Various Gallus varius hybrids: variation in junglefowl hybrids and Darwin's interest in them

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Various *Gallus varius* hybrids: variation in junglefowl hybrids and Darwin's interest in them

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Summary.—Hybrids between Green Junglefowl *Gallus varius* and domestic fowl *G. gallus domesticus* confused several 19th-century ornithologists. The plumage of these hybrids is so unlike the colours and patterns of either of the parent species that they were considered to be distinct species: *G. aeneus* Temminck, 1825; *G. temminckii* Gray, 1849; and *G. violaceus* Kelsall, 1891. Darwin wanted to understand if *G. aeneus* and *G. temminckii* were hybrids or species, as part of his research on the origin of the domestic chicken. His view was that all domesticated fowl have a single wild ancestor, Red Junglefowl *G. gallus* (formerly *G. bankiva*). A hybrid specimen now present in the bird collection of the Natural History Museum at Tring played an important role in Darwin's reasoning and, although the conclusions he drew from this specimen were incorrect, his single-ancestor origin theory for domesticated fowl stands.

'These hybrids were at one time thought to be specifically distinct, and were named *G. aeneus.* Mr. Blyth and others believe that the *G. Temminckii* is a similar hybrid' (Darwin 1868a: 234–235).

In general, junglefowl species of the genus *Gallus* have a rather confused nomenclatural history. Ceylon Junglefowl *G. lafayettii*, for example, was named three times due both to its sexual dimorphism (males and females were each described as separate species) and to natural variation within the species (van Grouw *et al*. 2017). Other reasons why species were named more than once was that, historically, scientists were less likely to be aware of one another's work or might simply ignore prior descriptions and rename species.

George Kearsley Shaw (1751–1813) was the first to describe and name Green Junglefowl *G. varius* (Fig. 1), which is endemic to Indonesia. The origin of the species, which he called Variegated Pheasant *Phasianus varius*, was unknown to Shaw, but he thought it was probably an Indian bird (Shaw 1798). Whether Coenraad Jacob Temminck (1778–1858), the first director of the State Museum of Natural History (now Naturalis Biodiversity Centre in Leiden, was aware of Shaw's work is unknown, but he subsequently named and described the species both from specimens he had seen in the Paris museum, collected on Java by the French botanist and ornithologist Jean-Baptiste Leschenault de La Tour (1773–1826), and from those in his private collection which he received from the governor of Java (Temminck's own collection helped found the Leiden museum). Temminck named the species *G. furcatus* (from Latin furca: two-pronged fork), 'Cock with the forked tail' (Temminck 1807: 1807, 1813: 261–266, see Fig. 2). Thomas Horsfield (1773–1859) in turn named the species *G. Javanicus*, based on a specimen at that time in the Museum of the Honourable East India Company in London (Fig. 3), despite referring to Shaw's *varius* (Horsfield 1822). Although vols. 1–2 of the *Manuel d'ornithologie* (Temminck 1820a,b) had been Horsfield's guide to most of the genera in his 1822 publication, it nevertheless appears that he was unaware of the

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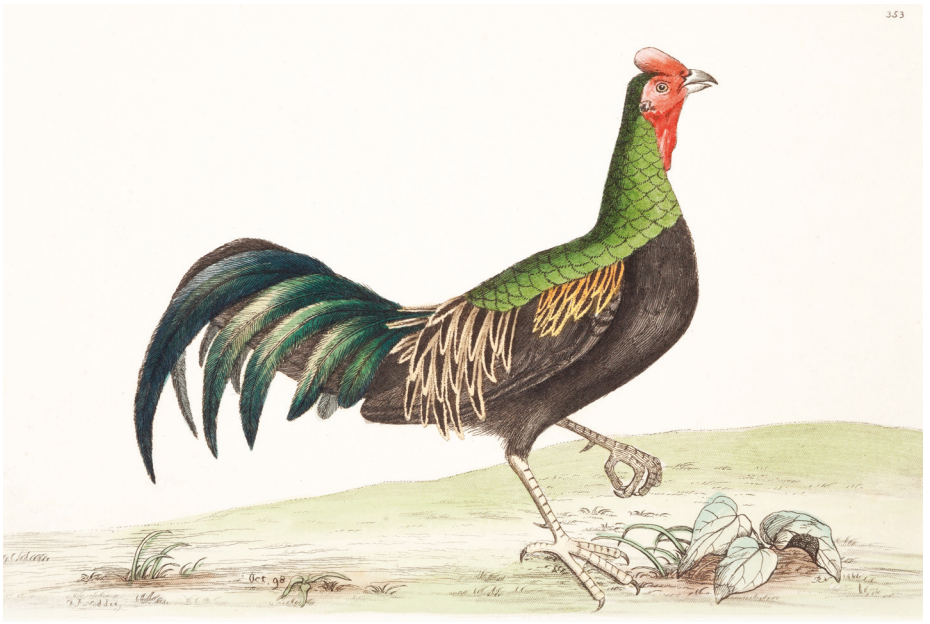

Figure 1. Pl. 353, Variegated Pheasant *Phasianus varius* in Shaw 1798 (Harry Taylor, © Natural History Museum, London)

