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Complete Mitochondrial Genome Analysis Clarifies the Enigmatic Origin of Haplogroup D in Japanese Native Chickens

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Japanese native chickens (JNCs) comprise approximately 50 breeds, making Japan a diversity hotspot for native chicken breeds. JNCs were established through the repeated introduction of chickens from foreign countries. Jidori, which is the generic name of JNC breeds whose ancestral morphology resembles that of their wild progenitor (red junglefowls), is generally thought to have propagated from north East Asia (Korea and north China) to ancient Japan. However, mitochondrial haplogroup D, which is abundant in Island Southeast Asia (ISEA) as well as the Pacific but relatively rare in other regions, can be observed in some Jidori breeds (e.g., Tosa-Jidori, Tokuji-Jidori) with high frequency, leading to speculation that chickens from ISEA or the Pacific also contributed genetically to JNCs. To test this hypothesis, we sequenced the mitochondrial genomes of Jidori breeds and conducted phylogeographic analysis. Our results indicate that the JNC Haplogroup D belongs to Sub-haplogroup D2, which is currently only observed in Xinjiang, northwest China, and not to Sub-haplogroup D1, which is widely distributed in the ISEA–Pacific region. The other mitochondrial haplogroups of Jidori examined in this study also showed affinity to those of chickens native to north East Asia. Therefore, our findings support the north East Asian origin hypothesis for Jidori.

Key words: Austronesian, Pacific chickens, Sub-haplogroup D1, Sub-haplogroup D2, Tokuji-jidori

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Introduction

Domestic chickens have played an important role in human history, not only as a source of animal protein, but also in a socio-cultural context (Herrera *et al*., 2020). Additionally, domestic chickens have been translocated to every inhabited region of Earth from their domestication origins through human mediation (migration and trading) because of their small body size compared with that of other common livestock. Accordingly, it is important to elucidate when and from where chickens have propagated to gain a better understanding of historical interactions among ethnic groups in terms of material and non-material cultures.

Japan is a diverse hotspot of chicken breeds, and Japanese native chickens (JNCs) comprise approximately 50 breeds (Tsudzuki 2003). Domestic chickens are thought to have been repeatedly introduced from foreign countries into Japan, establishing the extant varieties of JNCs in a multi-layered manner (Oana 1951, Oka *et al*., 2007, Yonezawa *et al*., 2020). Archaeological evidence suggests that chickens were first brought to Japan during the Yayoi period (1000–300 BCE to 300 CE) for ritual purposes rather than as a food resource (Eda 2018). Chickens also play an important role in Japanese myths, as described in chronicles such as *Kojiki* (712 CE) and *Nihon Shoki* (720 CE). Thus, considering the deep impact of chickens on the spiritual culture of ancient Japan, clarifying the geographic origins of JNCs can provide considerable information to broaden our understanding of how the basis of ancient Japanese culture was established through intercommunion with other cultural spheres.

Here, we focus on "Jidori," which is the generic name for JNC breeds that retain the morphologically ancestral characteristics seen in their wild progenitors (the red junglefowls),

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because Jidori is thought to have been introduced to Japan at an early stage of Japanese history, probably during the Yayoi period (Oana 1951). The mitochondrial haplotypic components of JNCs present considerable similarities with those of native chickens in north East Asian regions as well as Tibet and Taiwan, suggesting that JNCs, including Jidori, were repeatedly introduced mainly from Korea or North China (Yonezawa *et al*., 2020). On the other hand, the proportion of mitochondrial Haplogroup D, which is particularly abundant in Island Southeast Asia (ISEA: mainly Indonesia and the Philippines) and the Pacific islands but relatively rare in other regions, occurs at a high frequency in JNCs (Miao *et al*., 2013, Oka *et al*., 2007, Hata *et al*., 2020, Yonezawa *et al*., 2020), especially in Tosa-Jidori and its related breeds (e.g., Uzura-Chabo) as well as Tokuji-Jidori. Tosa-Jidori is a small Jidori breed that is regarded as the most ancient JNC breed. Accordingly, Oka *et al*. (2007) suggested that some JNC breeds, such as Tosa-Jidori, originated directly from the ISEA, rather than from China and Korea.

