Full Issue

Source: Bulletin of the British Ornithologists' Club, 146(2) : 115-224

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v146i2.2026.a9

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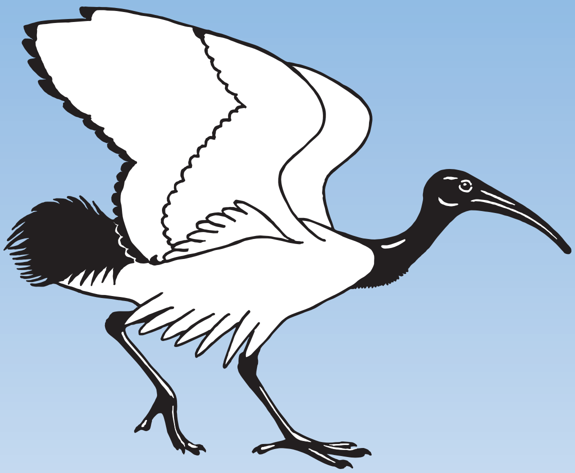
Bulletin of the British Ornithologists' Club



Volume 146 No. 2 (Online)
June 2026

ISSN 2513-9894 (Online)

Bulletin of the British Ornithologists' Club
ISSN 2513-9894 (Online)
Edited by Guy M. Kirwan
Associate Editors: Bruce M. Beehler; Lincoln Fishpool; Juan Freile;
Matthew R. Halley; Flavia Montaño-Centellas; Robert Prŷs-Jones; Christopher J. Sharpe
Volume 146 Number 2, pages 115–220

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E-mail: info@boc-online.org
Tel. +44 (0)208 8764728 / 07919174898

Registered Charity No. 1169733

www.boc-online.org

Published by the British Ornithologists' Club
Typeset by Eng-Li Green, New Mexico, USA

Bulletin of the
BRITISH ORNITHOLOGISTS' CLUB

Vol. 146 No. 2 Published 3 June 2026

CLUB ANNOUNCEMENTS

The 1,018th meeting of the Club was held in the upstairs room at the Barley Mow, 104 Horseferry Road, London SW1P 2EE, on 23 March 2026. Seventeen people were present: Mr M. Andrews, Mr P. Belman, Mr R. Bray, Mr G. Candelin (*Speaker*), Dr R. A. Cheke, Mr S. Chapman, Mr R. Dickey, Mr A. Jackson, Dr S. Portugal, Dr R. Prŷs-Jones, Ms B. Pugh, Dr A. Richford, Ms K. Rooke, Mr D. G. D. Russell, Mr C. W. R. Storey (*Chairman*), Mr S. Thompson and Ms J. White.

30 Years in the Tower by George Candelin. Seventy years after David Lack published his ground-breaking *Swifts in a tower*, the Club welcomed George Candelin, the current 'Keeper of the Swifts' at the Oxford University Museum of Natural History, who gave an excellent overview of this pioneering long-term study. Lack joined the BOC in 1942 and in May 1947 (the same year that he founded the Wytham Tit Project) he and his wife, Elizabeth, installed nest boxes in the tower of the University Museum to study the colony of swifts. Now one of the longest continuous studies of a single bird species in the world, this study of *Apus apus* continues to contribute substantially to our knowledge of this fascinating species.

George, ex-Chairman, now President, of the Oxford Ornithological Society (www.oos.org.uk), has been involved in this research for 30 years. His talk detailed how the study has evolved and expanded over time. The season starts in April, before the Swifts return around the first week in May. Regular visits to the tower record the weather, number of birds per box, as well as nest building, brooding or aggression between adults. For nearly 80 years, these data, as well as the number of eggs laid, young hatched and juveniles fledged have been carefully recorded for each nest box. Gradually building a huge, unparalleled, dataset, which is increasingly important as the climate changes and insect abundance declines. Swift numbers in the UK were not systematically monitored prior to the BTO Breeding Bird Survey (BBS) was launched in 1994, and this long-term project continues to be critical, especially as the BBS indicates a 68% decrease in breeding numbers in the UK from 1995 to 2023.

