

FIVE-TOED CHICKENS: THEIR ORIGIN, GENETICS, GEOGRAPHICAL SPREADING AND HISTORY

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Abstract. The five-toed chickens have been well known in the history of agriculture and zoology for a long time. Genetically, they represent a mutation of developmental gene(s) that leads to the polydactyly condition observed in five-toed chicken breeds found in China, Japan, England, France, Russia, Turkey, Poland, and Lithuania. We analyzed the ancient and contemporary literature and hypothesize that the polydactyly mutation occurred more than one time and independently in Europe, Asia and, maybe, in the other parts of the world. If the five-toed chickens had several centres of origin or, at least, two in Europe and Asia, the question arises how they were distributed to other parts of the world. We may suggest that they passed along the known ways in history as other chicken populations did. Events in human history that involved chicken diffusion have been occurring over thousands of years, might repeat in opposite directions, and could not always be traced. Recent molecular studies may provide new insight into the problem of the polydactyly and its origin in chickens.

Key words: domestic fowl, distribution, heredity, centres of origin, mutation, polydactyly.

Introduction

Development of extra toes, or polydactyly, is an unusual trait in chickens and in the class Aves in general. Almost all birds have four digits. The prehistoric Archaeopteryx had four toes on the feet and three digits on the wings, whereas the bulk of the avian progenitors — reptiles — possess five and most mammals have also five toes. Five toes in certain chicken breeds are deemed to be a reverse mutation from their distant ancestors or to be a new character not related to the ancestral forms. Origin and historical distribution of the five-toed chickens is not clear yet, though we know that they are currently spread in Europe and Asia. It is well known that first domestic fowls came from Asia to Europe. However, it is uncertain whether the five-toed chickens were brought from Asia to Europe and by what paths, or they originated independently in these two parts of the world.

In this paper, we make an attempt to shed light on some of these problems using available information. Unfortunately, this information is incomplete through the absence

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of archaeological data for five-toed chickens and lack of detailed data for the extant local populations of polydactylous chickens (except for Russian populations). On the other hand, many ancient and modern zoologists and poultry scientists wrote about the five-toed chickens. Since very little critical historical research has been undertaken up to date regarding the origin and spread of the five-toed chickens, we offer this literature investigation supplementing it, where appropriate, with the data from history, geography, genetics and our own observations.

Genetics of polydactyly

What is known about the genetic control of polydactyly? William Bateson (1861–1926), one of the founders of classical genetics gave in 1894 a detailed description of polydactylism in birds including chickens developing five and even six toes (Bateson 1894). Later on, Bateson, Punnett and Hurst (as reviewed by S.G. Petrov 1941) examined heredity of this trait in chickens and showed its incomplete dominant inheritance. Although birds normally carry four toes, sometimes two or three, very rarely a bird may carry five or more toes, as a supposedly reverse mutant deviation from the normal condition or as a new formation. Several distinct chicken breeds have polydactyly as a pure breed characteristic; sometimes this genetically controlled trait can also be unexpectedly found in some local populations and in breeds that have not had it before. This phenomenon may be observed for other dominant or incompletely dominant chicken genes. For instance, there are known cases of spontaneous mutations (or modifications) in the genes for frizzle (*F*), fibromelanosis (*Fm*), naked neck (*Na*), and silver (*S*) as observed by poultry breeders and scientists, including our own observations on occurrence of polydactyly, and described in the literature (e.g., Jones 1921).

The remarkable genetic mutation of polydactyly has been known for centuries and transferred to genotype of a number of modern chicken varieties, the phenomenon being also known in other classes of higher vertebrate animals. From classical poultry genetics (Crawford 1990), it is well known that polydactyly is due to the autosomal gene *Po*, and the basic mode of its inheritance is incomplete dominance. On the other hand, polydactyly is a complex trait influenced by modifier and suppressor genes. Another complication in the inheritance of this trait is the suggestion that some polydactylous as well as nonpolydactylous breeds carry suppressor genes that can completely inhibit the expression of polydactyly in genotypically polydactylous chickens. In the ancient and contemporary five-toed breeds the most probable and frequent gene is the mutant *Po*, with the exception of the chickens, in which the second mutant allele of this gene, *Po^d* (duplicate polydactyly), or a mutation *po-2* (recessive polydactyly) is clearly involved.