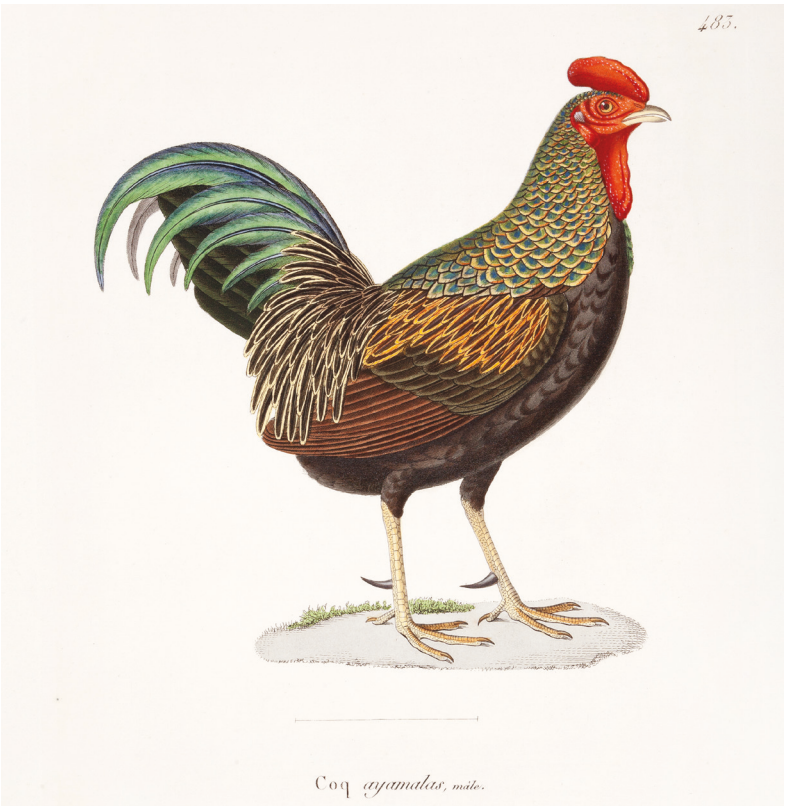

Figure 2. Lithograph of *Gallus furcatus*, 'ayam-alas', pl. 483 in Temminck's *Planches coloriées* (1829); the lithograph was after a drawing by the French natural history illustrator Nicolas Huet le Jeune (1770–1830) (Harry Taylor, © Natural History Museum, London)

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Figure 3 (above). Type specimen of *Gallus javanicus* Horsfield, 1822 (NHMUK Vel.Cat. 34.2a), collected in Java by Horsfield between 1811 and 1817, during which period Java formed part of British possessions in Indonesia (Harry Taylor, © Natural History Museum, London)

Figure 4 (left). Bekisar; a hybrid between a Green Junglefowl cock and a domestic chicken hen; the single throat wattle of Green Junglefowl is dominant in inheritance over the double wattles in chickens and therefore present in hybrids (© Cemani Farms, Subang, West Java, Indonesia)

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name *furcatus* for this species mentioned by Temminck (1820a: xc). So overall this junglefowl species was scientifically named three times.

Besides the synonymy in the different pure species, hybrids between Green Junglefowl and domesticated fowl *G. gallus domesticus* added to the nomenclatural chaos in the genus *Gallus*. In Indonesia, especially on Java, these hybrids were deliberately bred. Because of their beautiful, but wholly different plumage, ornithologists believed that they were distinct species and, again, these hybrids were scientifically named three times as distinct taxa: *G. aeneus* Temminck, 1825; *G. temminckii* Gray, 1849; and *G. violaceus* Kelsall, 1891. Here we review these names and present additional information on extant hybrid specimens, including the three different types, of which some were known to Darwin.

Gallus varius hybrids

The first-generation hybrid offspring of a *G. varius* cock and a domesticated chicken hen is called Bekisar in Indonesia (Beebe 1921: 249). The practice of hybridisation to produce Bekisar is ancient and probably commenced on the Kangean Islands in the Java Sea. Only the male hybrids are valued for their peculiar voice while the female hybrids were killed, at least formerly. Their call consists of the prolonged notes of Green Junglefowls combined with the volume of domestic fowl. Each cock has his own unique voice which carries long distances. They were prized by the boat cultures of Indonesia, which placed them in bamboo cages in their canoes and used them to maintain communication with other boats, even in the roughest seas.

While on Java, William Beebe (1877–1962), an American ornithologist, noticed the large diversity in these birds: 'some of these hybrids are huge creatures, with enormous pendant combs and beautiful plumage, whilst others are small and bantam-like with absurdly short legs' (Beebe 1921: 249). The large diversity in Bekisar, both in size and colour, is caused predominantly by the domestic fowl parent, depending on the inheritable features present in the breed of chicken used for the cross with Green Junglefowl. All dominant features present in the domestic hen will be present in the hybrid. What all Bekisar have in common, however, is their single throat wattle (Fig. 4), which is also present in *varius* and is dominant in inheritance over the double wattles of Red Junglefowl and its domestic varieties.

Another feature of all Bekisar cocks is their peculiar voice which lacks cadence or definiteness. Their calls are loud prolonged screams which can carry for at least 1 km. In Beebe's time the value of the bird was usually in the loudness and the piercing quality of its crow, which also needed to be drawn-out and monosyllabic. Among the poorer classes, however, another standard of vocal excellence was common: birds with a short, abrupt crow; more like that of the wild *varius*, but with a persistence which, according to Beebe (1921: 261), 'would drive a white person insane', were valued over other individuals.

Besides their use among boat cultures, by others their vocal characters were then mainly used for gambling purpose. Breeding and keeping Bekisar is still common and popular on Java for the latter reason—to match them in vocal competition—and 'good singing birds' are highly priced. To gain an impression of the diversity in colour, shape and size of these hybrids, search on the internet for images of 'bekisar' or 'ayam bekisar'.

Bronzed Cock *Gallus aeneus* Temminck, 1825

Temminck (*in* Temminck & Laugier de Chartrouse 1825) described a 'new species' of junglefowl, based on a specimen (Fig. 5) he had seen in the 'Muséum d'Histoire naturelle de Paris'. He named it *G. aeneus*, the bronzed cock (French: coq bronzé), a name originally linked to this specimen by Georges Cuvier (1769–1832) who, however, never described it