George also drew attention to the other biologically fascinating inhabitants of the nest boxes, the Flat Fly *Crataerina pallida*, a species of biting fly in the family of louse flies Hippoboscidae, whose lifecycle is inextricably linked with the Common Swift. George finished his talk by giving a short overview of the variety of swift nest boxes commercially available, suggesting that lightweight but durable boxes featuring a bottom entrance are preferable, and have the highest occupancy. He also stressed optimal positioning out of direct sunlight, under deep eaves, on walls that do not receive direct sun in undisturbed areas away from potential attack by rodents, ideally 5 m above ground level with uncluttered adjacent airspace. The talk provided a fascinating and timely overview of an inspirational ecological study that continues Lack's work to research these cherished harbingers of summer.

Douglas G. D. Russell

NEW ASSOCIATE EDITOR

We are pleased to welcome a new Associate Editor with immediate effect. Matthew R. Halley is an ornithologist and historian from Pennsylvania, USA. He serves as Research Director and Curator of Birds at the Delaware Museum of Nature & Science (Wilmington) and is a Research Associate at the Academy of Natural Sciences of Drexel University (Philadelphia). His research is primarily focused on the evolution, systematics and nomenclature of American and Asian birds, often informed by intensive research in manuscript archives. Halley is the former editor of *Cassinia*, historic journal of the Delaware Valley Ornithological Club, and sits on the Board of Editors of *Neotropical Naturalist* (Eagle Hill). He has been a prodigious contributor to *Bull. Brit. Orn. Cl.* since 2016.

ISSN-2513-9894
(Online)

CORRIGENDUM

In *Bull. Brit. Orn. Cl.* 146(1): 110, in the legend to Fig. 5, both of the specimen registration numbers are missing a digit: they should read 'AMNH 260191 left, AMNH 260190 right' (not 26191 and 26190 respectively). We thank Tom Trombone for pointing out this error.—The Hon. Editor

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The BOC has since 2017 become an online organisation without a paying membership, but instead one that aspires to a supportive network of Friends who share its vision of ornithology—see: http://boc-online.org/. Anyone wishing to become a Friend of the BOC and support its development should pay UK£25.00 by standing order or online payment to the BOC bank account:

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Friends receive regular updates about Club events and are also eligible for discounts on the Club's Occasional Publications. It would assist our Treasurer, Richard Malin (e-mail: rmalin21@gmail.com), if you would kindly inform him if you intend becoming a Friend of the BOC.

The *Bulletin* and other BOC publications

Since volume 137 (2017), the *Bulletin* of the BOC has been an online journal, published quarterly, that is available to all readers without charge. Furthermore, it does not levy any publication charges (including for colour plates) on authors of papers and has a median publication time from receipt to publication of five to six months. Prospective authors are invited to contact the *Bulletin* editor, Guy Kirwan (GMKirwan@aol.com), to discuss future submissions or look at http://boc-online.org/bulletin/bulletin-contributions. Back numbers up to volume 136 (2016) are available via the Biodiversity Heritage Library website: www.biodiversitylibrary.org/bibliography/46639#/summary; vols. 132–136 are also available on the BOC website: http://boc-online.org/

BOC Occasional Publications are available from the BOC Office or online at info@boc-online.org. Future BOC-published checklists will be available from NHBS and as advised on the BOC website. As its online repository, the BOC uses the British Library Online Archive (in accordance with IZCN 1999, Art. 8.5.3.1).

ISSN-2513-9894
(Online)

Neotype designation for *Pterocles orientalis* (Linnaeus, 1758)

by Jiří Mlíkovský & Alexander L. Bond

Received 12 August 2024; revised 5 January 2026; published 3 June 2026

http://zoobank.org/urn:lsid:zoobank.org:pub:FAD7BD66-FD1E-40CB-A8C9-12E0B27A9DD5

Summary.—For more than a century the name *Tetrao orientalis* Linnaeus, 1758, has been applied consistently to the Black-bellied Sandgrouse *Pterocles orientalis*, following the detailed analysis of Hartert (1917), and is in no dispute and is accepted here. However, under the current *International code of zoological nomenclature*, the taxonomic meaning of a species-group name is defined solely by its name-bearing type, not by prevailing usage or historical interpretation. Linnaeus explicitly based *Tetrao orientalis* on a composite set of published sources referring to different taxa, and no lectotype or neotype has ever been designated. As none of the original specimens associated with these sources is known to survive, the name currently lacks a Code-compliant type fixation. We therefore do not revise or question the established application of *Pterocles orientalis* but formally anchor that universally accepted usage by designating a neotype in accordance with Art. 75 of the *Code*, thereby ensuring long-term nomenclatural stability.