The earlier classical observations on complex genetic nature of the chicken polydactyly condition have lately been supplemented with molecular studies showing involvement of more than one gene in the polydactyly manifestation (Arisawa *et al.* 2006; Huang *et al.* 2006). Arisawa *et al.* (2006) detected expression of the sonic hedgehog homolog (*Drosophila*) (*SHH*), bone morphogenetic protein 2 (*BMP2*), and homeobox protein *hoxd13* (*HOXD13*) genes in the presumptive region of the extra digit in the leg buds, and expression of *SHH* and *HOXD13* in the presumptive area of the extra digit in the developing wing bud of Japanese Silkie embryos. Huang *et al.* (2006) found one single nucleotide polymorphism within an exonic (coding) sequence of the limb region 1 homolog (mouse) gene, *LMBR1*, that showed a strong association with the polydactyly in a Silkie population. The association was supposed to be explained by a changed gene splicing effect or, more prob-

ably, by other regulatory mechanisms involving *SHH*. These authors also mapped *LMBRI* on chromosome 2 between the *MCW071* and *ADL0270* microsatellite markers.

The five-toed trait expression in chickens is also subject to environmental factors. As shown by Walter Landauer (Landauer 1948) and others, the expression of polydactylism can be suppressed or shifted to different phenotypes by exposing the developing embryos to low temperatures and injecting them with colchicine and insulin, and can be increased by selection. Impact of environmental factors on polydactyly expression was also found in other animals, for instance, in anurans and other amphibians (Lada 1999; Vorobyeva 1999). Thus, polydactyly stems from morphogenesis disturbance at earlier stages of limb development and may occur as a response to unfavourable environmental conditions, as a reversed or *de novo* mutation, as a modification and as a result of epigenetic processes.

Breeds of five-toed chickens

At present, the main known five-toed breeds are (fig. 1–7): Dorking, Lincolnshire Buff (England), Houdan, Faverolles, Meusienne (France), Sultan (Turkey), Silkie (China), Beijing Fatty (China, partly five-toed), Japanese Silkie (or Ukokkei, Japan), and Pavlov (Russia, in the past partly five-toed). Historically, there might be few more polydactylous breeds, e.g., the original Polish (Poland) and Antokolka (Lithuania*) chickens (Roszkowski & Wartacz, published online; Hutt 1949).

Four breeds, Lincolnshire Buff, Houdan, Faverolles and Meusienne, are believed to have one common source of the fifth toe, the Dorking breed. In spite of its excellent qualities, at present the Dorking is only raised by fanciers in UK, and the breed population number is not very high. Judging from the personal communication data provided by Mrs. Victoria Roberts, Secretary of The Dorking Breed Club, and based on the triennial survey in 2002 among 56 fancy breeders (50%), there was a total of 841 Dorking birds. The Houdan is an ancient French five-toed breed, and similar five-toed chickens were also present in old *Belgica*. La Perre de Roo wrote that “*common fowl* with five toes is found in the neighbourhood of Courtrai, Bruges, Ghent, and other Belgian towns, and also in the northern departments of France, where it has a high and well-merited reputation” (de Roo 1902, as quoted by Brown 1906). Jean-Claude Périquet (1994), speaking of the Houdan, adds: “As for the five toes, it seems that this peculiarity comes from a common five-toed hen (that was very spread in Normandy) rather than from the Dorking”. The latter statement is contradictory to the accepted opinion that Houdans derived from the Dorking. So, it seems that Dorkings are the oldest fowl among the modern European five-toed breeds that are still present at both borders of the English Channel. In the European five-toed breeds, the fifth toe is turned back and up, while there is a split of the first toe in the Japanese Silkie that may be controlled by the other genes.

As for the origin of the other above-mentioned breeds and the source of their fifth toe, this is still unclear. Regarding the Japanese Silkie (or Ukokkei), Arisawa *et al.* (2006) consider that its roots lead to China or India. Some assumptions exist with regard to the Russian origin of the Sultan breed as stated by the German zoologist Bruno Dürigen (1853–1930): “Turkish [or Sultan chicken]. This crested, leg feathered and bearded chicken — *Gallus domesticus* barbato-cristatus, plumipes [bearded, crested and leg feathered domestic cock] reminds among all crested chickens mostly a presumable ancestral form, a leg

* This breed might have originated from Poland as suggested by Hutt (1949) and confirmed by Yu.I. Dmitriev (2008, pers. comm.).

feathered, bearded and crested chicken which is native to Russia for centuries [i.e., Pavlov (or Russian)]” (Dürigen 1921). Although the Pavlov (fig. 6) was quoted by Dürigen as the most probable ancestor of the Sultan breed, there was actually no evidence (archaeological, historical or genetic) for such a conclusion, so this question — Sultans from Pavlovs or vice versa? — is still open. The Pavlov breed was extinct by the beginning of the 20th century (Moiseyeva 1992, 2006). Now it is being reconstructed from several specimens taken from Siberia and Austria. In the process of restitution of Pavlovs, the breeders found about 20–30% of five-toed individuals in their progeny (Yu.I. Dmitriev 2008, pers. comm.).

