Temminck's Gallus giganteus; a gigantic obstacle to Darwin's theory of domesticated fowl origin?

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Source: Bulletin of the British Ornithologists' Club, 140(3) : 321-334

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v140i3.2020.a5

Temminck's *Gallus giganteus*; a gigantic obstacle to Darwin's theory of domesticated fowl origin?

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Received 16 April 2020; revised 25 June 2020; published 21 September 2020

http://zoobank.org/urn:lsid:zoobank.org:pub:C30BF513-EE1C-4CCE-A5FD-0AD4A53E9A58

Summary.—In 1813, based on the single foot of a large chicken, Temminck named a 'new' species of junglefowl, *Gallus giganteus*. He considered this 'species' the ancestor of several large domesticated chicken breeds and believed it was one of six wild ancestral species of domestic fowl. Temminck's hypothesis was rejected by Blyth who thought Red Junglefowl *G. gallus* was the sole ancestor. The arrival into Britain of several very large Asian chicken breeds in the mid-19th century led to speculation that Temminck's *G. giganteus* may have been their wild ancestor. Darwin, who had initially agreed with Blyth, noted several peculiarities in the Cochin, a large Asian breed, which he concluded might not have been achieved by selective breeding, and questioned whether *G. giganteus* was involved in their ancestry. Temminck's giant junglefowl appeared to be a significant hurdle for Darwin in his effort to prove a single ancestral origin for domestic chickens.

'*My very decided opinion*, that we may seek in vain for wild types of *G. giganteus*' (letter from Blyth to Darwin, 1856).

'We have not such good evidence with fowls as with pigeons, of all breeds having descended from a single primitive stock' (Darwin 1868: 239).

In the mid-19th century, prompted by the arrival of very large Asian chicken breeds into Britain, a heated debate ensued over whether the domesticated chicken had a polyphyletic origin (from multiple ancestral wild species) or a monophyletic origin (a single wild ancestor). Initially the first-named hypothesis was generally accepted, but Darwin (1859) in his *Origin of species* supported a monophyletic origin following Blyth (1847).

At the time a number of large and exotic-looking chicken breeds reached Britain as a result of the opening of additional ports in the Far East at the end of the First Opium War (1839–42, see Appendix 1). After studying several of these large breeds (some skeletal material from the relevant specimens is still present in the bird collections of the Natural History Museum at Tring; NHMUK), Darwin began to question his prior belief in a single ancestor. Having defended the idea of a monophyletic origin in support of his theory of natural selection (1859), he sought to test this hypothesis by disproving the (former) existence of other possible ancestors mentioned by earlier workers (see van Grouw *et al*. 2017). Temminck's Giant Junglefowl was one of Darwin's obstacles.

Temminck's Giant Junglefowl *Gallus giganteus*

At some point, Coenraad Jacob Temminck (1778–1858), first director of the State Museum of Natural History in Leiden, received from Batavia (modern-day Jakarta, Indonesia) a single foot belonging to a very large fowl. Believing it to be that of a large species of wild junglefowl that occurred in the forests of southern Sumatra and western Java, Temminck (1813: 84–86) named it 'Jago Cock' *Gallus giganteus*. It was twice the size of a common domestic chicken and the large, robust spur was 5 cm in length (Fig. 1). Temminck noted (1813: 84) that William

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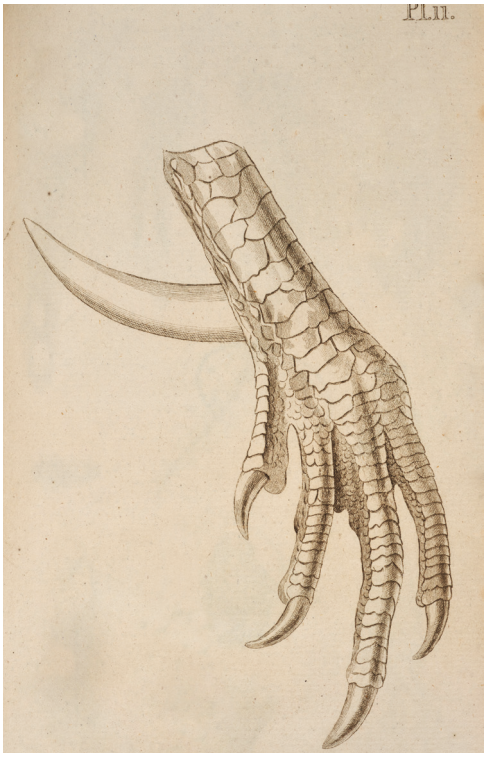

Figure 1. Pl. 2 in Temminck 1813, depicting the foot of *Gallus giganteus* (© Jonathan Jackson, Natural History Museum, London)

Figure 2. Pl. 44, Malabar cock *Gallus giganteus*, by Benjamin Waterhouse Hawkins in Gray & Hardwicke's *Illustrations of Indian zoology* (© Ben Nathan, Natural History Museum, London)

Marsden (1754–1836) had used the name 'Jago'—from the Sumatran or Malay 'Jago' for a breed of chicken used for cockfighting (Dixon 1848: 176)—writing 'The jago breed of fowls, which abound in the southern end of Sumatra, and western of Java, are remarkably large: I have seen a cock peck off of a common dining table: when fatigued, they sit down on the first joint of the leg, and are then taller than the common fowls' [this typical resting position is displayed by many large, long-legged, fighting breeds] (Marsden 1783: 98).