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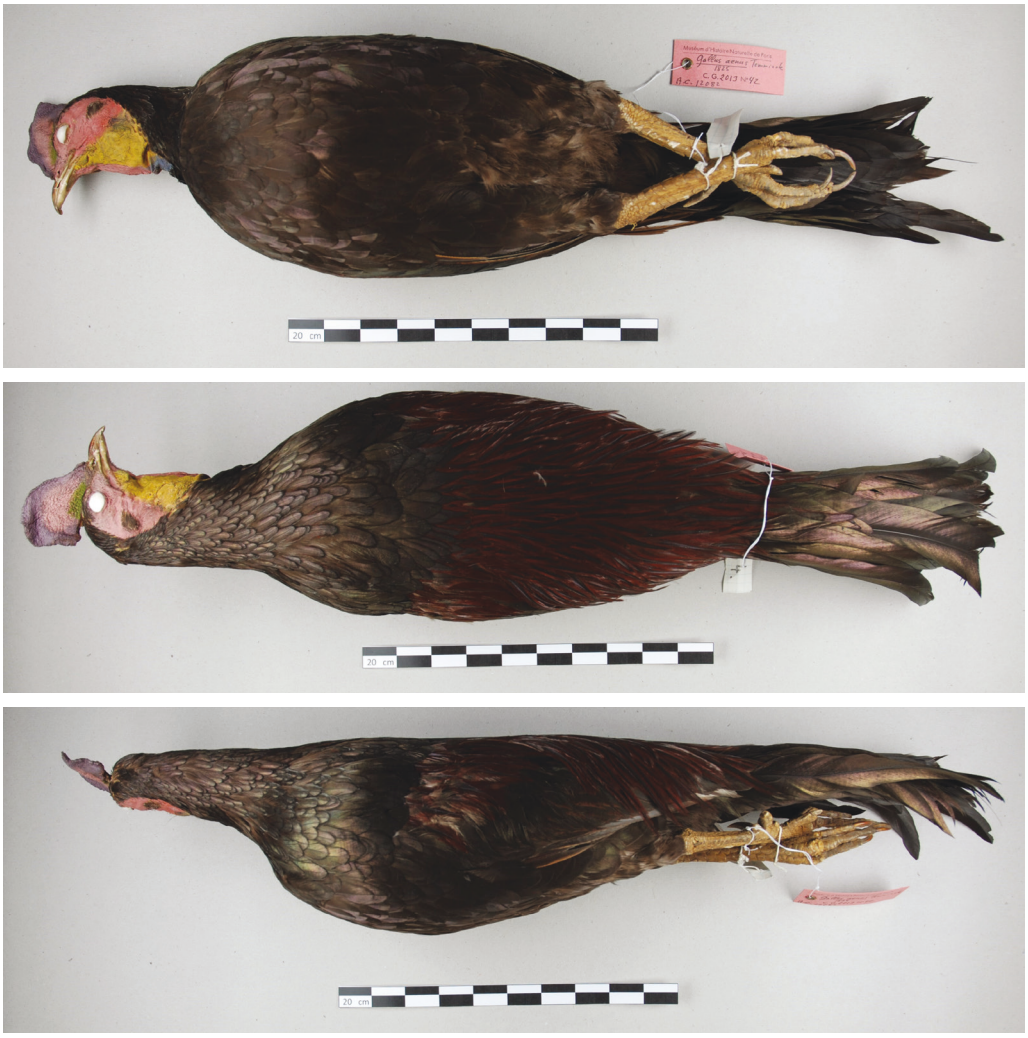

Figure 5. Holotype of *Gallus aeneus* Temminck, 1825 (MNHN.ZO.2013.42), collected by Pierre-Médard Diard between December 1818 and August 1819 on Sumatra (© Muséum National d'Histoire Naturelle, Paris)

as such (Voisin *et al*. 2015). The specimen was first figured, together with his description, in Temminck's *Planches coloriées* (1825, pt. 63, pl. 374; see Fig. 6).

The type specimen of *G. aeneus* was sent to the Paris museum by Pierre-Médard Diard (1794–1863), a French naturalist and explorer, who collected it at Pitat-Lanoago in Bencoolen (Lesson 1836: 378). Bencoolen was then a British possession (1685–1824) on the west coast of Sumatra (modern Bengkulu Province, Indonesia). Together with Alfred Duvaucel (1793–1824), another French explorer and a stepson of Cuvier, Diard was invited by Thomas Stamford Raffles (1781–1826), then Governor-General of Bencoolen (1817–22), to accompany him to the Malay Peninsula, Singapore and Sumatra to collect animals. Their first collecting trip started in December 1818, but in March 1820 Diard and Duvaucel fell out with Raffles over the division of the material, effectively terminating their cooperation! The reason for their conflict is explained differently by French and British sources. According to the French (Cuvier 1821) there was an agreement that half of the material collected would be sent to Paris, but Raffles nevertheless requisitioned most of it for the East Indian Company

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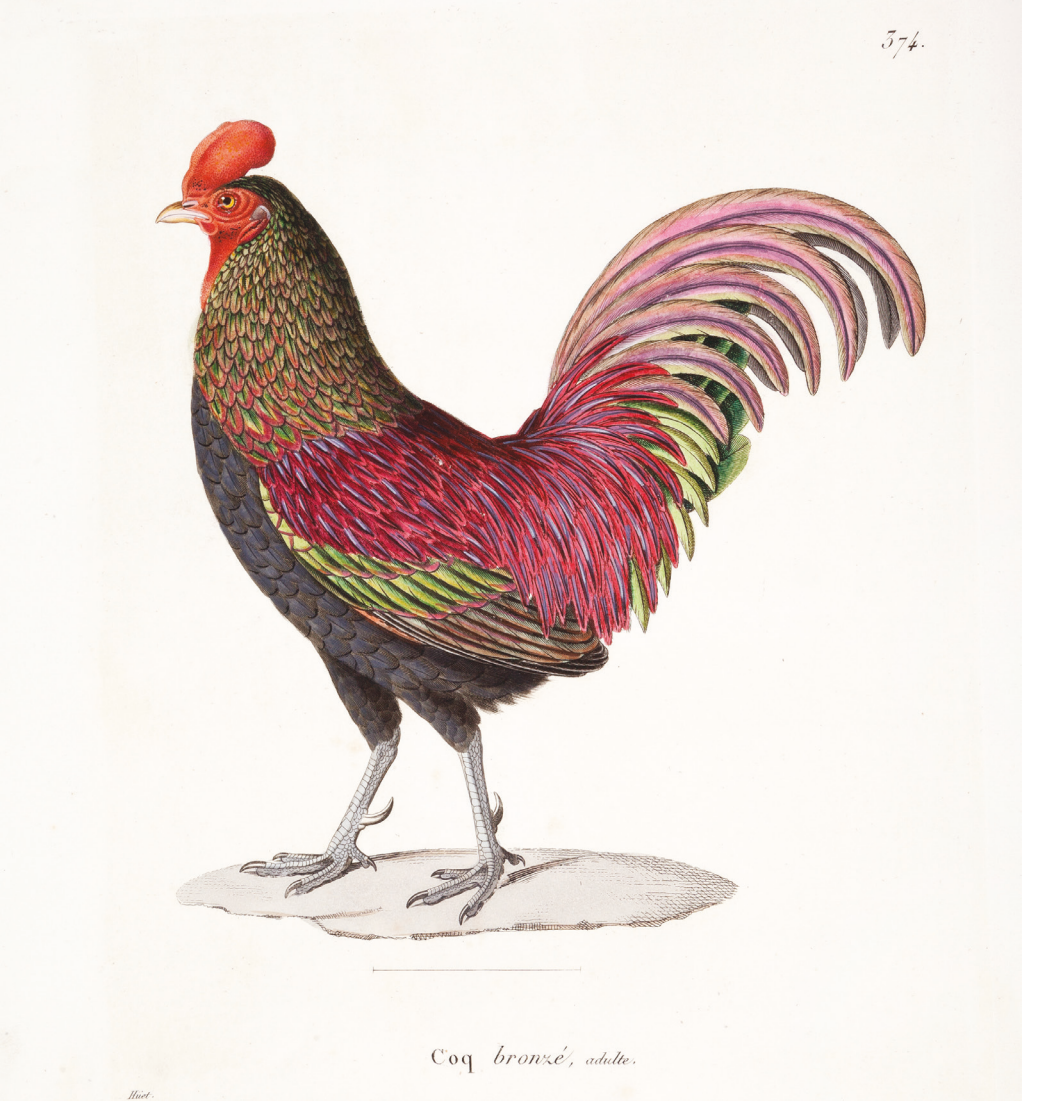