The German zoologist and Russian academician, Peter Simon Pallas (1741–1811), did not mention five toes in Pavlovs, maybe, because this breed was partly five-toed, but he found other five-toed chickens widespread in Russian Empire (Pallas 1811). Pallas’ observations about chickens were chiefly done during his two scientific expeditions across Russia (1768–1774, 1793–1794), in which he took part by invitation of Russian Empress Catharine II the Great. The expedition routes included regions of both European and Asian parts of the Russian Empire (Yuzhakov 1904). Among the nine chicken populations Pallas (1811) described, three were five-toed (as designated by Greek letters α , δ and ϵ). Then, in the vast Russian Empire — and who knows since how many centuries — there were four sorts of five-toed chickens: rural hens, English, Silkie (Pallas’ varieties α , δ and ϵ , respectively), and partly Pavlovs.

In order to complete the information on five-toed chickens in Russia, we can take into account the data obtained by A.S. Serebrovsky in the expeditions in 1926–1933 across some parts of the Soviet Union (Serebrovsky 1935; archival materials*) as well as our own observations. As a result of a survey done by Serebrovsky and his colleagues among 58 local populations in 23 regions of the European and Asian parts of the USSR, the five-toed fowls occurred with the following frequencies: Shabalino (Vyatka Krai), 1.01%; Bashkiria, 0.05%; Livny (Orel Region), 1.2%; part of North Ossetia, 0.42%; Kabarda, 1.33%; and Balkaria, 0.11%. According to an unpublished N.I. Vavilov Institute of General Genetics survey of collection populations at the Kuchino State Breeding Farm, Moscow Region in 1979, we found out four five-toed individuals (9.3%) out of 43 dwarf chickens of various origins. According to S.G. Petrov (1941), a member of the Serebrovsky’s expedition, there was definitely no import of five-toed breeds into the surveyed regions, although it remains unknown what polydactyly type was observed in the studied populations. As for the Kuchino State Breeding Farm populations, there was a split of the first toe in the five-toed dwarf individuals similar to what can be seen in the Japanese Silkie.

As for the other five-toed breeds, they have a lesser recognition and distribution, except Silkies and Faverolles that are quite popular among chicken fanciers. The famous Italian explorer Marco Polo (1254–1324) was probably the first European who observed the Silkie-like chickens in China in 1271–1275 (Polo 1954). However, he did not mention how many toes they had. Up to date, there are five breeds called Silkie that have the black skin but only one of them is five-toed (Xu & Chen 2003).

Origin and history of domestic chickens

To understand origin and distribution of polydactylous chickens, we will briefly describe the origin centres of the domestic fowl and routes, by which chickens were spread all over the world.

* Russian Academy of Sciences Archive, Collection 1595, Nos. 482, 486, 487.

An earlier hypothesis about chicken origin and spread claims that chickens were first domesticated in the region of Indus Valley (Mohenjo-Daro and Harappa) and then brought to Mesopotamia and Greece, whence the Celts obtained and dispersed them throughout Europe and finally to Britain in the late Iron Age (Darwin 1868; Ivanov 1924; Wood-Gush 1959; Zeuner 1963). A northern route from India to China (1400 BC) and thence to Russia was one of several routes proposed by Sir Edward Brown (1851–1939), all using India as original base (Brown 1929). This point of view had been prevailing for a quite long period. More recently, China (Ho 1977) and Southeast Asia (West and Zhou 1988) were named as the centres of chicken origin, while Akishinonomiya *et al.* (1994–1996) pinpointed Thailand and neighbouring countries. Darwin (1868) adhered to the opinion that chicken domestication occurred in South East Asia and wild fowls were domesticated by the Malays. According to new estimates (Ho 1977; Plant 1986; West and Zhou 1988; Crawford 1995), domestication of chickens dates back about 6,000–8,000 BC.

As compiled by Barbara West and Ben-Xiong Zhou (West and Zhou 1988), of the 90 sites across a vast territory in Europe and Asia for which evidence of chickens was found, seventeen were contemporary with or earlier than 3,200–3,000 BC when domestic chickens first reached (or originated in) India, including China (6,000 BC), Iran (3,900 BC), Turkey (2,900 BC), Romania (6,000 BC), Greece (Neolithic period, 8,000–3,000 BC) and Ukraine (4,000 BC). Here, it is important to understand that these data often belonged in certain cultural layers where chicken remains had been found and these periods might have lasted long enough, but they do not mean exact dating of archaeological findings. West and Zhou (1988) concluded that chickens were first domesticated in Southeast Asia well before the 6th millennium BC and taken north to become established in China by ca. 6,000 BC, whence they were later introduced to Japan via Korea during the Yayoi period (300 BC–300 AD). Therefore, domestication occurred in India much later, either independently or as a diffusion from Southeast Asia. Yet, as long as the archaeological studies continue, it is early to make final conclusions about chicken origin and distribution in the past.