Temminck (1813: 86, 1815: 653–654) grouped the different varieties of large-sized domesticated chickens as a single taxon; *Gallus patavinus* [from Padua], adopting the name used by Mathurin Jacques Brisson (1760: 170) for two large breeds, one from Italy and the other from France. In Temminck's opinion all of these large varieties had *G. giganteus* as their wild ancestor, giving the name *G. giganteus* a higher rank than *G. patavinus*. No formal code for zoological nomenclature existed at the time, and naturalists held different opinions as to how to apply scientific names (Gassó Miracle 2011), resulting in domestic varieties sometimes also being named scientifically.

Thereafter, Temminck's giant junglefowl was increasingly referred to as a domestic form, rather than a wild species. John Latham (1823: 164–165) described the 'Jago Cock' *G. giganteus* of Temminck as a wild junglefowl, from Sumatra and Java. However, he also mentioned the 'Malabar Cock' as a very large, domesticated fighting chicken from India which was not infrequently brought to England on ships belonging to the East India Company (Malabar is in coastal south-west India). It was depicted in two plates (see Figs. 2–3) in the *Illustrations of Indian zoology* by J. E. Gray (1832) but was described as being

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Figure 3. Pl. 45, Malabar hen *Gallus giganteus*, by Benjamin Waterhouse Hawkins in Gray & Hardwicke's *Illustrations of Indian zoology* (© Ben Nathan, Natural History Museum, London)

Figure 4. Black-breasted Red Malay cock, one of the tallest breeds of chicken, originally bred for cockfighting but nowadays for exhibition alone (© Paul Hassell & Martin Stephenson)

the same as Temminck's *G. giganteus*. The birds pictured resemble the Aseel, an Indian breed used for cockfighting (see Appendix 2).

William Henry Sykes (1832) reported that *G. giganteus* was known by the name of the 'Kulm Cock' by Europeans in India. He knew it only as a tame bird and believed it had been introduced to the Subcontinent by Mussulmans (Muslims) from Sumatra or Java. Sykes brought two cocks and a hen to England in June 1831 which, according to him: 'bore the winter well. The hen laid freely, and had reared two broods of chickens.' These birds probably were the first Malay-type fowl (see below) brought to England.

Almost certainly Temminck's large fowl foot belonged to a very large and long-legged domestic local variety used for cockfighting, a popular activity for centuries in South-East Asia. These local varieties were probably the precursors of the modern Malay, a breed of fighting chicken now kept solely for exhibition. It is one of the tallest chicken breeds and cocks may stand >90 cm high (Fig. 4). As this foot, which would be the holotype of *G. giganteus*, is not present in the bird collection of the Leiden museum (P. Kamminga pers. comm.) and its current whereabouts, if still extant, are unknown, we cannot be certain as to its true identity.

Temminck's polyphyletic origin theory

Temminck's (1815: 653–663) belief in a polyphyletic origin for domesticated fowl was based on the ideas of the French naturalist Georges–Louis Leclerc, Comte de Buffon (1707–85). Temminck supported Buffon's (1772: 166) belief that the wild Red Junglefowl (*coq sauvage de l'Asie*, wild cock of Asia) most closely resembled the majority of European

ISSN-2513-9894 (Online)

chicken varieties as this species had the same shape, colour (black-breasted red), feather structure and comb type as many domestic chickens. Although no other wild junglefowl species were known in Buffon's time, he considered that certain extremely large chicken breeds may possess another, unknown, wild species as ancestor. Buffon (1772: 177) listed seven 'giant' domesticated chickens mentioned by earlier workers as descendants of this unknown ancestor.