Austronesian people are widely distributed in the ISEA and Pacific and further present in Madagascar. Although no genetic evidence supports the arrival of Austronesians to the Japanese Archipelago in ancient times (GenomeAsia100K Consortium 2019, Gakuhari *et al*., 2020, Wang *et al*., 2021, but see also Matsumoto, 2009), several archaeological (Oda, 1992, Yamagiwa *et al*., 2019) and linguistic (Hudson, 1999, Robbeets, 2017) studies suggest signatures of ancient cultural interactions between Austronesian and Japanese people. Furthermore, Tokutaro Yasuda (1898−1983) investigated the appellations of chicken breeds in Southeast and East Asian countries and pointed out some similarities between Malay, Indonesian, and Japanese appellations (Matsumura 1977). Therefore, the hypothesis described in Oka *et al*. (2007) is attractive in taking account of the material and non-material cultural interactions between Japanese and Austronesian cultural spheres, as suggested in the *Ocean Road* hypothesis by Kunio Yanagita (1875−1962).

However, Haplogroup D also occurs at low frequencies in North China and surrounding regions (Miao *et al*., 2013, Huang *et al*., 2018). Xiang *et al*. (2014) further demonstrated that the frequency of Haplogroup D increased episodically in Middle China from 2000 to 3000 years before present, roughly corresponding to the Yayoi period (1000−300 BCE to 300 CE). Therefore, the north East Asian origin hypothesis of Haplogroup D for JNCs cannot be rejected. The proportion of Haplogroup D in each Asian chicken population is shown in Fig. 1. Since variable haplogroup nomenclature has been used by different research groups (Liu *et al*., 2006, Oka *et al*., 2007, Xiang *et al*., 2014), we followed the definition proposed by Liu *et al*. (2006), updated by Miao *et al*. (2013) and Huang *et al*. (2018), unless noted otherwise.

The current difficulties in elucidating the geographic origins of JNC breeds arise mainly from the low resolution of phylogeographic structures based on mitochondrial D-loop sequence analysis. This study aimed to examine the geographic origin of Jidori breeds, focusing on the north East Asian origin hypothesis and the ISEA–Pacific origin hypothesis, based on mitochondrial genome analysis.