West and Zhou (1988) also concluded that chickens from China were possibly spreading to European Celts via tribes of Russian steppe (Barbara West) or along the Silk Road to Turkistan (Ben-Xiong Zhou). In the literature on chicken dispersion from a domestication centre(s), including the key study by West and Zhou, the Great Silk Road is often indicated as a probable way of chicken transportation from Asia to Europe. The road existed back in 16th to 2nd centuries BC, up to the Middle Ages and even later, depending on sources of historical information. More importantly, there were very ancient ways that were partly utilized in the later times and became a part of the Great Silk Road (A.M. Petrov 1995). These ways were not paved in one direction but the Eastern (China) and Western (the rest of Eurasia) macrocivilisations were moving toward each other. Thus, most trans-Asiatic routes formed a broad historical-cultural corridor of international communication from China to Black and Mediterranean Seas that would be called the Great Silk Road. However, a closer look at Silk Road-related sources raises doubts about its significant role in transferring chickens from Asia and Europe that opposes the accepted point of view. According to A.M. Petrov (1995), a participant of the UNESCO Great Silk Road expedition in 1989, this way would be too long, hard and unsafe so that it took two or three years for merchants and travellers to get from a place of departure to a destination. Often, the trails were narrow paths where one was unable to use pack animals. Some of the road areas were just strewn with human and animal bones. Taking into consideration an exceptional hardship of Silk Road trips, S.G. Petrov (1941) entirely denied its significance for bringing chickens from Asia to Europe. However, there could be a compromise between two extreme points of view concerning the Silk Road involvement into the chicken transit: chickens might have

been transferred within easier lengths of road. There was another, sea way discovered and established later to connect Asia and Europe via Indian Ocean. All these facts interplay in our case of describing the real time and spatial momenta for export of goods and food sources, including chickens, in the old times.

Agricultural and zoological literature evidence

Mediterranean area. Since there is a controversial opinion concerning the time of emergence of five-toed chickens in the Mediterranean area as well as their distribution routes, we will now review ancient historical literature related to the subject. In the European Mediterranean area, there were famous ancient encyclopaedists and zoologists that wrote many works in the field of natural sciences and agriculture, including poultry breeding. However, we cannot utterly rely upon their evidences, since not all of their legacy has survived till the present and, if survived, their texts have been recopied many times and translated into various languages, which appears to distort their content. Another circumstance that should be borne in mind is knowledge level at that time, which falls short of the contemporary science development. Nonetheless, the aggregate of statements of various authors and their analysis have a great cognitive value and can reflect the reality better than single facts.

The great Greek zoologist Aristotle (384–322 BC) was the first Mediterranean writer, who wrote a lot about chickens. Regretfully, not all of Aristotle's works devoted to the description of various animal species have reached modern days. The examination of the known Aristotle's texts (Aristotle 1971a 1971b) made by one of us (EC) has not revealed any records of polydactylous birds among chicken populations in Greece at that time. Yet, it is known that Aristotle would not pass over in silence number of toes in other animals.

Only in 37 BC the five-toed chickens appeared in the Latin literature, when Varro (116–27 BC), Roman writer first described chickens to be chosen for best reproduction that should have “ruddy plume, black quills, odd toes, large heads, upstanding comb”, and be “corpulent” (Varro 1974). After Varro, in the 1st century AD, two Roman authors, Pliny the Elder (23–79) and Columella (4–ca. 70), both mentioned about five-toed chickens. Pliny the Elder (ca. 77) wrote about chickens with “*digits imperious*” (“odd number of toes”) and “*aliquant et super IIII digits traverse undo*” (“sometimes also with a toe obliquely arranged besides the four toes”).

The more evident text regarding five-toed chickens is that of Columella who wrote twelve volumes on agriculture in the mid 1st century AD. From his treatise *De re rustica* (Columella 1977) we can learn: “The reproducer females should therefore be of reddish colour, square-built, broad breasted, with large heads, red upstanding little combs, white earlobes, and in this respect they [earlobes] must be as largest as possible, nor with an even number of claws: and precisely they are considered the most prolific those who have five toes.”

We can say that both Varro's and Columella's descriptions can be quite applied to the Dorking of today, except for earlobes. Columella quoted white earlobes, although they were omitted or forgotten by Varro. At present, the Dorking earlobes are red, though often slightly tinged with white (Brown 1906). The red earlobes of the modern Dorking and its white eggshell are quite compatible from a genetic point of view, such as are genetically compatible white earlobe and brown eggshell in some Spanish breeds, for instance, Catalana del Prat, Vilafranquina negra, and Penedesenca (according to descriptions of these breeds elsewhere, e.g., Orozco 1989 and Scherf 2000).

The Greek geponic writer Nicolaus Florentinus (first half of the 3rd century AD, as cited by Gessner 1555), probably from Roman Bithynia, who in the 3rd century AD wrote *Georgica* in at least eleven books, said that the special hens were given five toes almost by lot. In our opinion, this statement sounds like a very attentive remark about the strange phenotypic behaviour of this trait when the chickens are not mated in purebred as in all likelihood was happening in old times.