Temminck (1813: 86, 1815: 664) considered these seven large-sized varieties to be descendants of wild *G. giganteus*. He also acknowledged that there was ample evidence for the ongoing transformation of animals at the hand of man, and was familiar with the wide range of different morphological characteristics in chickens achieved by artificial selection (Temminck 1815: 654–659). Among all these traits, however, were five characters already mentioned by Buffon (1772: 170–178), which, Temminck felt, were so peculiar that they could not have been the product of artificial selection. These were: (1) giant body size; (2) fibromelanosis (abnormal accumulation of dark melanin pigment in skin and connective tissue formations); (3) silky plumage (feathers without hooklets); (4) frizzled plumage (feathers that curl outwards); and (5) rumplessness (without a tail). Temminck (1813: 76, 1815: 653–654, 660–663) presumed that these characteristics originated from five additional ancestral Asian species, each possessing one of these distinct traits. The species were: (1) *G. giganteus*: ancestor of all large poultry breeds; (2) *G. morio*: the alleged ancestor of all dark-skinned breeds; (3) *G. lanatus* which presumably gave rise to chickens with silky plumage; 4) *G. crispus* which was responsible for curly (frizzled) feathers and, finally; (5) *G. ecaudatus*, ancestor of all rumpless fowl (see van Grouw *et al*. 2017). Temminck adopted the names, except *giganteus*, used by Latham (1790) for domesticated breeds with these traits.

Figure 5. Engraving of the Cochin China Fowl kept by Queen Victoria at Windsor, by Samuel Read (1816–83), published on 23 December 1843 in *The Illustrated London News* (© Illustrated London News Ltd / Mary Evans, London)

ISSN-2513-9894 (Online)

In France, the polyphyletic theory of the origin of domesticated chickens was generally accepted. The naturalists Georges Cuvier (1832: 244) and René Primevère Lesson (1836), for example, shared the view of Buffon and Temminck. Lesson (1836: 367) wrote: 'Mr. Temminck has followed Brisson in his distinctions of the breeds of fowl, while introducing numerous new facts, which helped in providing clarity concerning one of the most obscure points of ornithology [the origin of domestic fowl]. Although we are still far from a complete classification, the fact is that we possess now a few wild ancestors which shed more light on this genus [*Gallus*] than in the era of Brisson, Montbeillard and Buffon'.

As already mentioned, several decades after its description Temminck's giant junglefowl was generally considered to be a domestic form rather than a wild species. Dixon (1848: 176) stated: 'No ornithologist now ranks this bird as a distinct species.' However, in the 1840s several breeds of very large chickens were brought to England from the Far East (Fig. 5; see Appendix 1). They caused a sensation among fanciers and naturalists because of their large size. Due to their unusualness, Temminck's giant junglefowl was yet again raised as the possible wild ancestor of these and other large breeds. For example, the French physician, botanist and geologist Dominique Alexandre Godron (1807–80) was certain that Red Junglefowl was the sole ancestor of European poultry breeds, but suggested that *G. giganteus* might be the common ancestor of Asian ones (Godron 1859: 446–447).

Blyth's monophyletic origin theory

Edward Blyth (1810–73), curator of the Asian Society of Bengal in Calcutta, rejected Temminck's polyphyletic theory, suggesting that individual varieties of domesticated chicken are neither separate species nor subspecies, but had evolved by artificial selection from a single wild ancestor, the Red Junglefowl *G. gallus* (Blyth 1847).

Blyth published his monophyletic theory in more detail in 1851. At that time five 'species' of wild junglefowl were known to Blyth: (1) Grey Junglefowl *G. sonneratii*, (2) Ceylon Junglefowl *G. lafayettii*, (3) Green Junglefowl *G. varius*, (4) Bronzed Junglefowl *G. aeneus* (a hybrid, but not yet recognised as such; see van Grouw & Dekkers 2019), and (5) Red Junglefowl *G. gallus*. In summary, some of Blyth's arguments in favour of a sole ancestral origin were as follows: (1) regarding *G. sonneratii*: 'The very peculiar plumage of the cock, and every note uttered by either sex, totally separate it from every domestic breed'; (2) *G. lafayettii*: 'which is peculiar to Ceylon, and at once completely distinguished from the common fowl by its red-edged yellow comb, and extremely different voice in every note uttered'; (3) *G. varius* and (4) *G. aeneus*: 'a single throat-wattle, and no neck-hackles'; and (5) *G. gallus*: 'Domestic cocks of various breeds, may often be found to match, feather by feather, with the wild bird …; and the voice is absolutely that of an English game fowl.' Further he wrote: 'You may rest perfectly assured that there is no wild silky fowl, or feather-legged, or crested, or black-skinned, or gigantic, frizzled, & c.' (Blyth 1851).

Darwin was interested in Blyth's monophyletic theory. In their correspondence, Blyth (1855b) explained his theory further by presenting more examples in favour of Red Junglefowl, ending his argument: '[Red Junglefowl] essentially conforms to the type of the domestic fowl in all its multitudinous varieties, fully as much so as the Mallard does to the domestic drake; or the wild to the tame Turkey!' And in a subsequent letter he firmly stated, '*My very decided opinion*, that we may seek in vain for wild types of *G. giganteus*, &c' (Blyth 1856).

