. Of particular significance was the fact that all 12 specimens of *G. gallus* have two copies, regardless of subspecies. These observations on copy numbers of the 60-bp-long unit are consistent with the above mentioned notion about the order of divergence of the four species. All nine domestic fowls examined had the same copy number as *G. gallus*, again implying that the genealogical origin of the domestic fowls is monophyletic descending from *G. gallus* alone.

A Single Cluster Composed of a Continental Population of *G. g. gallus* and *G. g. spadiceus*. As shown in Fig. 2, *G. g. gallus* and *G. g. spadiceus* do not form two separate clusters in the phylogenetic tree. It seems that *G. g. gallus* is divided into two separate populations: (i) an island population from Sumatra and a (ii) continental population. *G. g. spadiceus* is more

closely allied with a continental population of *G. g. gallus* than an island population of *G. g. gallus* is to its continental relation. Thus, the subspecies status given to *G. g. spadiceus* might be questioned. On the other hand, *G. g. bankiva*, which inhabits the Indonesian islands of Sumatra, Java, and Bali, is a very distinct entity that is clearly separate from *G. g. gallus* as well as *G. g. spadiceus*; thus, its subspecies status appears to be well-deserved.

Geographical Differentiation of *G. g. gallus*, *G. g. spadiceus*, and Domestic Fowls. West and Zhou (1) suggested that chickens were first domesticated in Southeast Asia and were taken north to become established in China, possibly spreading to European Celts through tribes of the Russian steppe. Our phylogenetic tree seems to be consistent with their contention for the following reasons.

According to the phylogenetic tree (Fig. 2), domestic fowls including Indonesian races belong to the same cluster as a continental population of *G. g. gallus* and *G. g. spadiceus* sampled from Thailand and its adjacent areas. On the other hand, three specimens of *G. g. gallus* from South Sumatra form a separate cluster as already noted, yet native domestic fowls from the same island belonged to the cluster in which a continental population of *G. g. gallus* and *G. g. spadiceus* from Thailand were included; e.g., two *ayam kokok balenggek* from West Sumatra. Accordingly, an independent domestication event in Sumatra from its own *G. g. gallus* can be excluded. It suggests that the original domestication took place in Thailand and its adjacent regions and subsequently dispersed to West Sumatra in Indonesia.

West Sumatra in Indonesia is known as Minangkabau. It is worth noting that the people of Minangkabau have developed unique culture and *ayam kokok balenggek* is adopted as a symbol of the Solok prefecture in Minangkabau (10). It is quite possible that this domestic fowl has been highly esteemed in Minangkabau because of its novelty, implying that *ayam kokok balenggek* had been brought to West Sumatra from elsewhere. These facts support our notion that Indonesian native domestic fowls have been transferred to Indonesia from Thailand and its adjacent regions.

Sequence Differences Between *G. g. bankiva* and Other *G. gallus* Subspecies. As already noted, it is clear in Fig. 2 that *G. g. bankiva* is a very distinct entity from *G. g. gallus* and *G. g. spadiceus* in the phylogenetic tree. In fact, the numbers of nucleotide substitutions separating *G. g. bankiva* from other

GC bankiva15	1	AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	241	GG bankiva15	TAG	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300
GC bankiva18		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GG bankiva18	TAG	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC bankiva19		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GG bankiva19	TAG	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC gallus11		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC gallus11	TAG	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC gallus39		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC gallus39	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC gallus41		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC gallus41	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC gallus58		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC gallus58	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC gallus8		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC gallus8	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC gallus10		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC gallus10	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC spadiceus3		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC spadiceus3	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC spadiceus4		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC spadiceus4	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
GC spadiceus5		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	GC spadiceus5	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
G_lafayettei1		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	G_lafayettei1	TAAT	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
G_lafayettei2		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	G_lafayettei2	TAAC	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
G_sonneratii		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	G_sonneratii	TGG	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
G_varius2		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	G_varius2	TAA	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
G_varius32		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	G_varius32	CAA	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
G_varius50		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	G_varius50	CAA	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
G_varius6		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	G_varius6	CAA	---CTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
Cemani		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	Cemani	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
Ayam63		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	Ayam63	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
Ayam71		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	Ayam71	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
Pelung		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	Pelung	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
Bantam8		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	Bantam8	CAG	---TTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
Barred_Plymouth		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	Barred_Plymouth	CAG	---CTC	CAAA	CAACCTA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
Nagoya		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	Nagoya	CAG	---TTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
White_Leghorn1		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	White_Leghorn1	CAG	---TTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
White_Leghorn2		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	White_Leghorn2	CAG	---TTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
White_Leghorn3		AATTTTAA	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	CCCCCAGGGG	White_Leghorn3	CAG	---TTC	TAA	CCAATA	CCAAGCACC	TAACATGAA	TGGTTACAGG	ACATAAC	300	
C_coturnix		AAC	---ACTT	TTTAAACCTA	ACTCCCTAC	TAAGTGTACC	CCCCCTTCC	C_coturnix	ATAG									

