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Authors: Grouw, Hein van, Dekkers, Wim, and Rookmaaker, Kees

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On Temminck's tailless Ceylon Junglefowl, and how Darwin denied their existence

by Hein van Grouw, Wim Dekkers & Kees Rookmaaker

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Summary.—Ceylon Junglefowl was described in 1807 by the Dutch ornithologist Coenraad Jacob Temminck. The specimens he examined were tailless ('rumpless') and therefore he named them *Gallus ecaudatus*. In 1831 the French naturalist René Primevère Lesson described a Ceylon Junglefowl with a tail as *Gallus lafayetii* (= *lafayettii*), apparently unaware of Temminck's *ecaudatus*. Subsequently, *ecaudatus* and *lafayettii* were realised to be the same species, of which *G. stanleyi* and *G. lineatus* are junior synonyms. However, Charles Darwin tried to disprove the existence of wild tailless junglefowl on Ceylon in favour of his theory on the origin of the domestic chicken.

'The tailless cock inhabits the immense forests of the island of Ceylon' (Temminck 1813: 268).

'... but this statement [tailless fowls are wild in Ceylon] ... is utterly false' (Darwin 1868: 259).

Ceylon Junglefowl *Gallus lafayettii* is one of four species in the genus *Gallus* in South and South-East Asia. It is confined to Sri Lanka, where it is the national bird. At the end of the 18th century, three specimens of a tailless variety were sent from Sri Lanka to Holland, where they were added to the collections of Coenraad Jacob Temminck and Johan Raye van Breukelerwaert. Fowl without tail are called 'rumpless' by poultry keepers and geneticists, explained as the hereditary absence of some or all tail bones (Crawford 1990). In domestic fowl the condition has been known for centuries: rumpless domestic chickens were illustrated by the Italian naturalist Ulisse Aldrovandi (1600) as Persian fowl (Fig. 1). Linnaeus (1758) correctly considered the rumpless Persian fowl a variety of Red Junglefowl *G. gallus*, naming it *Phasianus gallus*, var. γ. ecaudatus. Latham (1790) transferred it to the genus *Gallus* and elevated it to a species as *G. ecaudatus* (see Appendix).

Darwin also was familiar with rumplessness as a variety in domestic chickens and used it as an example of deleterious variants, which in his opinion, if they occurred in animals in the wild, would be removed from the general population by natural selection (Darwin 1868). In this paper we provide evidence that Darwin did not believe in the former existence of wild rumpless junglefowl on Ceylon. Furthermore, he was unaware that these were in fact a variety of Ceylon Junglefowl and he also did not realise that the evidence for this, Temminck's specimens in Leiden, still existed.

Temminck's rumpless Ceylon Junglefowl

Coenraad Jacob Temminck (1778–1858) became the first director of the State Museum of Natural History (RMNH, now Naturalis Biodiversity Center) in Leiden following its foundation in 1820. Temminck's own ornithological collection had previously been enriched via contacts with many travellers and collectors, due to the senior position of his father Jacob in the Dutch East India Company (Hoek Ostende *et al.* 1997). Temminck started



Figure 1. Engraving of Aldrovandi's (1600) rumpless Persian hen and Persian cock (Harry Taylor, © Natural History Museum, London)

to catalogue his birds in 1799, when he allocated numbers up to 333, adding to these in subsequent years until the list was printed in 1807 (Stresemann 1953). Entry 257 catalogued two specimens of rumpless fowl from Ceylon: '(257) Gallus ecaudatus (*primus*) (Mas) *Temm. Gall.* – Le coq sans croupion, ou le Wallikikili de Ceylan (Mâle) (*Espèce primitive*) – *Temm. Gall. v.1. pl. Enl.*' (Temminck 1807: 145).



Figure 2. Lithograph of Gallus ecaudatus, based on specimen RMNH. AVES.224888 (Fig. 3), by Jean-Gabriel Prêtre prepared c.1806 for an illustrated work in three volumes that Temminck intended to publish on pigeons and Galliformes. Only the volume on pigeons was published, in 1808, and the two volumes on Galliformes never appeared due to a conflict between Temminck and the French illustrator of the first volume, Pauline Knip (Dickinson et al. 2010). Instead, Temminck later published Histoire naturelle générale des pigeons et des gallinacés in three volumes (1813-15) without any colour illustrations. The reference 'Gall. v. 1. pl. Enl.' in Temminck's published catalogue (1807) refers to the first of the two unpublished volumes on Galliformes, which would have been vol. 2 of the complete work (Naturalis Biodiversity Center, Leiden)