In his *Origin of species* Darwin (1859: 18–19) gave great credit to Blyth's monophyletic theory: 'Mr. Blyth, whose opinion, from his large and varied stores of knowledge, I should value more than that of almost any one, thinks that all the breeds of poultry have proceeded from the common wild Indian fowl (Gallus bankiva)' [Red Junglefowl]. He later, however,

ISSN-2513-9894 (Online)

began to question this view: 'We have not such good evidence with fowls as with pigeons, of all breeds having descended from a single primitive stock' (Darwin 1868: 239). Although he generally believed that Temminck's *G. giganteus* was a domestic variety—having also examined a specimen in the British Museum (Darwin 1868: 235, see Appendix 2)—based on his own research (see below), he did consider that there may be reasonable arguments in favour of a polyphyletic origin after all: '… even if it be admitted that *G. bankiva* [Red Junglefowl] is the parent of the Game breed, yet it may be urged that other wild species have been the parents of the other domestic breeds; and that these species still exist, though unknown, in some country, or have become extinct' (Darwin 1868: 237).

Darwin's proof of monophyletic origin

Artificial selection applied by breeders of domesticated animals and cultivated plants was an important analogy for Darwin to illustrate the mechanism of evolution by natural selection in nature. Darwin (1859: 30) wrote: 'The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds.' To show that artificial selection based on 'the adding up of small, natural occurring variations' could result in such a great diversity within a single species, it was important for Darwin to prove that the great diversity came from the same ancestor, e.g. a monophyletic origin. To demonstrate that artificial selection can cause extreme osteological variation within a single species, Darwin conducted comparative studies on the skeletons of domesticated animals, including pigeons, ducks and chickens.

For his study on fowl Darwin (1868: 260) examined morphological variation in 80 skeletons and skulls, including three Red Junglefowl specimens, of 16 different breeds. Approximately half of the specimens were received from William Bernhardt Tegetmeier (1816–1912), Darwin's most important advisor on pigeons and poultry, and a vital link to the fanciers' community. By comparing domestic chicken skulls with those of Red Junglefowl (Fig. 6), which he considered the 'wild-type standard', Darwin (1868: 260–266) observed that a history of strong selective breeding had significantly increased osteological diversity in chicken skulls. The skeletal material included also seven specimens of the large Cochin breed (Fig. 7, see also Appendix 1), two of which are still at NHMUK (Fig. 8A–B).

Figure 6. Skull of male Red Junglefowl *G. gallus* from Darwin's collection, NHMUK 1868.2.19.59, the museum labels and accompanying note expressing Blyth's compliments. Darwin received this specimen from Blyth, who wrote: 'By the steamer which conveys this letter, you will also receive a fine skeleton of the Bengal Jungle-cock (care of Dr Horsfield, at the India-house)' (Blyth 1855a). Darwin considered the skull of Red Junglefowl as the 'wild-type standard' and compared it with skulls of domestic chickens to describe the differences (© Jonathan Jackson, Natural History Museum, London)

ISSN-2513-9894 (Online)

Figure 7. Buff Cochin cock; the Cochin, first introduced into Britain in 1847, does not originate from Cochinchina (Vietnam) but from China and is kept purely for exhibition. The Cochin is in many aspects very different from other breeds but, according to Darwin (1868: 260), 'All the characteristic differences of the Cochin breed are more or less variable and may be detected in greater or lesser degree in other [Chinese] breeds' (© Willem & Martijn Hoekstra)

Figure 8A–B. Two Cochin skulls from Darwin's collection, right a male, NHMUK 1868.2.19.70 (Darwin's no. 48) and left a hen, NHMUK 1868.2.19.55 (Darwin's no. 60). Sectioning of the hen's skull was performed by (or for) Darwin, as it was needed for a picture on p. 263 in *Variation under domestication*, 1868, vol. 1 (see Fig. 8B), wherein it is stated that the skull is of a male (© Jonathan Jackson, Natural History Museum, London)

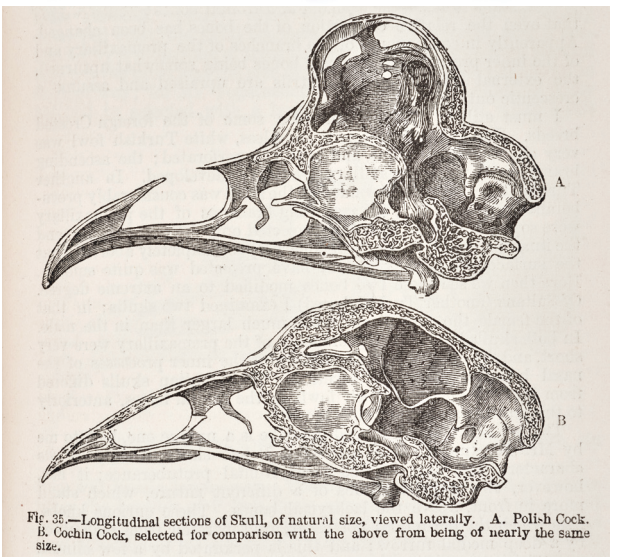

Fig. 35.—Longitudinal sections of Skull, of natural size, viewed laterally. A. Poli-h Cock. B. Cochin Cock, selected for comparison with the above from being of nearly the same size.