Black-bellied Sandgrouse *Pterocles orientalis* (Linnaeus, 1758) is a well-known species of the south-western Palearctic (Vaurie 1965, de Juana 1996, Madge *et al*. 2002, del Hoyo & Collar 2014). It was described by Linnaeus (1758: 161) as *Tetrao orientalis* based on published sources alone; Linnaeus had not seen any specimens of the species himself.

In particular, Linnaeus (1758) based his *orientalis* on the 'Tetrao orientalis' of Hasselquist (1757: 278–279), 'Perdix damascena' of Willughby (1676: 128) and 'Francolin' of Tournefort (1718a: "158" = 159). Of these sources, Hasselquist and Tournefort were personally acquainted with the bird they described, whereas Willughby (1676) took all his information from Aldrovandi (1600: 143). For Tournefort, Linnaeus (1758) referred to the Amsterdam edition of 1718 (Tournefort 1718a), although the work was originally published in Paris in 1717 (Tournefort 1717a: 412), then in Lyon in the same year (Tournefort 1717b: 111), and an English translation appeared in London in 1718 (Tournefort 1718b: 311).

Aldrovandi (1600: 143) had a single specimen to hand. He reported that the bird generally resembled Grey Partridge *Perdix perdix* (Linnaeus, 1758), but noted that it was markedly smaller and had yellow legs. Also, he remarked that the bird was brought to Italy from Damascus, then a city in the Ottoman Empire, now the capital of Syria. Aldrovandi's (1600) description of the bird and his figure (Aldrovandi 1600: 142; Fig. 1) show that 'Perdix damascena' is an *Ammoperdix* partridge, not a *Perdix* partridge or even a sandgrouse. The colour pattern of the head of the figured bird indicates that the specimen was a Sand Partridge *Ammoperdix heyi* (Temminck *in* Temminck & Laugier, 1825), which still occurs in Syria (Porter *et al*. 2024).

Tournefort (1718b: 311) reported that his 'Francolin' inhabits the island of Samos, Greece, adding the following information: 'Heath-cocks [= francolins] are not common there, but keep to the Sea-side between the little Boghas [= the strait between Samos and the Dilek Peninsula, Turkey] and Cora [= Chora], near a marshy Pool [uncertain, possibly Alyki wetland], which we have not omitted in our Chart; they call 'em Meadow-Partridge."

ISSN-2513-9894 (Online)

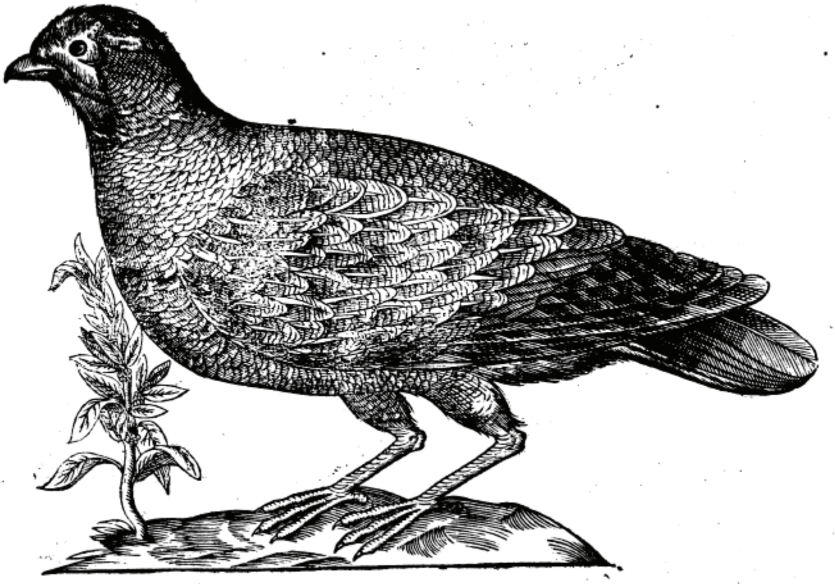

Figure 1. 'Perdix damascena'; after Aldrovandi (1600: 142), now considered a Sand Partridge *Ammoperdix heyi*.