Figure 6. Lithograph of *Gallus aeneus*, 'the Bronzed Cock', pl. 374 in Temminck's *Planches coloriées* (1825); the lithograph was after a drawing by the French natural history illustrator Nicolas Huet le Jeune (Harry Taylor, © Natural History Museum, London)

Museum. The English explanation (Raffles 1822, Raffles 1830: 372–373, 702–723), however, was that all the collected material belonged to the East Indian Company as the latter paid the collectors a monthly salary for their work, but that nevertheless the French had secretly sent many objects to Cuvier in Paris, including their notes and drawings. Whatever the truth, Diard and Duvaucel did send specimens to France, including this cock supplied to the Paris museum by Diard during his stay in Bangkok (Voisin *et al*. 2015).

Salomon Müller (1804–63), a member of the governmental Natural Sciences Commission for the Dutch East Indies (1820–50), was the first to recognise that Temminck's *G. aeneus* was not a species (Müller 1843: 210). In December 1825 Müller was sent to Java, in the role of taxidermist, to collect and prepare specimens for the Leiden museum. He was the longest-serving member of the Commission and remained in Indonesia collecting specimens until

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late 1836, when he was summoned by the goverment to return to the Netherlands to begin describing the material he and his colleagues had collected during the previous 16 years. Müller became one of the most important ornithologists of his era, and from the material he collected personally (*c*.6,500 bird skins) and that of his colleagues of the Commission he described and named more than 90 new species, of which at least 65 are still valid taxa (HvG pers. research). While describing and cataloguing the Galliformes, together with Herman Schlegel (1804–84) who was at that time still Temminck's assistant at the Leiden museum, Müller discovered that *G. aeneus* was merely a hybrid between *G. varius* and a domestic chicken (Müller 1843: 210).

Batavian Cock *Gallus temminckii* G. R. Gray, 1849

George Robert Gray (1808–72) also described a new species of junglefowl (Figs. 7–8), based on a specimen purchased by the British Museum in 1849 from the dealer Gustav Adolph Frank (1809–80). The specimen was said to be from Batavia (modern-day Jakarta), but its true provenance was unknown. According to Gray, presumably based on the similarities with *G. aeneus*, 'it has been thought right to name it provisionally *Gallus temminckii*, until it may be proved otherwise than a species' (Gray 1849). In the description, Gray also mentioned a living example in the London Zoological Gardens (Fig. 9) which in some respects agreed with the description of *G. temminckii,* but bore a closer resemblance to *G. aeneus* of Temminck. It is not at all clear if at that point Gray was aware of Müller's (1843) publication and that *aeneus* is a hybrid, as he ends his description: '...that people who have the means of studying these birds [*G. temminckii* and *G. aeneus*] in their native places may be induced to determine whether these examples may justly be considered species, or only hybrids of others that are already known to naturalists.'

Nearly 20 years later, based on the entry in the museum's catalogue ('GALLUS TEMMINCKII. The Batavian Cock. *a.* Batavia, male.'), it appears Gray (1867: 39) still considered his *temminckii* to be a full species. At some point, however, he must have recognised his mistake as on the back of the original label of the type specimen is written '?? Hybrid between *G. varius & G. Bankiva G. R. G*'.

Gallus violaceus Kelsall, 1891

In 1891, Harry Joseph Kelsall (1867–1950), a Lieutenant with the Royal Engineers in Singapore, described a new species of junglefowl based on a live bird held in confinement in the botanic gardens of Singapore (Fig. 10). It was obtained in 1890 from a Malay dealer who had at that time two, both males, for sale. According to the dealer, they came from Borneo, but their provenance was uncertain. Based on the conspicuous violet gloss on the hackles and tail feathers, which according to Kelsall was the most distinguishing feature of the bird, he named this 'species' *G. violaceus*. Kelsall further noted that his bird resembled *G. varius* in having only a single throat wattle, and in the hackles being round-tipped, rather than lance-shaped as in other members of the genus. It, however, differed from *G. varius* in its colouring and by having a serrated comb (Kelsall 1891). A few years later, two additional specimens, both males, came to his attention in the possession of an animal dealer in Singapore who thought they came from Java, but again provenance was uncertain (Kelsall 1894).