ISSN-2513-9894 (Online)

Figure 9. Dorsal view of a Cochin skull NHMUK 1868.2.19.70, left, showing a deep groove along the middle of the frontal bone, compared with Red Junglefowl *G. gallus* skull NHMUK 1868.2.19.59, right, showing the flat surface to the frontal bone (© Jonathan Jackson, Natural History Museum, London)

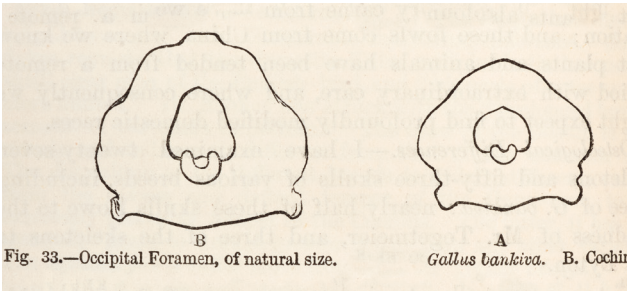

Figure 10. Illustration in Darwin (1868: 261) with the caption: '—Occipital Foramen of natural size. A. Wild *Gallus bankiva*. B. Cochin Cock.' In Cochin (B) the long axis of the occipital foramen is vertical, whereas in the Red Junglefowl (A) it is horizontal.' The occipital foramen is the large opening at the back of the skull through which the spinal cord enters the cranial cavity (© Jonathan Jackson, Natural History Museum, London)

Darwin observed several remarkable peculiarities in this breed, including in their skulls (Fig. 9–10), which did not occur in Red Junglefowl or any of the other breeds, and which, Darwin concluded, might not have been achieved by artificial selection (Darwin (1868: 261).

Despite the peculiarities he had found in the Cochin, the overall conclusions of his comparative study satisfied Darwin that domestic fowl has a monophyletic origin and he wrote 'The Cochin, with its deeply furrowed frontal bones, peculiarly shaped occipital foramen, short wing-feathers, short tail containing more than fourteen feathers, broad nail to the middle toe, fluffy plumage, rough and dark-coloured eggs, and especially from its peculiar voice, is probably the most distinct of all the breeds. If any one of our breeds has descended from some unknown species, distinct from G. bankiva [*Gallus gallus*], it is probably the Cochin; but the balance of evidence does not favour this view' (Darwin 1868: 260).

Discussion

The sole purpose of Darwin's studies on domesticated fowl (see Appendix 3) was to confirm Blyth's hypothesis of a monophyletic origin in order to validate his own theory of evolution by natural selection (1859). Without satisfactory 'proof', however, Darwin did not blindly allocate a monophyletic origin to all domestic species. Whereas the peculiar morphological differences found in fowl might be explained by a long history of strong selective breeding (Darwin 1868: 260), for the extreme diversity in dogs Darwin had no other explanation beyond a polyphyletic origin (Darwin 1859: 18). Even after prolonged research, Darwin remained convinced that several species of wolf and jackal, perhaps including one or more extinct species, had contributed to the various breeds of domestic dog (Darwin 1868: 26).

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Tegetmeier (1867: 75), who had closely followed Darwin's research (see Appendix 3), also supported the single-species ancestry of domesticated fowl. Less than four years after Darwin's death, however, Tegetmeier (1885) retracted his earlier belief in a monophyletic origin in an open letter to *The Field* (van Grouw & Dekkers 2019: Appendix). Disregarding his earlier confirmation of Darwin's opinion, Tegetmeier now used the differences in the Cochin skulls as a counter-argument against it as, in his revised opinion, poultry breeders could never have created the two peculiar differences by artificial selection: 'We have in the Cochin a fowl … with many structural peculiarities that could hardly have been induced by domestication. Thus the long axis of the occipital foramen in the Cochin is perpendicular, in our old breeds horizontal, a difference that could never have been bred for, and which it is difficult to see could be co-relative with any other change. The same may be said respecting the deep sulcus or groove up the centre of the frontal bone…' (Tegetmeier 1885). In his argument, Tegetmeier nowhere mentioned that the peculiarities in the Cochin skulls were discovered by Darwin. His letter was later reprinted in a book about poultry breeds by Brown (1906: 3–4) where it was seen by the American poultry geneticist Don Cameron Warren (1890–1994).