Figure 3. First syntype of *Gallus ecaudatus* Temminck, 1807 (RMNH.AVES.224888), adult, from Temminck's former private collection (Naturalis Biodiversity Center, Leiden)



Figure 4. Second syntype of *Gallus ecaudatus* Temminck, 1807 (RMNH.AVES.224889), juvenile, from Temminck's former private collection (Naturalis Biodiversity Center, Leiden)

The entry is bilingual, Latin and French. Therefore, both 'primus' and 'Espèce primitive' have the same meaning and suggest that Temminck thought these birds represented the ancestral type of rumpless domestic fowl. Temminck referred ('pl. Enl.') to a lithograph of one of the birds that he intended to add to a planned series of descriptions of pigeons and Galliformes; this was never published, but is preserved among his papers in the Naturalis Library, Leiden (Fig. 2).

Temminck (1813) provided more extensive details about the new species *Gallus ecaudatus*, 'named by me' (mihi). In Ceylon it was called *wallikikili* meaning 'cock of the woods'—a name later shortened to *wallikiki* by French authors and used for domestic, rumpless fowl. Temminck examined three specimens, all males (no hens): two in his own collection (as listed in Temminck 1807) and another adult owned by Johan Raye van Breukelerwaert, a rich merchant with an extensive bird collection who lived close to Temminck in Amsterdam. Temminck stated that his own tailless specimens were sent by an unnamed governor of Dutch Ceylon. The last two Dutch governors before Ceylon was ceded to the British in 1796 were Willem Jacob van de Graaf (governor 1784–94) and Johan van Angelbeek (1794–96). It is probable that Raye's specimen came from the same source. No other rumpless specimens of Ceylon Junglefowl have been recorded from Sri Lanka.

In 1820, Temminck's private collection became the nucleus of the new museum in Leiden, where many of these specimens are still present, including his two mounted *G. ecaudatus* in remarkably good condition. One is an adult with fully developed comb and wattles (Fig. 3), while the other is a young bird whose comb and wattles were just starting to develop (Fig. 4). The collection of Raye van Breukelerwaert was auctioned in July 1827. According to an annotated copy of the sales catalogue in the Naturalis Library, Lot 885



Figure 5. Holotype of *Gallus lafayettii* Lesson, 1831 (MNHN 2014-393) collected by Leschenault in Ceylon between July 1820 and February 1821 (Muséum national d'Histoire naturelle, Paris)

'Gallus ecaudatus, le Coq sans queue' was bought by 'RM', abbreviation of 'Rijks Museum' (RMNH) in Leiden (Raye 1827). However, Raye's specimen of *G. ecaudatus* is no longer present in Leiden and could have been exchanged, sold or destroyed during the intervening 190 years; its current whereabouts are unknown.

Lesson's 'tailed' Ceylon Junglefowl

In 1816 the French botanist and ornithologist Jean-Baptiste Leschenault de La Tour visited India to collect plants and to establish a botanical garden in Pondicherry. With permission from the British authorities he also visited Madras, Bengal and Ceylon (Ponthieu 1827). Returning in July 1822, Leschenault donated the birds he had collected to the Muséum national d'Histoire naturelle in Paris, including a specimen of a junglefowl from Ceylon clearly exhibiting a tail. The collection was revised by the French surgeon and naturalist René Primevère Lesson, who recognised the junglefowl as a new species *Gallus lafayetii* (Lesson 1831). The specific name commemorated the French aristocrat Gilbert du Motier, Marquis de La Fayette, who was a key figure in the French Revolution of 1789 and the July Revolution of 1830. Lesson (1831, 1836, 1838) consistently spelled the specific name *lafayetii*, while referring to the bird in French as 'Coq Lafayette'. Hence the spelling *lafayetii*



Figure 6. Oeillet Des Murs, *Iconographie ornithologique* (1845–49), pl. 18: 'Gallus lafayetii (Lesson) Coq de Lafayette' (Harry Taylor, © Natural History Museum, London)

is considered a lapsus (ICZN 1999, Art. 32.5.1) and the corrected spelling *G. lafayettii* is in common use (McGowan *et al.* 2017).

The brief description in Lesson (1831) provided only the provenance ('Coq sauvage de Ceylan') and plumage colour (in the male). Subsequently, Lesson may have discussed the classification of junglefowl with Temminck and his assistant Hermann Schlegel, who visited the Paris museum in April–June 1835 (Schlegel 1837, 1839, Zijderveld 2014). This is reflected in his subsequent publications (Lesson 1836, 1838), wherein he referred to Temminck (1813) and used the latter's more elaborate description. He copied the vernacular names for the species used by Temminck (Le Coq sans croupion ou wallikikili) which referred to the tailless form, and listed his *lafayettii* as a synonym of Temminck's *ecaudatus*.

