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Matrilineal Components and Genetic Relationship of Silkies from China and Japan

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Silkie is a famous black-bone chicken breed with beautiful silky feather. The unique medical property of this chicken was recorded in Chinese traditional medicine dictionary about 700 years ago. In this study, we analyzed the mtDNA D-loop sequence variation of 26 Bairong Silkies from Fujian Province, China, together with 100 reported Silkie mtDNAs from China and Japan, and studied their matrilineal components and genetic relationship. A total of 21 haplotypes were detected, which could be assigned to six haplogroups (A-E, G). Among them, haplogroups D and G were exclusively presented in Japanese Silkies and Chinese Silkies, respectively. Chinese Silkies had higher frequency of lineages belonging to haplogroups A, B, and E, and lower frequency of haplogroup C than Japanese Silkies. For the four Chinese Silkie populations, most of samples of Taihe, Chengdu, and Hubei Silkies were grouped in haplogroups A, B, and C, whereas most of Bairong Silkies were grouped in haplogroup E. Five haplotypes were shared by Japanese and Chinese Silkies. The genetic diversity of each Silkie population varied, but the overall diversity of Chinese Silkies was similar to that of Japanese Silkies. Taken together, our results confirmed the genetic connection between Chinese and Japanese Silkies, but also clearly showed that the matrilineal genetic structures of Chinese and Japanese Silkies had some differences.

Key words: d-loop, genetic diversity, matrilineal origin, mtDNA, silkies

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Introduction

The modern domestic chickens are now distributed worldwide and have evolved along with the development of human civilization. The origin and phylogeographic history of chickens across Eurasia have been extensively elucidated based on mitochondrial DNA (mtDNA) sequence variation (Fumihito *et al.,* 1994, 1996; Liu *et al.,* 2006a). The wildly accepted concept is that the progenitor of domestic chickens is red jungle fowls (*Gallus gallus*), and the highly divergent mtDNA haplogroups in domestic populations would suggest for multiple domestications in different regions, such as Yunnan, South and Southwest China and/or surrounding areas, as well as the Indian subcontinent (Liu *et al.,* 2006a). As the initially domesticated chickens were adapted to new environments and were subjected to different artificial selection pressures, populations with new characteristics were developed and further formed local breeds (Zárate *et al.,* 2006).

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Although most of domesticated chickens are used for meat consumption and egg production, the ornamental types have been prevailed worldwide today. Among them, the Silkie (*Gallus gallus domesticus*) is well known for its unique fluffy plumage feeling like silk. In China, Silkie is specially characterized by its unique medical property, which was recorded in Chinese traditional medicine dictionary about 700 years ago (Xie, 1995). There is no clear distinction between the Silkies and other chicken breeds at the matrilineal component level (Fu *et al.,* 2002; Liu *et al.,* 2006a). The exact scenario regarding where or when Silkies with the fur-like plumage were first cultivated was unknown. Most of the existing conventional literatures suggested for an origin in China. Other places in Southeast Asia, such as India, have also been proposed as the cultivation center for the Silkie breeds (Arisawa *et al.,* 2006). The domestication history of chicken in China could be dated back to 5400 BC (West and Zhou, 1989), but the first detailed description for the Silkies was recorded only 700 years ago (Xie, 1995). Nowadays, there are eight Chinese Silkie breeds/populations registered in the Domestic Animal Diversity Information System (DAD-IS, 2007) of the Food and Agriculture Organization of the United Nations (http://www.dad.fao.org/). All these breeds/populations could be assorted

into white feather type and black feather type based on the feather color (Qiu *et al.,* 1988). Among them, the Taihe Silkies and Bairong Silkies, which are distributed in Jiangxi Province and Fujian Province, respectively, are thought to be the ancestor populations of modern Silkies in China. Subsequently, these two breeds were diffused into other regions (Qiu *et al.,* 1988; Xie, 1995). Unfortunately, there is no strong evidence, especially for molecular data, to support this hypothesis.