At the beginning of the 14th century, Italian magistrate Pietro Crescenzi (ca. 1233–1320 or 1321) had also spoken about odd-toed chickens (Crescenzi ca. 1305, first printed in 1471), but we doubt quite a lot that Crescenzi was personally dealing with aviculture, or at least with poultry farming. Despite some disclaimer arising from uncertain biographical data, according to what he wrote on hens, Crescenzi had in our opinion no training and sometimes deeply misleading competence. The chapter devoted by Crescenzi to hens is nearly a faithful transcription of the text of Varro, without any addition of some personal experience. Therefore, Crescenzi is perhaps not a reliable source concerning the existence of five-toed chickens in Italy at the beginning of the 14th century.

The Swiss naturalist Conrad Gessner (1516–1565) in his *Historia animalium*, when dealing with the choice of best hens, quoted Pliny, Columella, obviously Varro, and Nicolaus Florentinus, as the literature sources of the five-toed chicken existence (Gessner 1555).

Ulisse Aldrovandi (1522–1605), the famous Italian naturalist, was astonished about the statement of Pliny the Elder and Columella that in Roman world the best chickens were the five-toed ones. Aldrovandi (1600) wrongly stated that never he had seen five toes neither in birds and chickens, but only in monsters: “Columella also appreciates those hens which have five toes, do not however have transverse spurs sticking out from their legs. Therefore, I am at a loss what to say about such toes since besides from an abundance of matter we see that five-toed feet are not observed in this genus of birds or in any other, except in freaks, such as that five-toed foot given me by an unknown person and which I keep in my museum.” Aldrovandi in his *Ornithologiae* unsparingly poured Gessner’s text, and passed over his quotation of both Varro and Florentinus about five-toed chickens.

Aldrovandi (1600) reasserts his ignorance that in his time five-toed chickens were unknown: “Columella says: “*They are considered very fertile those who have five toes, do not however have transverse spurs sticking out from their legs*”, a thing which is testified also by Pliny, whose words I quoted shortly before, when I said that in our age such hens do not exist.”

Thus, by the end of the 16th century, five-toed chickens were unknown, at least in Italy, to such a big naturalist as Aldrovandi. However, this statement turns out to be quite untrue. Surprisingly, one of us (IGM) discovered a big and unforgivable mistake of Aldrovandi. In particular, we found the watercolour pictures (Stromberg 1996) of a rooster and a hen from the Aldrovandi collection called “*grifutis pedibus*”, that is, with vulture hocks (fig. 7), which are practically alike the black-and-white images reproduced in Aldrovandi’s *Ornithologiae* (Aldrovandi 1600). Both these couples of chickens are five-toed, but Aldrovandi in describing them only said that they had yellow legs. Amazingly, their legs are not entirely covered by feathers: their five toes are very clearly visible, but Aldrovandi did not see them. They were almost uselessly photographically reproduced by his painters and engravers.

The corpulent and five-toed chicken, as well as that one fitting from a reproductive point of view and so appreciated by Varro and Columella, was a breed, which differed from the breeds raised and appreciated in Greece and known by Romans. We suggest that breed was a new and an imported breed, perhaps the Dorking.

We have no data about chickens' importation from Britain to Rome, but that geese were imported from *Gallia Belgica* to Rome was testified by Pliny the Elder (ca. 77). To sum up the provided literature testimonies of the ancient, medieval and more recent zoologists and poultry scientists with regard to time of origin of five-toed fowls in the European Mediterranean area, we come to the conclusion that, as likely as not, five-toed chickens were unknown in the Mediterranean basin in the times of Aristotle who never lived out of the Mediterranean shores. As for the later period of time, we already have a number of dicta by several writers that testified to the existence of pentadactylous chickens in this area. Among them, we can refer to Varro, Columella, Florentinus, Gessner (according to the literature data) and, with some degree of doubt, Pliny the Elder and Crescenzi. As shown above, at the time of Aldrovandi, five-toed chickens were also known in spite of missing this fact by Aldrovandi himself. A lesser number of authors (e.g., Cato the Elder ca. 160 BC; Belon 1555; Thompson 1966; Capponi 1979) did not mention this trait in fowls in their works.

Chickens in Ancient Britain. In the times of King Solomon (ca. 1035–922 BC), Phoenicians reached the Islands of Scilly off the south-western most tip of England, called *Cassiterides* in Latin, to buy up tin (*kassiteros* in Greek) (Bement 1867). In fact, it seems certain that in ancient times the British tin represented the main source for Eastern Mediterranean countries. There is an assumption that Phoenicians might have brought chickens from the East to be bartered with the prized metal (Bement 1867).