The holotype of *G. lafayettii* Lesson, 1831, collected by Leschenault is still in Paris (Fig. 5). It was figured in the third part (dated 1846) of the *Iconographie ornithologique* (Pl. 18) by Oeillet Des Murs (1845–49), after a drawing by Alphonse Prévost (Fig. 6).

Darwin's monophyletic theory on origin of domestic fowls

Research continues as to whether the origin of the domestic chicken is monophyletic (from one species) or polyphyletic (from multiple species, e.g. Erikson *et al.* 2008). It could be derived exclusively from *G. gallus* (formerly *G. bankiva*), or also contain elements of other species, extinct or otherwise. Temminck (1815) opined that domestic poultry breeds descended from six ancestral wild species, five living and one possibly extinct, and Lesson

(1836) shared this view. One of the extant ancestral species, in Temminck's opinion, was the rumpless *G. ecaudatus* from Ceylon, which he considered the wild ancestor of the domestic rumpless poultry breed 'Persian fowl'. The French zoologist Georges Cuvier (1832) also agreed with this, despite 'ecaudatus' having the characteristic rumplessness atypical for genus *Gallus*.

Charles Darwin, however, had come to the conclusion that the domestic chicken was monophyletic and had descended solely from Red Junglefowl: 'Most fanciers believe that they are descended from several primitive stocks. ... Most naturalists, with the exception of a few, such as Temminck, believe that all the breeds have proceeded from a single species' (Darwin 1868: 230). Darwin is known to have consulted Temminck (1813) from an entry in one of his notebooks (Darwin 1838–51). He also quoted it (Darwin 1868) and in 1858 wrote to his friend William B. Tegetmeier that 'I know Temminck's work' (Darwin 1858). To protect his theory as to the monophyletic origin of domestic chickens, Darwin appeared keen to disprove the (former) existence of Temminck's ecaudatus.

However, the two remaining specimens in the Leiden museum are silent witnesses to the former occurrence of *ecaudatus*; wild, rumpless Ceylon Junglefowl on the island at the end of the 18th century. These specimens do not display any characters to suggest hybridisation with domestic *G. gallus*. The rumpless condition probably arose as a spontaneous mutation in the wild population of Ceylon Junglefowl and then disappeared again. When the mutation first occurred, or how long such birds persisted is unknown. A similar mutation occurs in domestic chickens, wherein the lack of tail is a disadvantage in competing with rivals for mating, and mating success (i.e. fertilisation) is much lower in rumpless individuals, mainly because the tail serves as a counterbalance during copulation (Crawford 1990). This presumably also applied to the rumpless Ceylon Junglefowl and it can be assumed that this explains why the variety did not become established in the wild.

Darwin's rejection of rumpless Ceylon Junglefowl as ancestor

The proposition that Red Junglefowl is the sole ancestor of the present domestic breeds of chicken was an important part of Darwin's reasoning for his theory of evolution. In *The variation of animals and plants under domestication* (1868), Darwin disclosed his monophyletic theory on the origin of domestic chickens. He provided rationale to prove the significance of Red Junglefowl, and argued against the involvement of the other three wild junglefowl species. The possible role of extinct species, as Temminck had suggested, was not favoured: 'The extinction, however, of several species of fowls, is an improbable hypothesis, seeing that the four known species have not become extinct in the most anciently and thickly peopled region of the East' (Darwin 1868: 237).

Darwin, unaware that *ecaudatus* and *lafayettii* were the same species, discussed the possibility that Ceylon Junglefowl is an ancestor of the domestic chicken, but found that the evidence argued against this: 'Ceylon possesses a fowl peculiar to the island, viz. *G. Stanleyi*; this species approaches so closely (except in the colouring of the comb) to the domestic fowl, that Messrs. E. Layard and Kellaert [*sic*] would have considered it, as they inform me, as one of the parent-stocks, had it not been for its singularly different voice. This bird crosses readily with tame hens, and even visits solitary farms and ravishes them. Two hybrids, a male and female, thus produced, were found by Mr. Mitford to be quite sterile: both inherited the peculiar voice of *G. Stanleyii*. This species then, may in all probability be rejected as one of the primitive stocks of the domestic fowl' (Darwin 1868: 234). Darwin here used the name *G. stanleyi* for Ceylon Junglefowl following then common usage in Britain (see Appendix). He relied on two independent experts on Ceylonese birds: Edgar Leopold

Layard, a British colonial civil servant and ornithologist, and Edward Frederik Kelaart, a Ceylon-born physician and naturalist.