Silkie is one of the most popular and ubiquitous ornamental breeds in Japan. Silkie is called "Ukokkei" in Japanese and is mainly distributed in Tokyo, Mie, Osaka, Hiroshima, Yamaguchi and Kagawa Prefectures (Chang and Huang, 2003). There are about 50 native chicken breeds in Japan, which could be divided into entertainment, egg, and/or meat production groups. The entertainment group could be further classified into two subgroups according to their introduction history, with one being introduced to Japan more than 2, 000 years ago and the other one during the early Edo Era (1603–1867) from China or India (Chang and Huang, 2003; Arisawa *et al.,* 2006). Based on these founder breeds, other Japanese breeds were subsequently developed via artificial selection programs by the end of the Edo Era (Arisawa *et al.,* 2006). Komiyama and colleagues (2003, 2004) suggested that all Japanese domesticated chickens were originated independently from Southeast Asia and the mainland China. Our later reanalysis of the gamecock mtDNAs in China and Japan demonstrated a genetic pattern consistent with the proposed dual origin of Japanese gamecocks, but also left room for a single origin of Japanese gamecocks from China (Liu *et al.,* 2006b). Recently, Oka *et al.* (2007) provided further mtDNA data to support the multiple origins of Japanese native chickens.

Mitochondrial DNA has been proved to be a very useful genetic marker in elucidating the origin of domestic animals, such as duck (He *et al.,* 2008), Cattle (Lai *et al.,* 2006; Chen *et al.,* 2008), and Goat (Liu *et al.,* 2009). The domestication history and phylogeographical relationship of modern chickens in China and Japan have been elaborately explored by using mtDNA sequence variations (Fumihito *et al.,* 1994, 1996; Komiyama *et al.,* 2003, 2004; Liu *et al.,* 2006a, b; Oka *et al.,* 2007), as well as, microsatellite DNA polymorphisms (Takahashi *et al.,* 1998). However, the matrilineal components of the Silkie breeds distributed in China and Japan and their genetic relationship have not been sufficiently characterized or discussed. In this study, we compared the mtDNA control region (D-loop) partial sequence variation of the Silkies from China and Japan. Our results provided insightful information regarding the breed formation history and subsequent diffusion route of the Silkie.

Materials and Methods

Sampling and Reported Data

We collected 26 Bairong Silkies from Fujian Province. These samples were sequenced according to the procedure described in our previous study (Liu *et al.,* 2006a) and were deposited in GenBank under accession numbers GQ 227993-GQ228018.

The previously reported sequences (27 Taihe Silkies from Jiangxi Province, 15 Chengdu Silkies from Sichuan Province, 24 Hubei Silkies from Hubei Province, China; Liu *et al.,* 2006a) were also used for comparison in this study. Thirty-four Japanese Silkies were retrieved from GenBank. All together, 126 mtDNA D-loop partial sequences were analyzed in this study (Table 1).

Data Analysis

The mtDNA sequences were aligned with the reference sequence of *G. g. domesticus* mitochondrial genome (Desjardins and Morais, 1990). Sequence variations were exported using MEGA 3.1 (Kumar *et al.,* 2004). We followed the classification system in our previous report (Liu *et al.,* 2006a) to classify each mtDNA into respective haplogroups/clades. An unrooted Neighbor-joining (NJ) tree of the haplotypes was subsequently constructed using the Kimura two-parameter model in MEGA 3.1, following the same rationale as discussed in our previous study (Liu *et al.,* 2006a). To provide a better view of the genetic relationship of the haplotypes in these geographic populations of Silkies, a median-joining network was constructed using program Network 3.1 (http://www.fluxus-engineering.com/sharenet.htm; Bandelt *et al.,* 1999). Finally, the haplotype diversity (h) and nucleotide diversity (π) for each Silkie population (Nei, 1987) were estimated using DnaSP 4.10 (Rozas *et al.,* 2003).

Results

A total of 27 polymorphic sites, including 26 transitions and one transversion, were found in 126 mtDNA sequences (each with a length of 519 bp). Twenty-one haplotypes were defined and all of them could be found in the data set reported by Liu *et al.* (2006a) (Fig. 1). The 21 haplotypes could be classified into six haplogroups (A-E, G). Briefly, six haplotypes belonged to haplogroup A, two haplotypes in haplogroup B, two haplotypes in haplogroup C, three haplotypes in D haplogroup, seven haplotypes in haplogroup E, and one haplotype in haplogroup G. Among them, haplotypes A2, C1, B1, E1, and B13 were dominant and were shared by 23, 22, 21, 20, and 12 samples, respectively. Nine haplotypes occurred in one sample. Each of the seven haplotypes (A6, A11, A18, D6, D13, E6, and E9) occurred in 2–4 samples. Haplotypes A 2 and B1 were shared by individuals from all four Chinese Silkie populations and one Japanese Silkie population. However, haplotypes E1 was shared by 19 individuals exclusively from the Bairong Silkies and one Japanese Silkie. When we counted the number of haplotypes according to the Silkie populations, 13 haplotypes were detected in Japanese Silkies, five haplotypes in Bairong Silkies, seven haplotypes in Taihe Silkies, five haplotypes in Chengdu Silkies, and five haplotypes in Hubei Silkies.