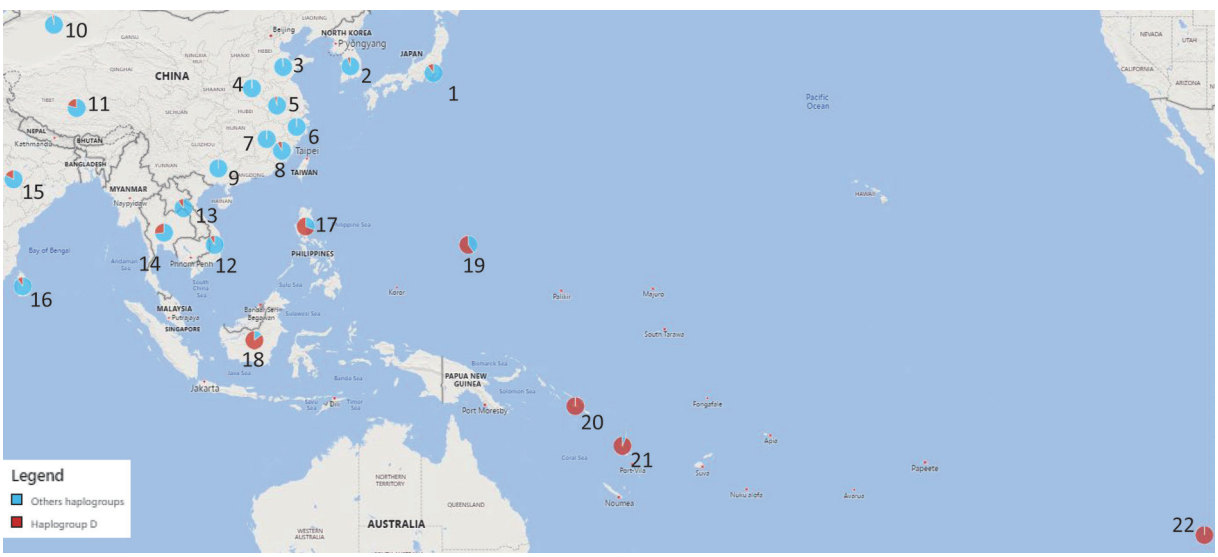

Fig. 1. **Distribution and frequencies of Haplogroup D in Asia and the Pacific.** The frequencies of Haplogroup D (red) and other haplogroups (blue) in each region are shown in pie charts. The locality names are as follows: 1. Japan, 2. Korea, 3. Shandong, China, 4. Henan, China, 5. Anhui, China, 6. Zhejiang, China, 7. Jiangxi, China, 8. Fujian, China, 9. Guangxi, China, 10. Xinjiang, China, 11. Tibet, China, 12. Vietnam, 13. Laos, 14. Thailand, 15. India, 16. Sri Lanka, 17. Philippines, 18. Indonesia, 19. Guam, 20. Solomon Islands, 21. Vanuatu, 22. Easter Island.

Materials and Methods

Purified DNA samples of JNCs provided by FASDA (The Foundation for Academic Specimens of Domesticated Animals) were used for the experiments. The complete mitochondrial genome sequences of Tokuji-Jidori (two individuals) and Aizu-Jidori (one individual) were determined using the procedures described by Osman *et al*. (2021), and they were deposited in DDBJ under accession numbers LC627429–LC627431. Details of these breeds are provided in the Supplementary Materials. The complete mitochondrial genomes of 236 domestic chickens and red junglefowls were retrieved from NCBI, except for sequences reported by Huang *et al*. (2018), which were kindly provided by Prof. Xun-He Huang for this study. These 236 published sequences and the three new sequences obtained in this study were automatically aligned using the MAFFT program ver. 7.428 (Rozewicki *et al*., 2019). A maximum likelihood (ML) tree was constructed using the IQ-TREE program ver. 2.1.1 (Nguyen *et al*., 2014) with the TN93+F+I+Γ model selected by the Bayesian information criterion (BIC). To evaluate the confidence of internal nodes, the bootstrap (BP) method was applied with 10,000 replications. Differences between the likelihood scores of the ML tree topology and alternative topologies were statistically evaluated using the Kishino–Hasegawa (KH) test (Kishino and Hasegawa 1989). Bayesian inference was conducted to reconstruct a phylogenetic tree using MrBayes ver. 3.2.7 (Ronquist *et al.*, 2012) using the Markov Chain Monte Carlo (MCMC) method for 10,000,000 generations. Trees were sampled every 1,000 generations, and the first 1,000,000 generations were discarded as the burn-in period. The convergence of the parameters was confirmed by checking that the effective sample sizes (ESSs) for all parameters were >200 using TRACER ver. 1.7. (Rambaut *et al*., 2018). Because the TN93 model is not available in MrBayes, the second-best model in BIC (the HKY+F+I+Γ model) was used for this analysis. Nucleotide diversity within the populations and net genetic distances among them were estimated using MEGA ver. 7 (Kumar *et al*., 2016). The uncorrected p-distances between individuals under the complete deletion option were used to compute these statistics. Phylogenetic relationships among populations were inferred using the Neighbor-Net method (Bryant and Moulton, 2004) in SplitsTree ver. 4 (Huson and Bryant, 2006) based on net genetic distances. If the net genetic distance between populations had a negative value, we used a value of zero instead.

Results

A simplified ML tree for 239 chickens and red junglefowls, as inferred from their complete mitochondrial genome sequences, is shown in Supplementary Fig. S1. The Bayesian phylogenetic tree revealed fundamentally consistent branching patterns (data not shown). These topologies are essentially in agreement with those of previous trees (Miao *et al*., 2013, Huang *et al*., 2018). One Tokuji-Jidori (TKJ06) used in this study belonged to Haplogroup D (Figure 2), and the other (TKJ08) belonged to Haplogroup A (Supplementary Fig. S2), based on maximum support values. In contrast, the Aizu-Jidori (AIZ25) used in this study belonged to Haplogroup C (Supplementary Fig. S3). Here, our discussion is focused on Haplogroup D, and the detailed arguments for Haplogroups A and C are presented in the Supplementary text.

