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Monophyletic Origin of Domestic Fowls

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論文内容の要旨

With the aim of elucidating the evolutionary origin of junglefowls and their domestication processes, the author conducted molecular evolutionary analyses of mitochondrial DNAs for various kinds of birds belonging to the subfamily Phasianinae. He then found that the real matriarchic origin of all the domestic fowls examined in the present study was an Asian continental population of *Gallus gallus gallus*. The phylogenetic analysis conducted in this study also suggested that the continental population of *Gallus gallus gallus* is the monophyletic ancestor of all domestic fowls. These findings resolve the long-time controversy concerning monophyletic versus polyphyletic origin theories of domestic fowls.

The present thesis is composed of four chapters. In Chapter 1, as an introduction, the author described the evolutionary significance of the domestication processes of junglefowls and the overview of taxonomical problems of birds within the subfamily Phasianinae, particularly junglefowls and domestic fowls.

In Chapter 2, attention is focused on the molecular phylogeny of the subfamily Phasianinae. Comparisons of DNA sequences for mitochondrial control regions among 16 avian species belonging to the subfamily Phasianinae, revealed the following: (1) Generalized perdicine birds (quails and partridges) are descended from ancient lineages. Even the closest pair, the common quail of the Japanese subspecies (*Coturnix coturnix japonica*) and the Chinese bamboo partridge (*Bambusicola thoracica*), maintained only a 85.71% identity. (2) The 12 species of phasianine birds previously and presently studied belong to three distinct branches. The first branch is made up exclusively of members of the genus *gallus*, while the second branch is made up of pheasants of the genera *Phasianus*, *Chrysolophus* and *Syrmaticus*. Gallopheasants of the genus *Lophura* are distant cousins to these pheasants. The great argus (*Argusianus argus*) and peafowls of the genus *Pavo* constitute the third branch. Members of the fourth phasianine branch, such as tragopans and monals, were not included in the present study. (3) The one perdicine species, *Bambusicola thoracica*, is more closely related to the phasianine genera *Gallus* and *Pavo* than to members of other perdicine genera. The above might indicate that *Bambusicola* belongs to one stem of the perdicine lineage which later split into two sublineages that yielded phasianine birds; one evolving to *Gallus*, while the other differentiated toward *Pavo* and related genera. (4) Tandem duplication of the 60-base

unit was established as a trait unique to the genus *Gallus*, which is shared neither by pheasant nor by quail.

In Chapter 3, the author discuss evolutionary relationships between red and green junglefowls. The noncoding control region of the mitochondrial DNA of various gallinaceous birds was studied with regard to its RFLP (restriction fragment length polymorphism) and sequences of the first 400 bases. Unlike its close ally green junglefowl, the red junglefowl *Gallus gallus* is a genetically very diverse species; a 7.0% sequence divergence was seen between those from Thailand (*Gallus gallus gallus* and *Gallus gallus spadiceus*) and that of the Indonesian island of Java (*Gallus gallus bankiva*). Furthermore, the divergence increased to 27.83% when each transversion was regarded as an equivalent of 10 transitions. On the other hand, a mere 0.5-3.0% difference (all transitions) separated various domestic breeds of chicken from two subspecies of *Gallus gallus gallus* of Thailand, thus indicating a single domestication event in the area inhabited by this subspecies, with the red junglefowl being the origin of all domestic breeds. Only transitions separated six diverse domesticated breeds. Nevertheless, a 2.75% difference was seen between RFLP type I breeds (white leghorn and nagoya) and a RFLP type VIII breed (*ayam pelung*). The above data suggest that although the mitochondrion of RFLP type V is the main contributor to domestication, hens of other RFLP types also contributed to this event.