The phylogenetic relationship among the six haplogroups was displayed in the NJ tree (Fig. 2a), and was

Table 1. **Sample information and genetic diversity of Silkies**

Breed	No.	Location	GenBank Accession number	Haplotype diversity	Nucleotide diversity	Reference
Bairong Silkie	26	Fujian, China	GQ227993-GQ228018	0.462±0.114	0.00509±0.00182	This study
Taihe Silkie	27	Jiangxi, China	AY465988-AY465991; AF512221-AF512233, AF512273-AF512282	0.838±0.034	0.01123±0.00109	Liu *et al.,* 2006a
Chengdu Silkie	15	Sichuan, China	AF512060, AF512062-AF512075	0.848±0.061	0.00811±0.00202	Liu *et al.,* 2006a
Hubei Silkie	24	Hubei, China	AF512189-AF512209; AF512234-AF512236	0.764±0.042	0.00812±0.00146	Liu *et al.,* 2006a
Subtotal in China	92	—	—	0.851±0.015	0.01168±0.00052	
Japanese Silkie	34	Japan	AB007733, AB007735, AB007740, AB007746, AB007747; AB114070, AB114071; AB263947-AB263970, AB263974-AB263976	0.841±0.056	0.01219±0.00106	Data deposited in GenBank by Miyake, T.
Total	126	—	—	0.882±0.012	0.01298±0.00030	

	11222222	2222233333	3333334						
	2269111244	4568900011	2344664	B	T	C	H	J	
	1979027523	6611626805	2027376	R	H	D	B	P	T
ST	CCCTTGTTGT	CTCACCTCCC	TCAACTC						
A2	....C.....	....	....	1	6	5	8	3	23
A6	....C.....	.C........	....	-	3	-	-	1	4
A7	....C..C..	....	....	-	-	-	1	-	1
A11	....C.....	........T.	....	-	-	2	-	-	2
A16	..T.C.....	....	....	-	1	-	-	-	1
A18	....CA....	....	....	-	-	2	-	-	2
B1	..T.CA.C..	T........T	....	2	7	3	6	3	21
B13	..T.CA.C..	T........T	.T.....	-	3	2	7	-	12
C1	..T.C..CAC	.C.G....T.	..G.TC.	1	6	-	2	13	22
C20	..T.C..CAC	.C.G...TT.	....TC.	-	-	-	-	1	1
D6	..T.C..C.C	.CTG..C.T.	..G....	-	-	-	-	3	3
D13	..T.C..C.C	.CTG..C.T.	....	-	-	-	-	3	3
D27	..T.C..C.C	.CTG....T.	..G...T	-	-	-	-	1	1
E1	..T.C.CC.C	.CT.....T.	......T	19	-	-	-	1	20
E3	..T.C.CC.C	.CT.....T.	.T....T	-	-	-	-	1	1
E5	..T.C.CC.C	.CT.....T.	....	-	1	-	-	-	1
E6	..TCC.CC.C	.CT.....T.	......T	3	-	-	-	-	3
E9	..T.C.CC.C	.CT.....T.	..G...T	-	-	-	-	2	2
E19	.TT.C.CC.C	.CT.....T.	.T....T	-	-	-	-	1	1
E20	TTT.C.CC.C	.CT.....T.	.T....T	-	-	-	-	1	1
G3	..T.CA.C.C	.CT.AT..TT	C..G..T	-	-	1	-	-	1

Fig. 1. **mtDNA sequence variations of 21 haplotypes identified in 126 Silkie samples collected in this study and from published sources.** The haplotypes were aligned to *G. g. domesticus* complete mtDNA sequence (Desjardins and Morais, 1990) and were defined according the classification system in our previous study (Liu *et al.,* 2006a). The number of individuals sharing the same haplotype in different populations is listed below the abbreviations for each population (BR-Bairong Silkie; TH-Taihe Silkie; CD-Chengdu Silkie; HB-Hubei Silkie; JP-Japanese Silkie). The column "T" shows the total number of individuals shared each haplotype. Dots (·) denote the identity with the reference sequence. Short lines (-) represent the absence of certain haplotype in the population.