Figure 2. 'Francolin'; after Tournefort (1717b: 111), an example of Black Francolin *Francolinus francolinus*.

This would not be sufficient to establish the taxonomic identity of this bird, but Tournefort provided an excellent picture of the bird (unnumbered and inserted on an unpaginated page in all cited editions), which clearly shows an adult male Black Francolin *Francolinus francolinus* (Linnaeus, 1766) (Fig. 2).

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Frederik Hasselquist (1722–52) was a Swedish naturalist and a student of Linnaeus (Bodenheimer 1951, Ståhlberg & Svanberg 2020, 2021). Following his death in Buca, Turkey, aged only 30, Linnaeus edited and oversaw the publication of his summarised travels and observations in the Middle East. In this publication, Hasselquist (1757: 278–279) provided a detailed description, but no figure, of what he referred to as male and female (the number of specimens examined by him is unknown) of 'Tetrao orientalis'. Despite that, the description allowed for a different taxonomic interpretation of the bird. Buturlin (1910) suggested that it was the Black Francolin, whereas Hartert (1917) provided evidence sufficient to identify it as Black-bellied Sandgrouse. Hasselquist (1757: 279) noted that the species occurs in 'Natolia' [= Anatolia, Asian Turkey].

Thus, Linnaeus (1758: 161) based his *Tetrao orientalis* on a mix of species, including Sand Partridge (Aldrovandi specimen from Syria), Black Francolin (Tournefort specimens from Greece) and Black-bellied Sandgrouse (Hasselquist specimens from Turkey).

Linnaeus's (1758) use of literature sources was more complex than early authors recognised. Whereas Svenson (1945a,b) and Mayr (1952) argued that Linnaeus based his descriptions on all the works he cited, subsequent research has revealed a more nuanced picture. Baum (1968) and Wheeler (1991) showed that Linnaeus often referred to his own earlier publications containing better data. Mlíkovský (2023) demonstrated that the situation was even more intricate and that Linnaeus sometimes failed to cite sources he actually used, whilst other cited works were at odds with his descriptions, suggesting he may have listed them as references without consulting them. Each Linnaean taxon therefore requires independent assessment to determine the actual basis of its description (Mlíkovský 2023).

Hartert's clarification

Buturlin (1910) misunderstood the abridged translations of Hasselquist and suggested that Linnaeus' (1758) *Tetrao orientalis* applies to the francolin. Hartert (1917) dealt with his arguments in detail, conclusively demonstrating that Linnaeus' description of *Tetrao orientalis* is based on Hasselquist (1757) alone and therefore applies unambiguously to Black-bellied Sandgrouse. At the same time, Hartert (1917) dismissed Linnaeus' (1758) references to Willughby and Tournefort in the erroneous belief that these were carelessly added and not part of the actual basis of the name. In any case, Hartert's (1917) action (see also Hartert 1920: 1502) resulted in a general acceptance of the species name *orientalis*, as published in the binomen *Tetrao orientalis*, for Black-bellied Sandgrouse.

However, under the *International code of zoological nomenclature* (ICZN 1999), long-standing and undisputed taxonomic usage does not by itself define the nomenclatural meaning of a species-group name. Since *Tetrao orientalis* was originally based on a composite set of sources and no name-bearing type has ever been designated, the name remains formally undefined under the Code, despite its stable application. Therefore the taxonomic meaning of *Tetrao orientalis* Linnaeus must be fixed via lectotypification (ICZN 1999, Art. 74) or neotypification (ICZN 1999, Art. 75).