Finally, in Chapter 4, the evolutionary origin and dispersal patterns of domestic fowls are discussed from various aspects of molecular evolution and human history. With the aim of elucidating in more detail, the genealogical origin of the present domestic fowls of the world, the author determined mitochondrial DNA (mtDNA) sequences of the D-loop regions for a total of 21 birds which belong to the red junglefowl (*Gallus gallus*) comprising three subspecies (6 *Gallus gallus gallus*, 3 *Gallus gallus spadiceus* and 3 *Gallus gallus bankiva*) and 9 birds representing diverse domestic breeds (*Gallus gallus domesticus*). He also sequenced mtDNAs from 4 green junglefowl (*Gallus varius*), 2 Cingalese junglefowl (*Gallus lafayettei*) and 1 grey junglefowl (*Gallus sonnerati*). He then constructed a phylogenetic tree for these birds using nucleotide sequences, choosing the Japanese quail (*Coturnix coturnix japonica*) as an outgroup. Moreover, he found that a continental population of *Gallus gallus gallus* was the real matriarchic origin of all the domestic species examined in the present study. It is also of particular interest to note that there were no discernible differences among *Gallus gallus* subspecies; *Gallus gallus bankiva* being a notable exception. This was because *Gallus gallus*

spadiceus and a continental population of *Gallus gallus gallus* formed a single cluster in the phylogenetic tree. One obvious and distinct feature that customarily separates *Gallus gallus gallus* from *Gallus gallus spadiceus* is the color of their ear lobes: white for the former and red for the latter. The fact that domestic breeds of the chicken are of two kinds as to color of ear lobes is a clear reflection of the contribution made by *Gallus gallus gallus* as well as by *Gallus gallus spadiceus* to their ancestry. *Gallus gallus bankiva*, on the other hand, is a distinct entity, thus, deserving its subspecies status. This implies that a continental population of *Gallus gallus gallus* was the monophyletic ancestor of all domestic breeds. The author also discuss the possible significance of the initial dispersal pattern of present domestic fowls, utilizing the phylogenetic tree.

論文の審査結果の要旨

本研究は、ニワトリ（家鶏）と野鶏を含む *Gallus* 属および近縁の属の鳥類の系統関係を、ミトコンドリア上の、遺伝子をコードしていない領域であるDループの塩基配列の変異を手がかりとして解明し、家鶏の起源を探ることを目的としている。

申請者はまずキジ亜科（Phasianinae）16種について塩基配列を決定し、分子系統樹を作成した。その中の *Gallus* 属および近縁の属の12種は明瞭な3群に分かれ、野鶏4種（共に *Gallus* 属）はその一つのクラスターを形成した。また、60塩基を単位とする縦列重複構造が *Gallus* 属に特異的に存在することが見出された。次に、2種の野鶏、赤色野鶏（*Gallus gallus*）と緑襟野鶏（*G. varius*）、および家鶏（*G. gallus domesticus*）を RFLP および塩基配列から比較した。赤色野鶏は緑襟野鶏との間で7%の配列の差を示すのに対し家鶏とは0.5～3%の差しかなく、赤色野鶏が家鶏の祖先種であることが示唆された。更に、タイ・インドネシアなど熱帯アジア各地から収集された赤色野鶏と在来家鶏を含む30サンプルを解析したところ、供試した家鶏はインドネシアの在来家鶏も含めて全てが、赤色野鶏の一亜種 *G. gallus gallus* のタイ国原産の系統群と一つのクラスターを作った。インドネシアには、この同じ亜種およびもう一つの亜種（*G. gallus bankiva*）に属する野鶏が分布しているが、それらはいずれも家鶏のグループとは遠縁であることがわかった。従来、家鶏の起源については一元説と多元説が対立していたが、本研究によって、少なくとも母系的には、赤色野鶏の一亜種 *G. gallus gallus* の中の熱帯大陸部の系統が単一の祖先であることが実証された。

本研究は1990年代の初めに開始されたものであり、棲息地におけるサンプルの収集、塩基配列の決定、分子系統樹の作成にいたる一連の研究の結果の大部分は、すでに3篇の原著論文として国際誌に発表済み、あるいは印刷中である。

以上を総合して、この論文の内容は本学の学位授与にふさわしい水準と判断した。