further demonstrated by a network graph (Fig. 2b). The topology of the tree based on the Silkie haplotypes was consistent with the pattern observed in a large domestic chicken data set (Liu *et al.,* 2006a). Among the 34 Japanese Silkies, 13 samples were distributed in haplogroups D and E, whereas the remaining 21 samples could be classified into haplogroups A, B, and C. For the Taihe, Chengdu, and Hubei Silkies, nearly all samples were distributed in haplogroups A, B, and C, with the exception of two samples belonging to haplogroups E and G, respectively. In contrast, 22 Bairong Silkies (84.6%) from Fujian, China, were distributed in haplogroup E, while four samples in haplogroups A, B, and C. Among the six haplogroups, D and G were exclusively found in Japanese Silkies and Chinese Silkies, respectively. The frequencies of haplogroups A, B, and E were higher in Chinese Silkies than in Japanese Silkies, but the frequency of haplogroup C was higher in Japanese Silkies (Table 2). Furthermore,

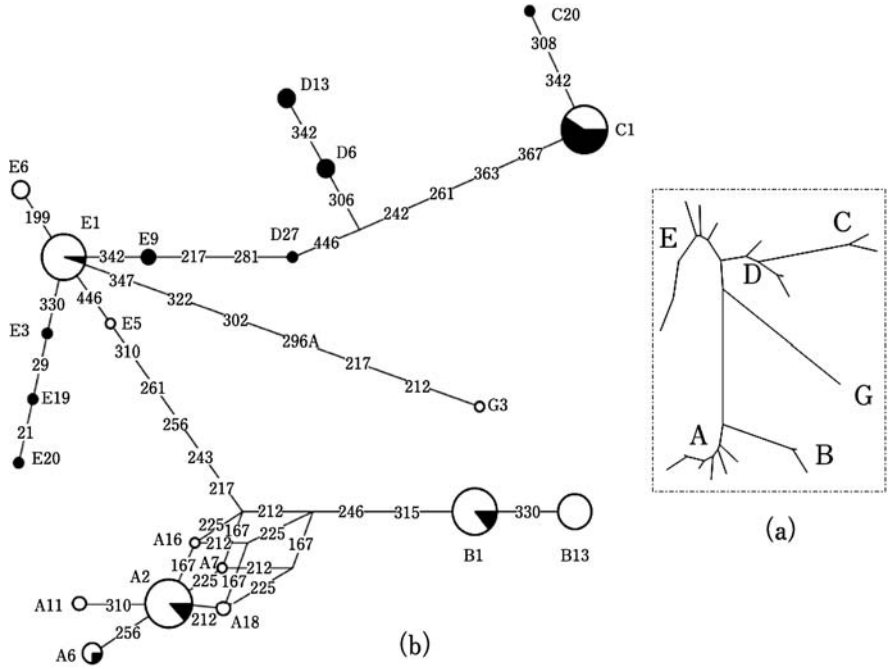

Fig. 2. **The unrooted neighbor-joining (NJ) tree (a) and the network graph (b) of the mtDNA haplotypes in Silkie samples.** The links are labeled by the nucleotide positions to designate transitions. Circle areas are proportional to haplotype frequencies. White and black colors were denoted for Chinese and Japanese Silkies, respectively.

Table 2. **Haplogroup distribution frequency in Chinese and Japanese Silkies**

Haplogroup	A	B	C	D	E	G
Chinese Silkies	31.5% (29/ 92)	32.6% (30/ 92)	9.8% (9/ 92)	0	25.0% (23/ 92)	1.1% (1/ 92)
Japanese Silkies	11.8% (4/ 34)	8.8% (3/ 34)	41.2% (14/ 34)	20.6% (7/ 34)	17.6% (6/ 34)	0
Total	26.2% (33/126)	26.2% (33/126)	18.3% (23/126)	5.6% (7/126)	23.0% (29/126)	0.8% (1/126)

Note: Haplogroups were defined in Liu *et al.* (2006a).

five haplotypes were shared by Japanese Silkies and Chinese Silkies, whereas eight haplotypes were exclusively found in Japanese Silkies.