Darwin's interest in *Gallus varius* hybrids

Charles Darwin (1809–82) was of the opinion that the domesticated chicken descended solely from one ancestor (monophyletic origin), namely Red Junglefowl *G. gallus* (formerly *G. bankiva,* Temminck). He used artificial selection applied by breeders of domestic animals

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Figure 7. Holotype of *Gallus temminckii* G. R. Gray, 1849 (NHMUK 1849.3.2.67), provenance unknown, but said to be from Batavia (modern-day Jakarta) (Harry Taylor, © Natural History Museum, London)

Figure 8. Engraving by Joseph Wolf (1820–99) of the holotype of *Gallus temminckii*, in Gray 1849 (Hein van Grouw, © Natural History Museum, London)

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Figure 9 (left). Engraving by Joseph Wolf of a hybrid junglefowl similar to *Gallus aeneus*, which was present in the London Zoological Gardens at the time, in Gray 1849 (Hein van Grouw, © Natural History Museum, London)

Figure 10 (below). Holotype of *Gallus violaceus* Kelsall, 1891 (ZRC 3.30131); at the time of description, 1891, this bird was still alive in the Singapore Botanic Gardens, but after it died was donated to the, then, Raffles Museum (© Kelvin Lim Kok Peng, Lee Kong Chian Natural History Museum at the National University of Singapore)

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as an important analogy to illustrate the mechanism of variation and selection in nature. The diversity of domesticated breeds all descended from a common ancestor, in this case Red Junglefowl, showed, in Darwin's opinion, how selection could modify a species. And, if artificial selection can be so powerful over a short time, what might natural selection achieve working over much longer periods?

Darwin very briefly mentioned the above poultry example in *On the origin of species by means of natural selection* (1859: 18–19), but described it in more detail in *The variation of animals and plants under domestication* (1868a: 225–275). As part of his poultry research, Darwin was interested as to whether *G. aeneus* and *G. temminckii* were species rather than hybrids (Darwin 1868a: 233–236). If the former, he needed to find arguments to eliminate them as possible ancestors of the domestic chicken in favour of Red Junglefowl. He had already rejected *G. varius* as ancestor, 'which differs in so many characters – green plumage, unserrated comb, and single median wattle – that no one supposes it to have been the parent of any of our breeds' (Darwin 1868a: 234). Regarding the true identity of *G. aeneus* and *G. temminckii*, he correctly relied on others, quoting Crawfurd (1856: 112): 'These hybrids [between *G. varius* and domestic fowl] were at one time thought to be specially distinct, and were named *G. aeneus*. Mr. Blyth and others believe that the *G. Temminckii* (of which the history is not known) is a similar hybrid' (Darwin 1868a: 234–235).

Darwin may, however, have found his first evidence for *aeneus* being a hybrid in Wagner (1847), as in his unpublished manuscript *Natural selection*, under footnote 13 (Chapter IX; hybridism), Darwin refers to Wagner's statement there that 'S. Müller and Schlegel have remarked that *Gallus aeneus* (pl. col. 374) is merely a hybrid of *G. furcatus* [*varius*] and a tame Hen.' *Natural selection* was the manuscript Darwin had originally intended to publish as the formal presentation of his views on evolution. It was, however, never completed because, prompted by Wallace's letter to him concerning the principles of evolution, Darwin hurriedly wrote and published *On the origin of species*, which was literally only an abstract of the manuscript. Compared to the *Origin*, the original long manuscript has more abundant examples and illustrations of Darwin's argument, plus an extensive citation of sources. *Natural selection* was transcribed after Darwin's death, and first published by Stauffer (1975).

Darwin was also in contact with Edward Blyth (1810–73), curator of the museum of the Asiatic Society of Bengal in Calcutta, about *G. aeneus* and *G. temminckii*. Blyth (1855b) wrote to Darwin that 'The *G. aeneus*, Temminck, is now known to be a hybrid raised in confinement between *G. furcatus* & a common hen.' In following letters he wrote: 'The *Gallus aeneus* of Temminck is a hybrid between *Gallus varius* (vel *furcatus*) & a common hen, often raised in captivity in Java' (Blyth 1856a), and, 'I have just received a large batch of the *Proceedings of the Zoological Society*; and find a *Gallus Temminckii* described by Gray (& it would seem also *figured*). I have no faith in it; suspecting it *very strongly* to be a hybrid of some kind, probably a cross between male *varius* (v. *furcatus*) and hen of the large Malayan breed of domestic fowls; while *G. aeneus*, Temminck, as we are assured by Schlegel, is mixed *varius* & (small?) common hen' (Blyth 1856b).

William Bernhardt Tegetmeier (1816–1912), Darwin's advisor on domesticated pigeons and fowl, wrote to Darwin: 'Did you ever see a half bred Gallus Varius? or Eneus [*sic*]? with common fowl.— He was some years since in the Zoological Gardens. He was remarkable as having transverse bright blue bands on his tail coverts like a so called "cuckoo cock". I have some of the feathers if you would like to see them' (Tegetmeier 1866a). Darwin (1866a) did like to see them, so Tegetmeier (1866b) sent them to Darwin who, when he returned the feathers by post, commented: 'they are extremely curious' (Darwin 1866b). In his *Variation under domestication*, Darwin briefly discussed 'cuckoo' markings in fowl as cases of analogous or parallel variation: 'the plumage of these birds is slaty-blue or grey, with each

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Figure 11. Male hybrid between Green Junglefowl cock and domestic chicken hen, bred and kept in the London Zoological Gardens in the 1850s and after its death donated to the British Museum (Natural History) (NHMUK 1857.11.9.1); the remarkable dark and pale barring on the feathers (the cuckoo pattern) is the result of a colour aberration known as 'sex-linked barring' which was inherited from the domestic hen; compare this specimen with the bird in Fig. 13 (Harry Taylor, © Natural History Museum, London)

feather transversely barred with darker lines, so as to resemble in some degree the plumage of the cuckoo' (Darwin 1868a: 244). By the term 'analogous or parallel variation' Darwin meant that similar characters occasionally occur in different varieties or races descended from the same species or, more rarely, in widely distinct species and was implying that these markings signified a reversion to an ancestral character.