Although Haplogroup D is not a dominant haplogroup in most regions of the world, it occurs at a high frequency in the Pacific region (Miao *et al*., 2013). In Figure 1, the proportions of Haplogroup D and other haplogroups are summarized, based on previous reports (Miao *et al*., 2013, Herrera *et al*., 2017, Huang *et al*., 2018). The frequencies of Haplogroup D in each region were as follows: 1. Japan (10.5%), 2. Korea (5.6%), 3. Shandong, China (1.7%), 4. Henan, China (0.6%), 5. Anhui, China (4.5%), 6. Zhejiang, China (0.5%), 7. Jiangxi, China (0.6%), 8. Fujian, China (8.2%), 9. Guangxi, China (0.5%), 10. Xinjiang, China (3.2%), 11. Tibet, China (20.7%), 12. Vietnam (9.7%), 13. Laos (10.1%), 14. Thailand (27.1%), 15. India (17.7%), 16. Sri Lanka (9.5%), 17. Philippines (69.0%), 18. Indonesia (85.6%), 19. Guam (60.0%), 20. Solomon Islands (100%), 21. Vanuatu (94.0%), 22. Easter Island (100%). Haplogroup D was also distributed at low or middle frequencies in the surrounding regions in the Pacific Ocean. However, as there are no diagnostic sites defining sub-haplogroups within Haplogroup D in the D-loop region, the detailed historical relationships among these populations are not well known. A magnified view of Haplogroup D, based on complete mitochondrial genome sequences, is shown in Fig. 2. As indicated by Huang *et al*. (2018), Haplogroup D can be separated into five sub-haplogroups (D1−D5). Sub-haplogroups D4 and D5 each consisted of a single wild individual: HXH23 from Guangxi, China for Sub-haplogroup D4 and HXH43 from Thailand for Sub-haplogroup D5. On the contrary, Sub-haplogroups D1 to D3 comprised of two or more individuals, and these three sub-haplogroups were supported by the maximum BP value and posterior probability (PP).

All domestic fowls from ISEA as well as the Pacific Islands belong to Sub-haplogroup D1. Those from mainland China (Yunnan) and continental Southeast Asia (Laos) were placed in basal positions in this Sub-haplogroup. Conversely, all chickens from islands (ISEA and Pacific) formed two major clades (the ISEA clade and the ISEA–Pacific clade), except for two individuals from Indonesia (Manado Sulawesi: KY039428) and the Philippines (Tugop: KY039399), which were placed at basal positions of Sub-haplogroup D1. The ISEA clade was moderately supported (BP: 41%; PP: 0.96) and consisted of Indonesian and Philippine chickens. Comparatively, the ISEA–Pacific clade was also moderately supported (BP: 75%; PP: 1), consisting of chickens from not only the Philippines but also New Guinea, Hainan (China), and the Pacific islands in Melanesia (New Caledonia, Vanuatu, Fiji) and Polynesia (Niue, Hawaii, Marquesas, Easter Island). Melanesian and Polynesian chickens formed a sub-clade (the Pacific subclade) within the ISEA–Pacific clade with the maximum support value.

Tokuji-Jidori (TKJ06) was placed within Sub-haplogroup D2. Currently, in addition to TKJ06, only one chicken of the