The mean haplotype diversity and nucleotide diversity were 0.882 ± 0.012 and 0.01298 ± 0.00030 for all chicken samples, respectively. For different Silkie populations, both the Chengdu Silkies (0.848 ± 0.061) and Japanese Silkies (0.841 ± 0.056) presented a high value of haplotype diversity. The Bairong Silkies had the lowest haplotype diversity (0.462 ± 0.114) and nucleotide diversity (0.00509 ± 0.00182). Overall, Chinese Silkies had a relatively equal diversity with Japanese Silkies (Table 1).

Discussion

With the improvement of living standard in China, to develop special and favorable strain/breed of farm animals has received more attention in recent years. Due to the medical property and beautiful appearance, many researchers have attempted to improve the production levels of Silkies (He, 2003). To know the genetic structure and diversity of certain domestic animal is essential for developing rational breeding programs. mtDNA sequence variations have been proved to be a useful tool in analyzing the genetic structure and tracing the matrilineal origin of domestic birds (Liu *et al.,* 2006a; He *et al.,* 2008). Fu and colleagues (2002) studied the genetic relationship between Silkies and other chicken breeds using mtDNA sequence variations, and detected no obvious differentiation. This result was further confirmed in our subsequent analysis of chicken mtDNA sequences from various

breeds (Liu *et al.,* 2006a). However, both studies did not discuss the genetic relationship between the Chinese and Japanese Silkies.

By employing the recently described chicken mtDNA classification system (Liu *et al.,* 2006a) and available mtDNA data, we compared the matrilineal components of Chinese and Japanese Silkies, with an intention to learn more about the past history of the Silkies. In particular, we collected new samples from the Bairong Silkie, which has been thought to be one of the ancestor populations of modern Silkies in China (Qiu *et al.,* 1988). Out of the nine highly divergent mtDNA haplogroups that were defined by Liu *et al.* (2006a), six were found in the 126 samples from Japanese and Chinese Silkies. Such a pattern further confirmed the complexity of domestic chicken matrilineal components at the breed level. Among the four Chinese Silkie populations, Bairong Silkies differed from the other three breeds/populations (Taihe, Chengdu, and Hubei Silkie) by harboring different frequencies of haplogroups. This difference, if not formed during the later breed selection and cultivation, would suggest for a different origin of Bairong Silkies. On this point, we would think that our result supported the notion for dual ancestor populations for modern Silkies in China (Qiu *et al.,* 1988; Xie, 1995). Normally, one would expect to detect higher genetic diversity in the founder or initial breed source population than in derived populations. However, we observed a very low genetic diversity in Bairong Silkies compared with the other Silkie populations, and this result would reject the presumably ancestral status of the breed. Because of wide application of intensive artificial selection during the breeding, the rejection of null hypothesis here is understandable. Nonetheless, the low genetic diversity of Bairong Silkie would call for essential attention for conservation and sustainable usage of this breed.

The relationship between Chinese domestic chicken and Japanese domestic chicken has been profoundly analyzed in previous reports (Komiyama *et al.,* 2003, 2004; Oka *et al.,* 2007). All these studies suggested that the Japanese domestic chickens were originated independently from Southeast Asia and the mainland China (Komiyama *et al.,* 2003, 2004; Oka *et al.,* 2007). In our previous study (Liu *et al.,* 2006a), we showed that the distribution of main mtDNA haplogroups in chicken presented geographic pattern: haplogroups A, B, and E were distributed ubiquitously in Eurasia; haplogroup C was prevalent in Japan and Southeast China; haplogroups F and G were exclusive to Yunnan, China; haplogroup E was dominated in Europe, the Middle East, and India. In this study, the 13 haplotypes identified in 34 Japanese Silkies belonged to five haplogroups. Specifically, the majority of Japanese Silkie samples (79.4%) could be classified into haplogroups C, D, and E. This pattern is in sharp difference with that of Chinese Silkies, in which haplogroups A, B, and E were prevalent. The high prevalence of haplogroup E in both Japanese Silkies and Chinese Silkies would point to their genetic connection in history. Conversely, the high frequency of haplogroup D, which has been found to be closely related to the distribution of the pastime of cock fighting (Liu *et al.,* 2006a, b), in Japanese Silkies distinguished itself clearly from the Chinese Silkies. In short, our results provided evidence for the genetic connection between Chinese and Japanese Silkies, but also demonstrated the difference between the matrilineal genetic structures of these Silkies.

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