Warren (1949) incorrectly assumed that Tegetmeier had performed the osteological research himself, and started his own to verify the structural differences in chicken skulls reported by Tegetmeier. Warren observed the occipital foramen (large opening at the back of the skull through which the spinal cord enters the cranial cavity) and the shape and structure of the frontal bones of 245 chicken skulls, representing 27 breeds and varieties. Among the 15 Cochin skulls used in his study a high incidence of grooves along the middle of the frontal bones was observed, albeit with no obvious differences in the shape of the occipital foramen (Warren & Smith 1949).

Red Junglefowl is currently recognised as the major ancestor of domestic varieties of chicken, but this does not preclude the participation of other species (Lawal *et al*. 2020). The presence of the gene for yellow skin, for example, in the genome of domestic chickens (Red Junglefowl has white skin), is derived from Grey Junglefowl *G. sonneratii* (Eriksson *et al*. 2008). Theoretically it takes only a single cross to release a variant ('foreign') gene into a population which, we stress, is categorically *not* the same as having multiple ancestors. Also, whatever changes a 'foreign gene' may produce in a species, its expression will nevertheless be mainly the result of information encoded in the total genome of that species, in this case Red Junglefowl. So, Darwin's (Blyth's) monophyletic theory still largely stands, and Temminck's *G. giganteus* was not a significant hurdle for Darwin after all.

Acknowledgements

We thank our referees for their helpful comments. Further, we are grateful to Alison Pearn and Rosemary Clarkson of the Darwin Correspondence Project (CUL) and Pepijn Kamminga, Naturalis Biodiversity Centre in Leiden, for providing information. We also thank Alison Harding, Librarian at NHMUK Tring, for making older literature accessible to us, Jonathan Jackson and Ben Nathan (NHMUK, London) for digital images of specimens and old illustrations, Lucinda Gosling (Mary Evans Picture Library, London) for a digital image of 'Her Majesty's Fowl', and Martin Stephenson and Paul Hassell, Willem & Martijn Hoekstra, and Sergio Calabuig for their photographs of various chicken breeds. We are indebted to our referees, as well as Kees Rookmaker and, especially, Katrina van Grouw for their constructive suggestions that improved the submitted manuscript considerably.

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Appendix 1: Queen Victoria's Cochin China Fowl

In 1843 Queen Victoria (1819–1901) was presented with some very large chickens from the Far East by Edward Belcher (1799–1877): two cockerels and six hens (Anon. 1843). These tall, single-combed and smooth-footed birds (Fig. 5) were obtained by Belcher, an Admiral in the British Royal Navy, in Cochinchina (a French colony encompassing the southern third of modern-day Vietnam). They became known as 'Cochin' or 'Cochin China Fowl' in Britain. Despite their name, these birds were not the precursors of the large, fluffy and feathered-foot chickens now known as Cochins (Fig. 6), which originated from Shanghai. The end of the First Opium War (1839–42, a conflict between Great Britain and China to control the opium trade) resulted in the opening of five Chinese ports, including Shanghai, to European vessels. As a result, a range of chicken breeds from the Far East were introduced to Europe, including, in 1847, from Shanghai, the precursors of modern Cochin in Britain. Poultry experts called them 'Shanghai Fowl' but ordinary poultry keepers, familiar with the names 'Cochin' or 'Cochin China Fowl' applied these names indiscriminately to any large chickens from Asia (Scrivener 2009: 55). The birds Darwin studied were 'Shanghai Fowl', the precursors of modern Cochin.

After cockfighting was officially banned in England and Wales (but not Scotland) in 1835, breeders found another way to have their birds compete, by exhibiting them. The arrival of various Asian poultry breeds during the mid-19th century contributed further to the change in public attitude towards the utility of poultry in Britain at that time. No longer considered to be a 'dunghill' chicken kept exclusively for eggs and meat, or for cockfighting, the breeding of fancy fowl for exhibition became a popular pastime among all social classes in Victorian Britain, and the first official poultry show was held in 1845 in London.

Appendix 2: Other specimens of large Asian chickens confused with wild species

Probably one of the first accounts of large Asian chickens was by Steven van der Hagen (1563–1621), First Admiral of the Dutch East India Company (1602–1800). During a trading voyage to the East Indies (modern-day Indonesia), in November 1604 van der Hagen visited the port of Pegu (modern-day Bago, Myanmar) and described the slaughter of 'giant' fowl: 'Much pork and chicken meat is eaten in this kingdom, & the cocks have throat & legs with an extraordinary width and force. When the women want to kill them, they are sitting on their necks & by this method they let them suffocate' (de Renneville 1705: 71). These large birds probably resembled Marsden's (1783) 'Jago fowl' from Sumatra and Java, and Temminck's *Gallus giganteus*.