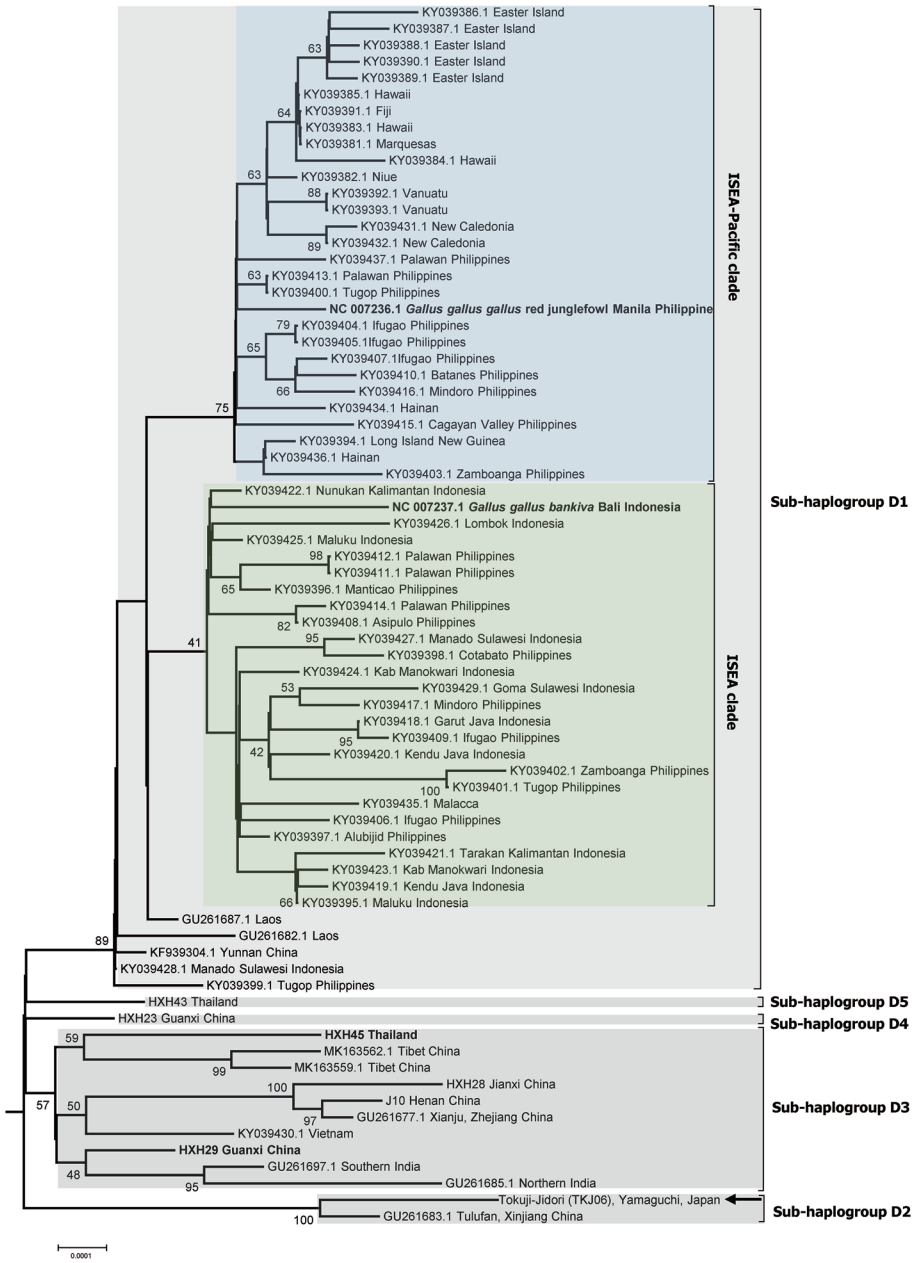

Fig. 2. **Phylogenetic relationships within Haplogroup D.** This figure shows a magnified view of Haplogroup D in the ML tree based on 239 chickens and red junglefowls (the complete tree is shown in Supplementary Figure S1). Nodal numbers indicate bootstrap probabilities with 10,000 replicates (only BP values > 40% are shown). Branch lengths were proportional to the number of nucleotide substitutions (scale bar indicates 0.0001 substitutions/site). Accession numbers, breed information (if available), and geographical information are provided for each individual. The JNC breed Tokuji-Jidori is marked with an arrow. Wild individuals are shown in bold font.

Tulufan breed from Xinjiang (China) is known to belong to this sub-haplogroup. Sub-haplogroup D3 consisted of red junglefowls from China (Guangxi) and Thailand, and domestic chickens from China (Zhejiang, Jianxi, Henan, Tibet), Vietnam, and India. Finally, the phylogenetic position of Tokuji Jidori (TKJ06) was statistically examined using the KH test. Although the phylogenetic hypothesis that TKJ06 forms a monophyletic group with HXH23 within Sub-haplogroup D5 could not be completely rejected (p=0.119), other alternative phylogenetic hypotheses that placed TKJ06 within Sub-haplogroups D1, D3, and D4 were rejected at a significance level of 5%.