Designating the specimen figured by Aldrovandi (1600) or that figured by Tournefort (1717a,b, 1718a,b) as the lectotype of *Tetrao orientalis* Linnaeus would destabilise zoological nomenclature, because the species name *orientalis*, now in general use for a sandgrouse species would be shifted to Sand Partridge or to Black Francolin, for which scientific names were introduced in 1766 and 1825, respectively, so that *Tetrao orientalis* (Linnaeus, 1758) would take priority.

Hasselquist (1757) described Black-bellied Sandgrouse to which the name *orientalis* is now generally applied. However, he was not specific as to the specimens he had to hand when he described the species, which makes it impossible to designate any one as

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the lectotype. None of the 16th–18th century specimens described by Aldrovandi (1600), Tournefort (1717a,b, 1718a,b) or Hasselquist (1757) is known to survive in any museum collection (*cf*. Steinheimer 2005). Thus, the only way how to fix the taxonomic meaning of *orientalis* in its current meaning is to designate a neotype, which we do here.

The original type locality of *Pterocles orientalis*

The type locality of a species-group taxon encompasses all localities from which the type material originated (ICZN 1999, Art. 76.1). In our case it is Damascus, Syria (Aldrovandi's specimen), the island of Samos, Greece (Tournefort's specimens), and Anatolia, Turkey (Hasselquist's specimens). Note that Anatolia has been a name for Asia Minor, i.e. for the peninsula that forms a large part of what is now Asian Turkey (Hopkins 1998, Kapucu & Palabıyık 2008). Hartert (1917) restricted the type locality to 'near Smyrna' [= Izmir] based on Hasselquist's travels (Ståhlberg & Svanberg 2020), which he later generalised without explanation as 'Anatolia' (Hartert 1920: 1502). Regardless, Hartert's (1917) restriction of the type locality would not be considered valid under the fourth edition of the *Code* (Art. 76) without the designation of a type specimen, as the type locality is intrinsically linked to a specimen (ICZN 1999, Art. 76).

Neotype designation

Neotype (designated herein): from the collection of the Natural History Museum, Tring, UK (NHMUK) 1881.5.1.4132 (Fig. 3), adult male collected by or for Henry James

Figure 3. Neotype of *Tetrao orientalis* Linnaeus, 1758: NHMUK 1881.5.1.4132, adult male from Trabzon, Turkey; see text for details. Scale bar = 50 mm (Jonathan Jackson, © Trustees of the Natural History Museum, London)

ISSN-2513-9894 (Online)

Figure 4. Labels attached to the neotype of *Tetrao orientalis* Linnaeus, 1758: NHMUK 1881.5.1.4132, adult male from Trabzon, Turkey; see text for details (Jonathan Jackson, © Trustees of the Natural History Museum, London). Note that the name *Pterocles arenarius* (Pallas, 1775) was widely applied to the species in question (Ogilvie-Grant 1893: 18–20) until Hartert (1917, 1920) showed that *Pterocles orientalis* (Linnaeus, 1758) has priority. It is now considered a subspecies of *Pterocles orientalis*, although there is little morphological distinction (Vaurie 1961, de Juana *et al.* 2020).

Ross (1820–1901) at 'Trebizond' [= Trabzon, Trabzon province, Turkey; 41.00°N, 39.72°E][1], presented by him to John Gould (1804–81) on 3 August 1839, and acquired by NHMUK with the Gould collection in 1881 (Sharpe 1906). Dickson & Ross (1840: 121) noted that this species (called by them '*Pterocles arenarius*') was common around Erzurum in north-eastern Turkey. No mention of the collection can be found in his correspondence (Ross 1902).