According to Carlos Adolfo Finsterbusch (1888–1970), Phoenicians were uppermost responsible of chickens' diffusion not only in the Mediterranean basin, but also in northern Europe, up to Ireland and England (Finsterbusch 1929). Their chickens were fighting birds and, without doubt, also table chickens, both used daily by Phoenicians. However, Finsterbusch points out that “before the Phoenician, the Britons had some sort of domestic fowl, apparently of Mongolic type.” This lead is very important because the presence in Britain of a domestic fowl of Mongolic type before Phoenician influence makes us think about an involvement by Celts. In fact, Dillon and Chadwicks (as referred to in Matthews 1993) traced back the first Celtic settlements in British Islands to late Bronze Age, namely around 1180 BC. But it was only towards 600–500 BC that Celts started their penetration into Gallia and partially also into Britain, overlapping agricultural populations that had lived there for millennia (from Palaeolithic until Bronze Age) and leading the breeding to prevail on cereal crop (as reviewed by Albino Garzetti (1914–1998) in Cesare [Caesar 1996b]). Ireland had been inhabited by Celts since the first half of 1st millennium BC but this country kept out of Roman and Germanic invasions.

Gaius Julius Caesar (100–44 BC) observed domestic fowl in Britain, when he crossed the English Channel to enter Britain twice in 55 and 54 BC. Stating in advance that Caesar directly knew only South-eastern Kent and Lower Thames area (and we think that when crossing the Thames he passed through Surrey and near Dorking), on occasion of this *second visit to Britain* he said that there was chicken, being that it was not eaten, likewise hare and goose (Caesar 1996a): “They do think unlawful to taste hare and hen and goose; nevertheless they raise them for sheer pleasure.”

Archaeological data cited by West and Zhou (1988) concerning chicken bones found in Great Britain are in agreement with the hypothesis of Finsterbusch about a likely chicken occurrence in Britain unrelated to a Phoenician influence, another sort of influence that we hypothesize as perhaps due to the subsequent waves of Celtic settlements. In fact, West and Zhou (1988) quoted eight British sites, each later than Mohenjo-Daro, but the finds in five of these eight sites date back to Iron Age. Of the five sites of Iron Age, there are certainly

three more ancient sites, and they date back to La Tène Age or late Iron Age (second half of 1st millennium BC). The remaining two sites are generically meant as of Iron Age, inasmuch as perhaps not datable with certainty.

Sándor Bökönyi (1926–1994), the prominent Hungarian archaeozoologist and former Director of the Archaeology Institute in Budapest, was a strong supporter of the hypothesis about poultry dispersion in Europe by Celts, though he did not mention five-toed chickens in his papers (e.g., Bökönyi 1991).

On the other hand, there is an opposite speculation that chickens were brought to the Celts by the Romans. This point of view was supported by Sir Edward Brown, outstanding writer on chickens. In his book *Races of Domestic Poultry* (Brown 1906) he is torn between the possibility that the Dorking was British or not. He was disappointed by the fact that there were not ancient written documents about Dorking (Brown 1906).

Discussion

In this article, we have discussed two basic issues of the spreading and emergence time of five-toed chickens. As a result of our investigation, we have broadened our outlook at the problem of polydactyly in chickens and discovered some new information about five-toed breeds and populations previously unknown or little known. Historical illustrations have been drawn by translating original texts into English and analyzing works of ancient, medieval and modern zoologists and poultry scientists concerning chicken pentadactyly.

Judging from the available information about diffusion of five-toed fowls, we should admit that the results of our search are not so definite as in the case of temporal parameters of their appearance. This can be explained by the fact that, as a rule, historical events underlying chicken dispersion, especially for the five-toed, have a multilateral vector as elucidated in detail in the previous sections. Hence it follows that analysis of historical processes cannot always be conducted with a mathematical accuracy and, sometimes, is simply impossible due to insufficient data. In our case, we have here one more complicating factor — genetics of pentadactyly, that is, its incomplete dominance and influence of some external factors on the trait expression, and therefore, possible modifications.

Nevertheless and despite the above complications, our analysis of the collected information allows framing a hypothesis about several scenarios for horizontal and vertical transmission of pentadactyly in chickens. First, this mutation could occur in China before Christian era and, then, transferred to Europe and other continents through various ways. In particular, its diffusion from Asia to Europe occurred through northern or southern routes, or both. Besides, dispersion of chickens was undoubtedly associated with historical events in the human society as discussed above.

Second, the chicken pentadactyly came into existence independently in Asia (China) and Europe (Britannia and/or Rome). We base this suggestion on the natural division of five-toed breeds into two groups: those that bear the Dorking genes in their genome, and breeds of unknown origin. Not all of these breeds have similar phenotypic traits. Since centuries or millenniums the Dorking, Houdan and other well known five toed breeds are still pentadactylous pure breeds and their genetic purity allowed and is still allowing the expression of their polydactyly.