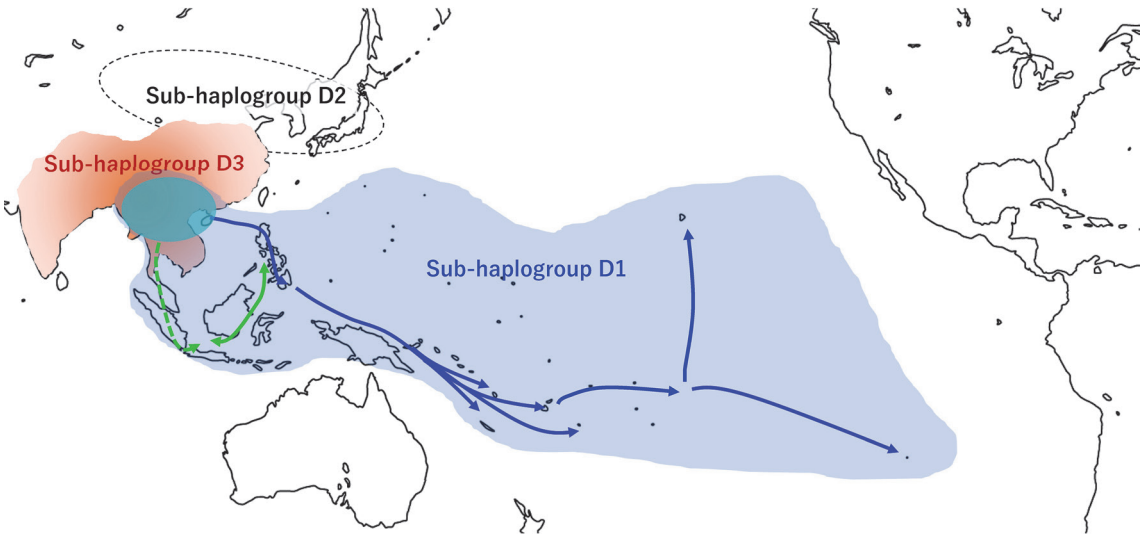

Fig. 3. **Putative geographical distribution areas of Sub-haplogroups D1−D3.** Putative distribution areas of the sub-haplogroups within Haplogroup D are shown. The precise range of Sub-haplogroup D2 is unknown, because only two individuals sampled from widely separated regions (Japan and Xinjiang, China) are known for this sub-haplogroup. The propagation routes of the ISEA clade (green arrows) and ISEA–Pacific clade (blue arrows) are based on phylogenetic branching patterns. Because the route(s) through which the ISEA clade was introduced to Indonesia and the Philippines could not be identified from the phylogenetic branching pattern, speculative propagation routes of the ISEA clade are indicated by the dashed and double-headed arrows.

The phylogenetic network among the populations based on Haplogroup D is shown in Supplementary Figure S4. This network also indicates that the ISEA–Pacific native chickens formed a distinct cluster, and native Japanese and Xinjiang chickens formed another independent cluster. This result also suggests that Haplogroup D in Japanese native chickens did not originate from the ISEA-Pacific native chickens.

Discussion

Our previous work based on D-loop sequences, suggested that Jidori breeds propagated from East Asia (Yonezawa *et al*., 2020). Yonezawa *et al*. (2020) focused on the evolutionary relationships among local populations because of the weak phylogeographic structure of domestic chickens. Here, we performed phylogenetic analysis based on the sequences of the complete mitochondrial genomes (Fig. 2, Supplementary Figs. 2 and 3). As discussed in the Supplementary Materials, Tokuji-jidori (TKJ08), belonging to Haplogroup A, and Aizu-Jidori (AIZ25), belonging to Haplogroup C, are thought to have originated from East Asia. Notably, the geographic origin of the ancestor of AIZ25 can be specified as the Yellow–Huai River Basin and Yangtze Plain (Supplementary figure 3) owing to the fine phylogeographic structure of Haplogroup C (Huang *et al*., 2018). Thus, phylogeographic analysis based on complete mitochondrial genomes can provide new insights into the origin of Jidori breeds at a high resolution. Therefore, we focused on the phylogeographic structure of Haplogroup D and discussed the enigmatic origin of this haplogroup in Japanese native chickens.