The same hybrid bird from the London Zoological Gardens is discussed in chapter 13, 'Reversion or Atavism', in *Variation* (Darwin 1868b: 39–40). Again he used the term 'reversion' to describe situations where a character previously observed in a taxon disappears in crosses and then resurfaces in later generations. Reversion was for him a form of ancestral inheritance; the return of characteristics of a distant ancestor; 'I owe to the kindness of this same excellent observer [Tegetmeier] the inspection of some neck-hackles and tail-feathers from a hybrid between the common fowl and a very distinct species, the *Gallus varius*; and these feathers are transversely striped in a conspicuous manner with dark metallic blue and grey, a character which could not have been derived from either immediate parent' (Darwin 1868b: 40). Tegetmeier, when asked his opinion about the latter statement, agreed (Darwin 1861, 1865). So both Darwin and Tegetmeier considered these blue tranverse bars on the hackles and tail feathers of this *varius* hybrid to be an ancesteral trait expressed by crossing, or by analogous variation. The hybrid which caused this discussion, or a very similar bird, was received by the British Museum in November 1857

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from the London Zoological Gardens and is currently still in the Natural History Museum's (NHMUK) collection at Tring (Fig. 11).

Both men drew the same conclusions about some additional specimens—skins of domesticated chickens from Borneo—sent to Darwin by James Brooke (1803–68), Rajah of Sarawak, in 1857. 'Sir J. Brooke sent me some skins of domestic fowls from Borneo', Darwin (1868a: 235) wrote, 'and across the tail of one of these, as Mr. Tegetmeier observed, there were transverse blue bands like those which he had seen on the tail-feathers of hybrids from *G. varius*, reared in the London Zoological Gardens. This fact apparently indicates that some of the fowls of Borneo have been slightly affected by crosses with *G. varius*, but the case may possibly be one of analogous variation.' Although we were unable to check this specimen, it is more likely that it was not a hybrid and that the transverse bars were caused by the cuckoo mutation which was, and still is, present in many domestic chicken populations. Cuckoo pattern in chickens is a dominant and sex-linked mutation, known as 'sex-linked barring' among poultry geneticists. This common heritable mutation rhythmically switches the production of melanin on and off during feather growth, resulting in alternating pale and coloured transverse bars over the total length of each feather (Crawford 1990: 126–128; see Figs. 12–13).

These Bornean skins were probably those that Darwin encouraged Tegetmeier to exhibit, together with those of other Asiatic domestic fowl, at a meeting of the Zoological

Figure 12. German Cuckoo, a breed of domestic chicken, male, in the traditional cuckoo pattern, commonly referred to as 'barred' by chicken fanciers, which is the combination of two different mutations; Black (gene symbol *E*), a dominant mutation which turns the wild type colour solid black, and sex-linked barring (gene symbol *B*) which switches the production of melanin on and off during feather growth, resulting in alternating pale and coloured transverse bars over the length of each feather (© Aad Rijs)

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Figure 13. Leghorn, a breed of domesticated chicken, male, in the variety 'gold barred', which is the result of the effect of sex-linked barring alone, without any other mutation; as sex-linked barring affects eumelanin (black) more than phaeomelanin (reddish brown), the alternating pale and coloured transverse bars are less conspicious in the 'golden' parts of the plumage; compare this bird with the specimen in Fig. 11 (© Aad Rijs)

Society (Anon. 1857, Darwin 1857, Tegetmeier 1857). Their current whereabouts, if they still exist, are unknown to us.

Discussion

One of the reasons why Darwin considered Red Junglefowl to be the sole ancestor of domestic fowl was that crosses between domesticated fowl and Red Junglefowl are fertile, while, according to the evidence available to Darwin, crosses with *G. varius*, *G. sonneratii* and *G. lafayettii* are rarely so. 'As I am informed by Mr. Crawfurd', Darwin (1868a: 234) wrote, 'hybrids are commonly raised between the male *G. varius* and the common hen, and kept for their great beauty, but are invariably sterile; this, however, was not the case with some bred in the Zoological Gardens.' Darwin also referred to Samuel James Augustus Salter (1825–97), who conducted crossing experiments with *varius* hybrids at the London Zoological Gardens during 1861–62, and reported low fertility among them (Salter 1863).

Hybridisation experiments in the London Zoological Gardens during 1884, however, revealed that all four *Gallus* species can produce fertile hybrids with domesticated fowl.

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These results persuaded Tegetmeier to repeal his earlier belief in a monophyletic origin of domestic fowl. In an open letter to *The Field*, Tegetmeier (1885, see Appendix) acknowledged that most poultry breeds indeed descended from Red Junglefowl, but suggested that a few large and distinct Asian chicken breeds were descended from some other species of wild junglefowl, now extinct.

So, less than four years after Darwin's death, his advisor Tegetmeier dismissed the single-species origin based on 'new' evidence which had not been available to Darwin. Although Darwin was correct as to the monophyletic origin of domesticated fowl, some of the evidence he used to corroborate his opinion was incorrect. For much of his hypothesis he had to rely on the accounts and observations of others, e.g. Blyth (1855a, 1856a), Crawfurd (1856: 112) and Salter (1863) regarding the fertility of hybrids, without knowing whether these were true.

Darwin's theory of evolution by natural selection rests on the premise of the heritability of variation, yet Darwin lacked knowledge of the mechanisms for this. Two views on inheritance were commonly embraced at that time: the inheritance of characteristics acquired during the lifetime of an individual (usually referred to as 'Lamarckian inheritance') and blending inheritance, in which the offspring is intermediate between the two parents. Both were at direct odds with natural selection as the mechanism for evolution. Darwin therefore formulated his own 'provisional hypothesis': pangenesis, a modified combination of the inheritance of acquired characteristics and the blending theory (Darwin 1868b: 357–404). In short, according to Darwin, minute particules called gemmules, produced by every cell, circulate around the body and can be modified throughout life. It is these gemmules, he maintained, that are passed to future offspring, subtly changing the information that is inherited. Depending on the number of gemmules received from both parents, the offspring may be more similar to one, or the other, parent. To explain 'reversion' and 'analogous variation', according to Darwin, gemmules could lie in dormancy then re-emerge to be manifest as ancestral forms.