Third, the five-toed mutants occurred several times and in several geographic areas. In the 20th century, we have evidence for this statement from the Serebrovsky's expeditions in 1926–1933 and recent observations in a population of dwarf

Silver Wyandottes at the All-Russian Poultry Research and Technological Institute, Sergiyev Posad.

Our suggestion about independent origin of five-toed chicken mutants is supported by recent discoveries (Huang *et al.* 2006) at the DNA level, showing the association between polydactyly and a mutation in the *LMBR1* gene that was observed in a Silkie population but was not found in two other polydactylous breeds (one from France). These findings may entail further evidence that different molecular genetic mechanisms may be involved in polydactyly manifestation in five-toed breeds of different origin.

In the course of our investigation, we have faced certain obstacles in finding the facts and interpreting the evidence. If at present there is no evidence about some fact or event, it does not necessarily mean that the fact or event has never existed. Moreover, great scholars of the past might have mistaken, too, and their statements require evaluation and testing. In our investigation and analysis, we have based ourselves upon certain methodological principles including, first of all, a better reliability of the sum of facts instead of single facts. For examining complex historical and biological processes, it seems more valid to avoid categorical conclusions that leave no degrees of freedom for alternative points because further search and discoveries can change an original point of view. In addition, application of logics, system approach, and available experience and knowledge to data analysis aids in understanding events that could happen either one way or another, or only one way, or some of them could never take place. These circumstances should be taken into consideration to resolve fully the problem of five-toed chicken origin.

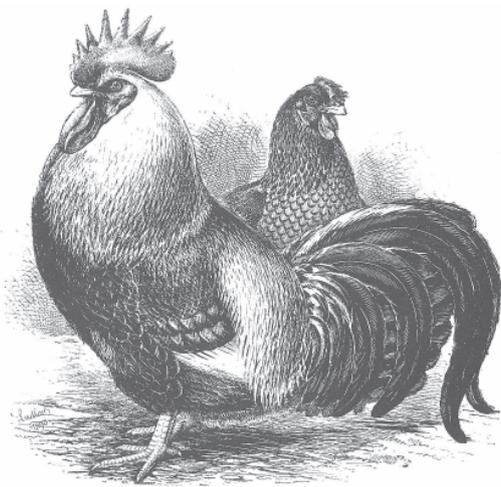


Fig. 1. Dorking (source: Brown 1906). This breed took its name from the town of Dorking in Surrey, UK. According to Brown (1906), the first definite description of the Dorking, or *Darking*, as it was then called, with details enabling us to recognize it, is found in Moubray [pseudo. of John Lawrence] (1815)

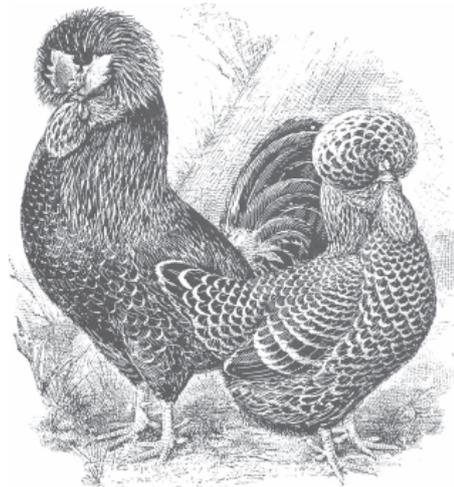


Fig. 2. Houdan (source: Brown 1906). The ancestor of this breed was likely living at the borders of *Belgica*, being that the town of Houdan lies about 60 km to the west of Seine and that this river was regarded as the western border of the territory occupied by ancient Belgians. At present, Houdan has about 3,000 inhabitants and is located in the Île-de-France region, Yvelines department (its capital is Versailles)

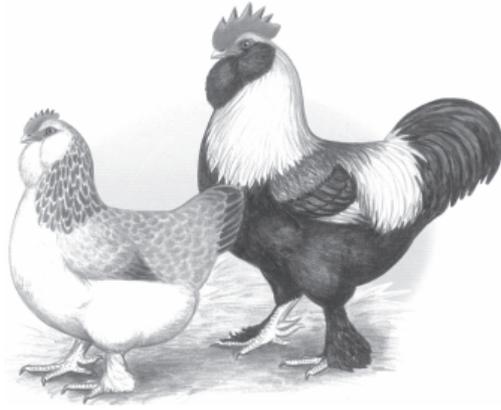


Fig. 3. Faverolles (source: Percy 2002). According to Brown (1906), this breed is mongrel of the Houdan with Dorking × Light Brahma. Created around 1870 in France, took its name from a village in the department of Eure-et-Loir, nearby Houdan, the latter belonging to the department of Yvelines