Two specimens of *G. giganteus* are mentioned in the *List of the specimens of birds in the collection of the British Museum* (Gray 1867: 39), and these, both cockerels, are still present at NHMUK, Tring. Gray grouped them as a variety of Red Junglefowl and referred both to Temminck's *G. giganteus*, and to Pl. 45 in *Illustrations of Indian zoology* (Malabar cock), which suggests that he considered them domestic varieties. NHMUK 1843.5.24.147 from 'India' is labelled *G. giganteus* (Fig. 11) and was probably the specimen examined by Darwin. It was purchased by the museum from John Leadbeater (1800–52), a dealer of natural history materials in London. The other specimen, NHMUK 1845.1.9.135 (Fig. 12), was received from the English naturalist, diplomat and ethnologist Brian Houghton Hodgson (1800–94) and came from Nepal. Although this specimen is recorded in the museum register as *Gallus bankiva* (the former name for Red Junglefowl), no species name appears on the specimen label, although 'Aseel' is written in pencil, presumably having been added later. The Aseel, or Asil, is a large, muscular breed created exclusively for cockfighting and originates from the Indian Subcontinent. Many different local varieties of Aseel occurred in India, differing mainly in size and weight. The first large 'fighting chickens' from India probably reached Europe in the second half of the 18th century, among them perhaps Latham's (1823) 'Malabar fowl'. Some breeds later contributed to the modern, commercial broilers (meat chickens). Their exhibition counterpart is known as Indian Game (Fig. 13). Others, still known as Aseel, have retained their traditional appearance (Fig. 14), but are now also bred and kept exclusively for exhibition outside Asia.

As Gray (1867) had already recognised that the two 'giant fowl' specimens in the collection were domestic varieties, one might expect that large Asian chickens used for cockfighting would no longer confuse museum ornithologists. However, in 1879 the British Museum's bird curator Richard Bowdler Sharpe (1847–1909) described a new species of junglefowl based on a specimen (Fig. 15) collected by Frederick William Thomas Burbidge (1847–1905) in the Sooloo Islands (modern-day Sulu archipelago, southern Philippines). Sharpe (1879) wrote: 'Mr. Burbidge procured a single example of this Jungle-fowl, which appears to be a very

ISSN-2513-9894 (Online)

Figure 11. Specimen of *Gallus giganteus* NHMUK 1843.5.24.147 from 'India', purchased by the British Museum in 1843 from John Leadbeater. This is, however, a domesticated variety of chicken bred for cockfighting and probably closely related to the breed known as Aseel. This is also the specimen examined by Darwin; '… and the specimen in the British Museum evidently has the aspects of a domestic variety' (Darwin 1868: 235) (© Jonathan Jackson, Natural History Museum, London)

Figure 12. Specimen of *Gallus giganteus* (Gray 1867: 39), NHMUK 1845.1.9.135, sent to the British Museum in 1845 by Brian Houghton Hodgson from Nepal; this is, however, a domestic variety of chicken bred for cockfighting and probably closely related to the Aseel breed (© Jonathan Jackson, Natural History Museum, London)

Figure 13. Jubilee Indian Game cock (or Cornish Game), a breed originating from Indian birds originally bred for cockfighting, but now kept exclusively for exhibition and which has changed dramatically in appearance. It is 'double muscled', a mutation in the myostatin gene resulting in more muscle tissue (breast meat) than normal (Aiello *et al*. 2018); and therefore is used to improve commercial broilers (© Willem & Martijn Hoekstra)

Figure 14. Pied Aseel cock, a breed that originates from Indian birds originally bred for cockfighting. Outside Asia it is now kept exclusively for exhibition, but breeders have preserved the original appearance of the ancestral type in the modern Aseel (© Willem & Martijn Hoekstra)

ISSN-2513-9894 (Online)

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Figure 15. Type specimen of *Gallus stramineicollis* (Sharpe 1879: 317), NHMUK 1883.9.20.25, which was initially assumed to represent a wild species; however, it is a domestic variety used for cockfighting on Borneo and the Philippines (© Jonathan Jackson, Natural History Museum, London)

Figure 16. Philippine Game cock, used for cockfighting in the Philippines, and on Borneo; it has not changed much in appearance being still used for this purpose, and is about twice the size of wild Red Junglefowl *Gallus gallus*, with similar proportions, but a small pea comb and no wattles (© Sergio Calabuig)

distinct species. He tells me that it was brought to the ship by one of the Sooloo natives alive, and he cannot vouch for its having been a wild bird. I have, however, shown the bird to Mr. Gould and other ornithologists; and they agree with me that it is probably a distinct species of Jungle-fowl. Governor Ussher also has seen the bird; and he tells me that he has never seen any domesticated Fowls in Borneo or the eastern islands which approached this species in the least.' The 'species' was named *Gallus stramineicollis* (Sharpe 1879: 317), presumably on account of its straw-coloured neck hackles.