As the transverse blue bars found in the hybrid are not present in *G. varius* and, according to Tegetmeier (Darwin 1861, 1865), neither in the domestic fowl parent, Darwin assumed they represented an ancestral form. The 'laws of inheritance' and the fact that genes are constantly passed from one generation to the next were unknown to Darwin. Whether the domestic hen indeed did not show any sign of 'barring' or Tegetmeier simply had not noticed it, we do not know; in some gene combinations the cuckoo phenotypic barring trait is hardly visible in female plumage, while in others it is completely masked. What we do know is that the plumage colour of the *varius* hybrid male in the London Zoological Gardens was not the result of reversion or analogous variation, but the result of the gene that codes for barring, present in the domesticated hen, being passed to her hybrid son.

While Darwin was still struggling to make pangenesis work, a monk experimenting with inheritance in pea plants in Brno had just discovered that each individual trait is inherited independently; sometimes visibly, sometimes not, depending on the combination of parental types, but remaining unchanged as each passes inexorably through the generations.

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photographs of chicken breeds. We are indebted to Kees Rookmaker and Katrina van Grouw for their constructive suggestions that improved the submitted manuscript considerably.

References:

Anon. 7 March 1857. Zoological – Feb 24. *Athenaeum J. Lit., Sci. & Fine Arts* 1857: 313.
Beebe, W. 1921. *A monograph of the pheasants*, vol. 2. H. F. & G. Witherby, London.
Blyth, E. 1855a. Letter to C. R. Darwin, 21 April 1855. Darwin Correspondence Project, letter no. 1670.
Blyth, E. 1855b. Letter to C. R. Darwin, 30 September or 7 October 1855. Darwin Correspondence Project, letter no. 1761.
Blyth, E. 1856a. Letter to C. R. Darwin, 23 February 1856. Darwin Correspondence Project, letter no. 1832.
Blyth, E. 1856b. Letter to C. R. Darwin, *c.*22 March 1856. Darwin Correspondence Project, letter no. 1845.
Crawford, R. D. ed. 1990. *Poultry breeding and genetics; developments in animal and veterinary sciences*, vol. 22. Elsevier, Amsterdam.
Crawfurd, J. 1856. *A descriptive dictionary of the Indian islands & adjacent countries*. Bradbury & Evans, London.
Cuvier, G. 1821. Notice sur les voyages de MM Diard et Duvaucel, naturalistes français, dans les Indes orientales et dans les îles de la Sonde. *Rev. Encyclopédique* 10: 473–482.
Darwin, C. R. 1857. Letter to W. B. Tegetmeier, 18 February 1857. Darwin Correspondence Project, letter no. 2054.
Darwin, C. R. 1859. *On the origin of species by means of natural selection*. First edn. John Murray, London.
Darwin, C. R. 1861. Letter to W. B. Tegetmeier, 22 March 1861. Darwin Correspondence Project, letter no. 3095.
Darwin, C. R. 1865. Letter to W. B. Tegetmeier, 7 April 1865. Darwin Correspondence Project, letter no. 4806.
Darwin, C. R. 1866a. Letter to W. B. Tegetmeier, 4 August 1866. Darwin Correspondence Project, letter no. 5176.
Darwin, C. R. 1866b. Letter to W. B. Tegetmeier, 10 August 1866. Darwin Correspondence Project, letter no. 5187.
Darwin, C. R. 1868a. *The variation of animals and plants under domestication*, vol. 1. John Murray, London.
Darwin, C. R. 1868b. *The variation of animals and plants under domestication*, vol. 2. John Murray, London.
Gray, G. R. 1849. Notice of two examples of the genus *Gallus*. *Proc. Zool. Soc. Lond*. 1849: 62–63.
Gray, G. R. 1867. *List of the specimens of birds in the collection of the British Museum*, pt. 5. London.
van Grouw, H., Dekkers, W. & Rookmaaker, K. 2017. On Temminck's tailless Ceylon Junglefowl, and how Darwin denied their existence. *Bull. Brit. Orn. Cl.* 137: 261–271.
Horsfield, T. 1822. Systematic arrangement and description of birds from the island of Java. *Trans. Linn. Soc. Lond*. 13: 133–185.
Kelsall, H. J. 1891. Description of a new species of jungle fowl, said to come from Borneo. *J. Straits Branch Roy. Asiatic Soc*. 24: 167–168.
Kelsall, H. J. 1894. Notes on *Gallus violaceus*. *J. Straits Branch Roy. Asiatic Soc*. 25: 173.
Lesson, R. P. 1836. *Compléments des oeuvres de Buffon*. *Oiseaux*, vol. 7. Pourrat Frères, Paris.
Müller, S. 1843. Bijdragen tot de kennis van Timor en eenige andere naburige eilanden. Pp. 131–310 *in* Temminck, C. J. 1840–47. *Land- en Volkenkunde. Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche bezittingen, door de Leden der Natuurkundige commissie in Indië en andere Schrijvers*. S. en J. Luchtmans & C. C. van der Hoek, Leiden.
Raffles, S. 1830. *Memoir of the life and public services of Sir Thomas Stamford Raffles, F.R.S. &c., particularly in the government of Java, 1811–1816, and in Bencoolen and its dependencies, 1817–1824; with details of the commerce and resources of the Eastern Archipelago and selections from his correspondence*. John Murray, London.
Raffles, T. S. 1822. Descriptive catalogue of a zoological collection, made on account of the Honourable East India Company, in the island of Sumatra and its vicinity. *Trans. Linn. Soc. Lond*. 13: 239–274.
Salter, S. J. A. 1863. Note on the fertility, inter se, of hybrids of different species of the genus *Gallus*. *Nat. Hist. Rev.* n. ser. 3: 276–279.
Shaw, G. 1798. *The naturalist's miscellany or Coloured figures of natural objects*, vol. 10. Nodder & Co., London.
Stauffer, R. C. ed. 1975. *Charles Darwin's Natural selection; being the second part of his big species book written from 1856 to 1858*. Cambridge Univ. Press, Cambridge, UK.
Tegetmeier, W. B. 1857. [Mr. Tegetmeier exhibited a collection of skins of new varieties of domestic fowls, the property of Mr. C. Darwin]. *Proc. Zool. Soc. Lond*. 1857: 46.
Tegetmeier, W. B. 1866a. Letter to C. R. Darwin, 2 August 1866. Darwin Correspondence Project, letter no. 5171.
Tegetmeier, W. B. 1866b. Letter to C. R. Darwin, after 4 August 1866. Darwin Correspondence Project, letter no. 5180.
Tegetmeier, W. B. 1885. The origin of the domestic fowl. *The Field* 26 September 1885: 467.
Temminck, C. J. 1807. *Catalogue systématique du cabinet d'ornithologie et de la collection de quadrumanes, avec une courte description des oiseaux non-décrits*. C. Sepp Jansz, Amsterdam.
Temminck, C. J. 1813. *Histoire naturelle générale des pigeons et des gallinacés*, vol. 2. J. C. Sepp & fils, Amsterdam & G. Dufour, Paris.