When Darwin discussed the four wild species of Asian junglefowl, he made no reference to the wild rumpless specimens Temminck named G. ecaudatus. Darwin (1868) was aware of Temminck's claim that wild rumpless specimens had been found in Ceylon, but his informants rather forcibly denied this. Layard (1851: 619) was undeniably clear that 'The rumpless fowl is not a wild inhabitant of this island, in spite of Temminck. It is a rather tame introduction from Cochin, I am told. I am sure it is not found wild in these parts. It may appear like boasting, but I can confidently say I am more acquainted with the Ceylon Fauna than any man living, and that if the bird had existed wild, I must have seen it.' Kelaart (1852), his second informant, failed to list rumpless junglefowl in his catalogue of birds of Ceylon. When Darwin met Kelaart by chance at the British Museum in 1856, he was offered help in regard to Ceylonese poultry (Darwin 1856) and must have been assured again that no wild rumpless junglefowl inhabited Ceylon (Darwin 1868). Edward Blyth, curator of the Museum of the Asiatic Society of Bengal in Calcutta, also proffered information about Asian wild junglefowl. In a letter to Darwin, Blyth stated 'Of the three wild typical Galli, one (G. Stanleyi, v. Lafayettei) is quite peculiar to Ceylon, and is abundantly distinct, specifically, from all domestic fowls' (Blyth 1855). None of them, apparently, realised that Temminck's birds constituted a rumpless variety of G. lafayettii.

Darwin, therefore, could quote adequate authority to state that a wild rumpless junglefowl did not exist in Ceylon in that era, and therefore could not have been ancestral to the domestic chicken. He did not believe that the rumpless fowls were a distinct species, as argued by the French surgeon and physiologist Paul Pierre Broca (1859). In fact he was quite adamant in his statement: 'An eminent physiologist [Dr. Broca] has recently spoken of this breed as a distinct species; had he examined the deformed state of os coccyx he would never have come to this conclusion; he was probably misled by the statement, which may be found in some works, that tailless fowls are wild in Ceylon; but this statement, as I have been assured by Mr. Layard and Dr. Kellaert [sic], who have so closely studied the birds of Ceylon, is utterly false' (Darwin 1868: 259).

Discussion

Darwin was misinformed and clearly unaware that Temminck's description of *G. ecaudatus* was based on actual specimens, and that these still existed in Leiden. He also appears not to have known about Lesson's publications, wherein *ecaudatus* and *lafayettii* are stated to be the same species. On the other hand, he was convinced by the statements of Blyth, Layard and Kelaart that there was no wild rumpless junglefowl on Ceylon, and that any tailless specimens had been in fact been imported domesticated ones. Of course, we now know that Temminck's specimens represent only a heritable aberration of Ceylon Junglefowl, but the fact remains that despite the belief of Darwin, Blyth, Layard and Kelaart, rumpless wild Ceylon Junglefowls did once occur on Ceylon.

Temminck and Lesson died long before Darwin published. Their role to correct Darwin's mistake could possibly have been assumed by Herman Schlegel, who succeeded Temminck as director of the Leiden museum in 1858. Schlegel (1860) acknowledged that Temminck's *G. ecaudatus* was not a species, but he believed that domestic, rumpless chickens derived from the rumpless variant of *G. lafayettii*. Schlegel considered species as fixed, and consequently he was strongly opposed to Darwin's theory of evolution (Zijderveld 2014). Darwin knew of Schlegel's opinions on species and evolution from remarks by his close friend, the British botanist and explorer Joseph Dalton Hooker (1845): 'I talked much with Schlegel, he is strongly in favour of a multiple creation & against migration.' Hence the two

men were discouraged to contact each other. If they had, Schlegel could have informed him that *ecaudatus* and *lafayettii* are the same species and that Temminck's specimens still existed, but so far no correspondence between Darwin and Schlegel has been found. However, if Darwin had known of the rumpless Ceylon Junglefowl it might have confused him. He may have changed his view on the origin of domesticated fowl and decided that the chicken was polyphyletic after all, just as he thought (incorrectly) was true of the domesticated dog (Darwin 1868). But these remain matters for speculation alone.

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- Addresses: Hein van Grouw, Bird Group, Dept. of Life Sciences, Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK, e-mail: h.van-grouw@nhm.ac.uk. Wim Dekkers, Jan van Eyckstraat 20, 5831 BN Boxmeer, the Netherlands, e-mail: wim.dekkers@kpnmail.nl. Kees Rookmaaker, Mijas Costa, Spain, e-mail: rhinorrc@gmail.com

Appendix: the confused nomenclature of the Ceylon Junglefowl

Ceylon Junglefowl Gallus lafayettii was scientifically named four times in a period of 40 years: ecaudatus Temminck, 1807; lafayetii (= lafayettii) Lesson, 1831; stanleyi Gray, 1832; and lineatus Blyth, 1847.