FIG. 1. The multiple alignment of mtDNA sequences for 32 specimens of junglefowls, domestic fowls and the common quail of Japanese subspecies.

two subspecies are quite large compared with the largest individual differences seen within *G. g. gallus* as well as *G. spadiceus*. Thus, *G. g. bankiva* is indeed deserving of its subspecies status within the species *G. gallus*. Because two

other subspecies of *G. gallus*, *Gallus gallus murghi* and *Gallus gallus jabouillei*, were not included in the present study, the validity of their subspecies status still remain as an open question.

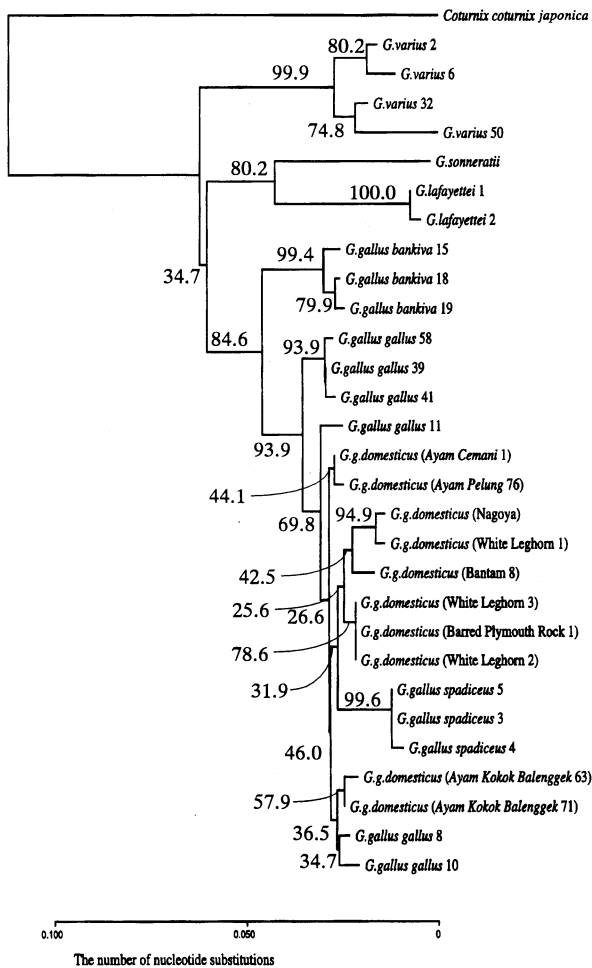


FIG. 2. A phylogenetic tree constructed by use of nucleotide sequence data.

Nevertheless, the monophyletic origin of domestic fowls from a continental population of *G. g. gallus* appears to be self-evident. The Indus valley where the domestication of chicken was evident at least 4000 years ago and still is the domain of *G. g. murghi*. Yet, the present study indicates that if *G. g. murghi* contributed to an independent domestication event, *G. g. murghi* should be genetically close to some of domestic fowls examined here. It naturally follows that *G. g.*

murghi had to be genetically indistinct from *G. g. gallus* as well as *G. g. spadiceus* of Thailand, thus, relinquishing its subspecies status. The same applies to another subspecies not included in the present study, *G. g. jabouillei*.

A Possible Significance of the Initial Dispersal Pattern of Domestic Fowls. As we have shown in this study, it is likely that all the domestic fowls have originated from the single domestication event in Thailand and its adjacent regions. The reason for the domestication of chickens is usually thought to be the securing the readily available source of protein and fat in the form of eggs and meats. However, there are other aspects. We should not forget that since the time immemorial, the chicken has often been associated with various religious services in different parts of the world, e.g., the cock as a harbinger of the sun rising again and cockfighting as a divine offering (11, 12). The initial dispersion of domestic fowls might have been due to the religious significance attached to the chicken. In particular, the fact that cockfighting is still very widely spread throughout Southeast Asian countries appears very significant in considering the reason for the initial dispersion of domestic fowls from the original site of domestication.

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