ISSN-2513-9894 (Online)

Temminck, C. J. 1820a. *Manuel d'ornithologie, ou, Tableau systématique des oiseaux qui se trouvent en Europe*, vol. 1. Second edn. H. Cousin, Paris.
Temminck, C. J. 1820b. *Manuel d'ornithologie, ou, Tableau systématique des oiseaux qui se trouvent en Europe*, vol. 2. Second edn. H. Cousin, Paris.
Temminck, C. J. & Laugier de Chartrouse, G. M. J. 1825. *Nouveau recueil des planches coloriées d'oiseaux*, pl. 374, pt. 63. Paris.
Temminck, C. J. & Laugier de Chartrouse, G. M. J. 1829. *Nouveau recueil des planches coloriées d'oiseaux*, pl. 483, pt. 81. Paris.
Voisin, C., Hennache, A. & Voisin, J.-F. 2015. List of type specimens of birds in the collections of the Muséum National d'Histoire Naturelle (Paris, France). 24. Cracidae, Odontophoridae, Phasianidae and Numididae. *J. Natl. Mus. (Prague), Nat. Hist. Ser*. 184: 1–42.
Wagner, J. A. 1847. Gallinaceae, Ornithology, Progress of Zoology in 1843. P. 80 *in* Reports on Zoology for 1843, 1844. The Ray Society, London.

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Appendix

Letter of W. B. Tegetmeier, *The Field* 26 September 1885, p. 467

THE ORIGIN OF THE DOMESTIC FOWL.

Sir,–The origin of all the different varieties or breeds of the domestic fowl is usually believed to be the common wild Indian jungle cock, the Gallus ferrugineus of modern naturalists, but known also as the Bankiva fowl (G. bankiva in the older books). This bird may be readily described as closely resembling a small black-breasted red game-cock, with a tail carried more horizontally than usual.

It may be regarded as most presumptuous in me to dare to contest the conclusions arrived at by the honoured master Darwin, with whom and for whom it was for some years my privilege to work; but a careful and extended consideration of the facts has led me to a different conclusion to that arrived at by him.

There are now existing four distinct and well-marked species of the genus Gallus, namely: (1) The common G. ferrugineus [*G. gallus*]; (2) the Sonnerat jungle cock (G. sonnerati of naturalists), so readily distinguished by the flattened shafts of the feathers in the male; (3) the jungle cock of Ceylon (G. stanleyi), which is confined to the island (this was admirably figured by the late T. W. Wood in illustration of a descriptive article of mine in *The Field* of Nov. 29, 1873); and (4) the fork-tailed or single-wattled cock of Java (G. furcatus).

That the domesticated fowl in India is derived from the first species is evident from the fact that sportsmen occasionally confound the wild and tame birds. This, taken into conjunction with the fact that hybrids with the other species bred in confinement have not been remarkably fertile, has led probably to the conclusion which has been arrived at; but this want of fertility has been due to the unnatural conditions under which the birds have been placed. Everyone at all conversant with poultry keeping knows that eggs laid by fowls in confined runs are mostly sterile, and it could hardly be expected that cross-breeding with distinct species would, under these conditions, conduce to greater fertility.

The hybrids between the different species of Gallus are, in many cases, perfectly fertile. Some years since, I saw at Clumber numerous game bantams roosting in the trees, that had for several generations been bred from a Sonnerat cock and domestic hens.

Last season [1884], at the Zoological Gardens, numerous half-bred birds were reared from G. stanleyi [*G. lafayettii*], and in former years many were bred from a single specimen of G. furcatus [*G. varius*]. There is no doubt that the several wild Galli will interbreed and produce fertile offspring as readily as do the corresponding and closely allied pheasants, in which the three species, the Chinese, the versicolor, and the Colchican, have become so mixed, that pure birds are rarer than mongrels.

I have no doubt in my own mind that the wild Galli have intermixed in not a few instances, and perhaps through not a few centuries, in producing our domesticated breeds.

But it is with regard to the eastern Asiatic type of fowl (absurdly known as Cochins and Brahmas) that my doubts as to the descent from the G. ferrugineus [*G. gallus*] are strongest.

We have in the Cochin a fowl so different from the ordinary domestic birds that, when first introduced, the most ridiculous legends were current respecting it. Putting these on one side, we have a bird 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. The extraordinary diminution in the size of the flight feathers and that of the pectoral muscles could hardly have been the result of human selection and careful breeding, as the value of the birds as articles of food is considerably lessened by the absence of flesh on the breast. Nor is the extreme abundance of fluffy soft body feathers a character likely

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to be desiderated in a fowl. The vastly increased size may have been a matter of selection, although, as the inhabitants of Shanghai feed their poultry but scantily, and, according to Mr. Fortune, mainly on paddy or unhusked rice, it is not easy to see how the size of the breed was obtained if, as generally surmised, it arose from the little jungle fowl [*G. gallus*].

Taking all these facts into consideration, I am induced to believe that the birds of the Cochin type did not descend from the same species as our game fowl. It may be asked what bird I would suggest as the origin of these eastern Asiatic breeds. In reply I would suggest the possibility, or even probability, of their being descended from some easily captured and readily domesticated short-winged species, that may have entirely passed into a state of domestication, as has the camel and the horse. I can see no inherent improbability in this suggestion, nor any fatal objection to the theory I have advanced. W.B. Tegetmeier.

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