- 1. Temminck (1807) described the 'Coq sans croupion' from Ceylon as *Gallus ecaudatus*. This name is preoccupied by *Phasianus ecaudatus* (Linnaeus, 1758), transferred to the genus *Gallus*, for a domestic variety of Red Junglefowl. However, this name might be invalid as domestic forms should not be named separately (ICZN 1999). If Temminck's *ecaudatus* is not preoccupied for that reason, it remains unavailable as it has not been used as a valid name for Ceylon Junglefowl post-1899 (ICZN 1999, Art. 23.9.1.1).
- 2. Lesson (1831) described the 'Coq Lafayette' from Ceylon as *Gallus lafayetii*. Lesson's name *lafayetii* should be corrected to *lafayettii*. It is commonly used and therefore takes priority (ICZN 1999, Art. 23.9.1.2).
- 3. Gray (1832) named the 'Stanley Hen' (without locality) as *Gallus stanleyi*. J. E. Gray, assistant keeper of zoology at the British Museum, together with T. Hardwicke, an army officer and naturalist, produced a major folio work, the *Illustrations of Indian zoology* (1830–35) containing 200 coloured plates, published without accompanying text. Pl. 43, painted by Benjamin Waterhouse Hawkins and published in April 1832 (Kinnear 1925), shows three hens of two species (Green Junglefowl *G. varius* and Red Junglefowl *G. gallus bankiva*) as



Figure 7. J. E. Gray, *Illustrations of Indian Zoology* (1832), pl. 43, which shows the females of three species of junglefowl, from left to right: Green Junglefowl *Gallus varius*, Ceylon Junglefowl *G. lafayettii* and Red Junglefowl *G. gallus bankiva*. Gray incorrectly thought that the Ceylon Junglefowl was a new species and named it Stanley Hen, or (in the index) Lord Stanley's Hen (Harry Taylor, © Natural History Museum, London)

well as a supposedly new species (Fig. 7) that Gray called 'Stanley Hen. Gallus stanleyi' in the caption to the plate, emended to 'Lord Stanley's Hen. Gallus Stanleyi, Gray' in the index of May 1832. It was named for Lord Edward Smith Stanley, 13th Earl of Derby, a passionate collector of animals, both living and dead (Fisher 2002) and President of the Zoological Society of London (ZSL) at the time. It is unknown where Waterhouse Hawkins saw the specimen shown on the plate. The other two species on Pl. 43 were kept at the time in the Gardens of the Zoological Society in Regent's Park (ZSL 1831, 1832), and perhaps the third species was held there as well. Alternatively, this hen might have been kept by Lord Stanley. However, there were no junglefowl in Lord Stanley's aviary at Knowsley Hall near Liverpool at that time (Woolfall 1990), nor are there any relevant specimens in Stanley's skin collection, now at the World Museums Liverpool (T. Parker pers. comm.). Consequently, the whereabouts and provenance of the type specimen are unknown. Sykes (1832), followed by Gray (1844), suggested that Gallus stanleyi was in fact a female Grey Junglefowl G. sonnerati.

4. Blyth (1847) described a new junglefowl from Ceylon as *Gallus lineatus*. The Museum of the Asiatic Society of Bengal in Calcutta in 1846 received a shipment of birds 'from Dr. Templeton, including some of considerable interest, – as the *Gallus stanleyi* of Gray, hitherto I believe only known from Hardwicke's published figure of the hen' (Blyth 1846: 314). The next year, Robert Templeton sent from Ceylon 'a second and new species of Jungle-fowl from that island (*Gallus lineatus*, nobis) additional to *G. stanleyi* of Hardwicke's illustrations – which latter has, I believe, been first verified from an actual specimen, previously transmitted to the Society by the same gentleman' (Blyth 1847: 211). Blyth provided no characteristics and his name must be regarded as a *nomen nudum* (ICZN 1999, Art. 12). When, in 1848, Blyth received a male junglefowl from Ceylon from Edgar Leopold Layard, he recognised that all three specimens were of the same species, which he listed as *Gallus stanleyi*, of which both *lafayettii* (erroneously spelled *Lafayettei*) and his *lineatus* were synonyms (Blyth 1849). Perhaps due to Blyth's authority, many British ornithologists continued to use the specific name *stanleyi* instead of *lafayettii* for Ceylon Junglefowl (e.g. Kelaart 1852, Layard 1854, Jerdon 1864, Blyth 1867, Legge 1875).