Governor Ussher who, according to Sharpe, had never seen fowl like this on Borneo or nearby islands clearly was not very observant. At the time cockfighting was common and popular throughout Indonesia and the Philippines. Local chicken breeds used (Fig. 16) closely resemble the specimen collected by Burbidge; a large fowl with the approximate proportions of a Red Junglefowl, but with a pea comb and no wattles (the mutation responsible for the comb also results in the absence of wattles). William Robert Ogilvie-Grant (1863–1924), who catalogued the gamebirds in the collection of the British Museum (Natural History), was probably first to recognise *G. stramineicollis* as being a domestic chicken (Ogilvie-Grant 1893: 343).

Appendix 3: Darwin's progressive view on the monophyletic origin of domesticated chickens

Compared to his pigeon research, Darwin's work on poultry is less well known and has received little attention from historians or scientists, despite that he devoted almost as much effort to the study of fowl as to pigeons. In addition to his comparative studies on chicken skeletons to demonstrate variation due to artificial selection, Darwin also conducted a crossing experiment with various poultry breeds to underpin Blyth's monophyletic theory. He received the chickens needed for this experiment from Tegetmeier in December 1858 (Darwin 1858), while writing *On the origin of species*.

Based on his earlier experiments with pigeons, Darwin knew which type of crosses he wanted to perform with chickens to achieve the best result. He procured 'a first-rate black Spanish cock, and hens of the following pure breeds,–white Game, white Cochin, silver-spangled Polish, silver-spangled Hamburgh, silver-pencilled Hamburgh, and white Silky. In none of these breeds is there a trace of red, nor when kept pure have I ever heard of the appearance of a red feather' ['red' was in Darwin's opinion the colour of Red

ISSN-2513-9894 (Online)

Junglefowl] (Darwin 1868: 240). The first chicks hatched in spring 1859 and were crossed the following spring to produce the second generation. The crossing experiment ended in November 1860 (Darwin 1855–68: 49), after these were fully grown and Darwin had observed the colour of their adult plumage. Some of the birds he had bred resembled the coloration of Red Junglefowl, which Darwin considered a reversion to the ancestral type (atavism), writing: 'In the case of pigeons, I have shown that purely-bred birds of every race and the crossed offspring of distinct races frequently resemble, or revert to, the wild rock-pigeon [*Columba livia*] in general colour and in each characteristic mark. With fowls we have facts of a similar nature, but less strongly pronounced' (Darwin 1868: 239). This was, in Darwin's opinion, sufficient evidence for a monophyletic origin of domestic fowl.

The first edition of the *Origin* was published on 24 November 1859, a year before Darwin's crossing experiment was completed. Therefore, he could not yet refer to his own findings regarding a monophyletic origin. In chapter one of the *Origin* Darwin (1859: 18–19) wrote: 'Mr. Blyth, whose opinion, from his large and varied stores of knowledge, I should value more than that of almost any one, thinks that all the breeds of poultry have proceeded from the common wild Indian fowl (Gallus bankiva)' [Red Junglefowl]. The same text appeared in the second edition, published on 7 January 1860, still before the end of his experiments.

In Darwin's lifetime six editions of the *Origin* were published: in 1859, 1860, 1861, 1866, 1869 and 1872, and a change in the text about his monophyletic poultry theory only appeared for the first time in the fourth edition. In principle it would have been possible to include the results of his crossings experiment in the third edition (published in March 1861). However, Darwin was awaiting comments from Tegetmeier on the results of the experiment, written up as a chapter on fowl in *The variation of animals and plants under domestication*. Although the chapter was submitted to Tegetmeier on June 1861 (Darwin 1861b), it was not returned to Darwin with his feedback until early 1865 (Darwin 1865)!

With the final results of his crossing experiments approved by Tegetmeier, Darwin (1866: 20) therefore added in the fourth edition of the *Origin*, to the earlier statement: 'having kept nearly all the English kinds [breeds] alive, having bred and crossed them, and examined their skeletons, I have come to a similar conclusion [as Mr. Blyth], – the grounds of which will be given in a future work [*Variation*, 1868].' After *Variation* was published, the final text in the fifth edition of the *Origin* read; 'Having kept nearly all the English breeds of the fowl alive, having bred and crossed them, and examined their skeletons, it appears to me almost certain that all are the descendants of the wild Indian fowl, Gallus bankiva; and this is the conclusion of Mr. Blyth, and of others who have studied this bird in India' (Darwin 1869: 20). This text remained unchanged in the sixth edition (1872: 14).

ISSN-2513-9894 (Online)