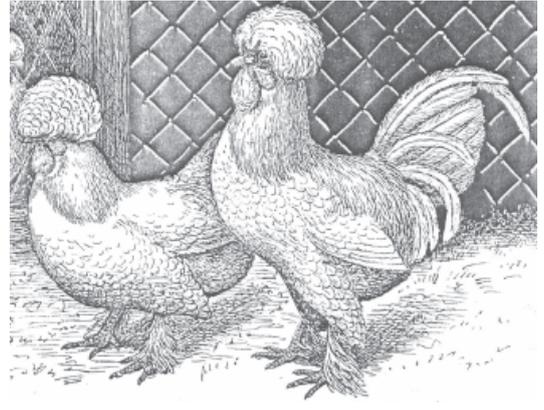


Fig. 4. Sultan (source: Dürigen 1921). According to Miss Elizabeth Watts (n.d. or 1860?), this fowl was sent her in England from Constantinople in 1854. The name of the breed was *Serai-Täook*, or better, *Saray Tavuk*, that is “*the hen of the Sultan’s seraglio*”

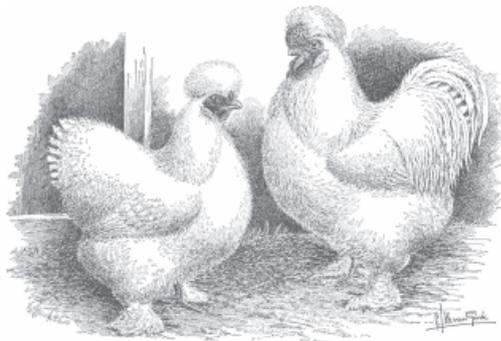


Fig. 5. Silkie (source: Nederlandse Bond van Hoender-, Dwerghoender-, Sier- en Watervogelhouders 1992). According to what is affirmed on the E Natural Health Center web site, this breed is native to China, TaiHe county, east of Wushan mountains, Jiangxi province, where it has been raising since more than 2,000 years

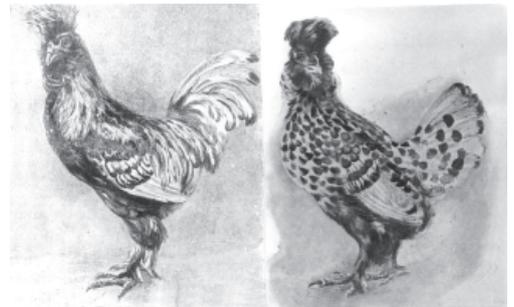


Fig. 6. A couple of the Pavlov Silver breed (source: Serebrovsky 1926): a cock (left) and a hen (right)



Fig. 7. Aldrovandi's (1600) five-toed cock (left) and hen (right) whose polydactyly was overlooked by Aldrovandi

Conclusions

Based on the analysis of the ancient literature and recent molecular studies, we hypothesize that the polydactyly mutant trait might have occurred more than one time and independently in, at least, two centres of origin, in Europe and Asia. The trait could be distributed to other parts of the world along the known ways in history as other chicken populations did. These ways included trade activities, military campaigns, migration of human populations, emergence and fall of ancient empires, discoveries of new lands, and exchanges between poultry farmers and between breed fanciers. Occurrence of these events in human history has been continuous over thousands of years and repeating in opposite directions. Earlier events might be hidden behind later ones, and the former, partly or fully, may not be traced due to the absence of available historical documents. Also, migration or re-occurrence of a mutant trait could not always be tracked back. Molecular studies on polydactyly candidate genes may provide a new information about this genetic condition and the origin of five-toed chickens.

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Аннотация. В статье представлен подробный анализ пород пятипалых кур, истории их наблюдения, данных об их распространении и последовательного молекулярно-генетического анализа сходств и различий между ними. Авторы подчеркивают, что пятипалость у кур возникла как отдельная мутация (мутации) генов, контролирующих развитие конечностей, а судя по тому, что такие породы встречаются в Китае, Японии, Англии, России, Турции и Литве, такая мутация (мутации) возникла достаточно давно. На основании выполненного анализа авторы приходят к заключению о том, что эта мутация могла возникать больше, чем однократно, и независимо друг от друга в Европе, Азии и, может быть, в других частях света. Если это предположение справедливо, возникает вопрос, как могла распространяться пятипалость из разных центров ее возникновения, в частности, из Азии и Европы. Авторы предполагают, что ее распространение шло параллельно распространению других популяций кур на протяжении сотен лет, иногда повторяясь в противоположных направлениях. Подчеркивается, что события в истории сельского хозяйства, которые сопровождались распространением разных пород кур, до сих пор остаются недостаточно исследованными. Авторы полагают, что молекулярно-генетические исследования генетических связей между популяциями пятипалых кур могли бы пролить свет на некоторые аспекты таких событий.