The branching patterns within Sub-haplogroup D1 suggest that the domestic chickens of Sub-haplogroup D1 propagated from continental Southeast Asia (including South China) to the Indonesia–Philippines region. Regarding the absence of Indonesian chickens in the ISEA–Pacific clade, it is also possible that this clade directly propagated from South China (Hainan Island) to the Philippines. Concerning the ISEA–Pacific clade, Pacific populations (Melanesian and Polynesian populations) arose through the dispersal of the Philippine population. The populations on Fiji, Hawaii, Marquesas, and Easter Island formed a small clade. This branching pattern is largely consistent with the historical scenario proposed by Thomson *et al*. (2014) based on ancient DNA analysis of Pacific chickens.

The dispersal processes of Pacific chickens largely reflect those of Austronesian people (Fig. 3). However, although it is generally accepted that Austronesian people originated in Taiwan (Melton *et al*., 1998, Lipson *et al*., 2014, Soares *et al*., 2016), the branching pattern of Sub-haplogroup D1 indicates their propagation from continental Southeast Asia (including South China) to the Pacific. This finding suggests that Austronesians did not possess chickens at the time of out-of-Taiwan migration (~4300 BCE: Diamond, 2000). Yonezawa *et al*. (2020) demonstrated that Taiwanese native chicken populations form a genetic cluster with North Chinese and West Chinese (e.g., Tibet, Qinghai, Xinjiang) native chickens, together with Japanese and Korean native chicken populations, and named this cluster the Northeast Group. These findings suggest that the native chicken population was introduced to Taiwan from mainland China after the exodus of Austronesians (Fig. 3). On the other hand, because of the considerable

migration of Han people from mainland China during or after the 17th century CE, the ethnic composition of the Taiwanese population drastically changed. Therefore, it is also possible that the genetic component of modern Taiwanese native chickens does not reflect that of ancient Taiwanese native chickens at the time of the exodus of Austronesians, if such chickens indeed existed. A detailed genetic analysis of native chickens kept by Taiwanese aborigines or ancient DNA studies of pre-17th century archaeological remains of chickens will be necessary to elucidate this issue in future research.

In comparison with Sub-haplogroup D1, taxon sampling within the Sub-haplogroups D2 and D3 is currently limited. However, for Sub-haplogroup D3, the inclusion of red junglefowls and geographic information on domestic and wild fowls suggests that members of this sub-haplogroup were domesticated in Southeast Asia, including South China, and then spread northward to the Yangtze Plain and westward to India (Fig. 3). In contrast, Sub-haplogroup D2 had no wild progenitors and only included two domestic fowls. Therefore, it is very difficult to establish a complete picture of the geographic range and route of propagation. The two domestic fowls in this sub-haplogroup were sampled from two widely separated regions, Japan and Xinjiang. Considering that Japanese and Xinjiang native chickens belong to the Northeast Group (Yonezawa *et al*., 2020), as mentioned above, the genetic compositions of the Japanese and Xinjiang native chickens are similar in the context of global comparisons. Thus, it is likely that Sub-haplogroup D2 was detected in other populations of the Northeast Group centered in North China (Fig. 3). Regarding the enigmatic origin of Haplogroup D in JNCs, the new findings in this study suggest that it originated from North China and/or its neighboring areas, such as Korea, rather than from the Pacific.

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Author Contributions

T.Y., M.N., Y.Y., T.S., K.K., H.O., H.E. and F.A. conceived and designed the study. T.Y., T.S., H.O., and F.A. obtained molecular data. T.Y., M.N., Y.Y., K.K., H.E., and F.A. performed data analysis and interpreted the results. T.Y. drafted the manuscript and M.N., Y.Y., T.S., K.K., H.O., H.E., and F.A. critically reviewed and improved the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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