The designation of a neotype for *Tetrao orientalis* Linnaeus, 1758, satisfies the provisions of Art. 75.3 of the *International code of zoological nomenclature* (ICZN 1999) as follows. (Art. 75.3.1) The neotype is designated expressly to clarify the nomenclatural definition of the nominal species-group taxon *Tetrao orientalis*, by fixing its taxonomic meaning to the universally accepted application of the name to *Pterocles orientalis*. Although usage of the name has been stable for more than a century, the original description by Linnaeus (1758) was explicitly based on a composite set of published sources referring to different taxa, and no lectotype or neotype has previously been designated; consequently, the name lacks a *Code*-compliant name-bearing type. (Art. 75.3.2) Diagnostic characters distinguishing *Pterocles orientalis* from other species of *Pterocles* are well described in the cited modern literature. (Art. 75.3.3) The neotype is fully documented by collection data, catalogue number, sex, plumage condition, and locality, and is thus unambiguously identifiable. (Art. 75.3.4) No original name-bearing type specimen is known to exist: Linnaeus (1758) based the name exclusively on published accounts, and none of the specimens described or figured by Aldrovandi (1600), Tournefort (1717a,b, 1718a,b), or Hasselquist (1757) is known to survive; extensive review of these sources has revealed no extant syntypes. (Art. 75.3.5) The designated neotype is consistent with the original concept of the taxon as demonstrated by Hartert (1917, 1920) and subsequent authors, who showed that the diagnostic basis of Linnaeus's name derives from Hasselquist's material and applies to Black-bellied

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[1] The species has never been known to breed in the Black Sea coastal region of Turkey and there is no suitable habitat for it do so in the immediate environs of Trabzon, at least in the present day (Kirwan *et al.* 2008; G. M. Kirwan *in litt.* 2026), although an 1833 watercolour by Godfrey Thomas Vigne (1801–63) depicts the township of Trabzon as surrounded by steppe-like habitat in the 1830s ('Trebizond', Victoria & Albert Museum Prints & Drawings Collection, SD.1086; https://collections.vam.ac.uk/item/O152694/trebizond-watercolour-vigne-godfrey-thomas/), which could have been inhabited or visited by sandgrouse. Moreover, in the past, localities were not understood as exactly as today, and the name of a centre was often applied to an entire region. Nevertheless, the specimen collected by Ross could have been a wandering individual from elsewhere in the country (at Erzurum, Dickson & Ross considered the species to be a summer visitor, arriving in early April and departing in late September), or perhaps even outside it. Morphologically, *P. o. orientalis* and *P. o. arenarius* are very similar, except that *arenarius* is 'somewhat paler' (Vaurie 1961); indeed the species is perhaps better considered monotypic (de Juana *et al.* 2020).

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Sandgrouse; the neotype agrees in all relevant characters with that interpretation. (Art. 75.3.6) The neotype originates from Turkey, within the geographic region (Anatolia) to which Hartert (1917, 1920) intended to restrict the type locality of *Tetrao orientalis*, and the selected specimen represents the nominate population to which all Turkish Black-bellied Sandgrouse are currently referred. Its selection therefore best serves nomenclatural stability. (Art. 75.3.7) The neotype is deposited in the Natural History Museum, Tring (NHMUK), a recognised scientific institution with appropriate facilities for the preservation and accessibility of name-bearing types. No specimens are available from İzmir; a mounted specimen at the University of British Columbia Beaty Biodiversity Museum (Vancouver, Canada; UBCBBM B016239) is indicated as being from İzmir, but it lacks original labels and provenance (I. Szabo *in litt*. 2026).

In light of this case, the complexity of situations involving Linnaeus' scientific names require some final consideration. Many of his scientific names for birds were based on a single specimen or source, and therefore there is no expectation of a mixed type series (e.g., Mlíkovský 2023). Of those that were based on a mixed type series comprising multiple recognisably distinct taxa, it is possible to identify a single specimen to which Linnaeus referred, either directly or indirectly, to designate a lectotype under Art. 74 of the Code (e.g., Mlíkovský 2023). In a minority of cases, as we have illustrated above, the mixed type series lacks any surviving specimens and thus designation of a neotype is required (e.g., Harrison 1947, 1954, Clancey 1948, 1950a,b,c, Gyldenstolpe 1957, Fjeldså 1973, Mlíkovský 2023: 1515).

Acknowledgements

We thank J. Jackson for photographing the neotype, and G. Kirwan and two reviewers for comments that improved this manuscript. For information on sandgrouse specimens in their care, we thank S. Frahnert (Berlin), I. Szabo (Vancouver) and T. Töpfer (Bonn).

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ISSN-2513-9894
(Online)

Polychromatic plumage gradients in Grey-cheeked Thrush *Catharus minimus* and Bicknell's Thrush *C. bicknelli* (Turdidae) and their taxonomic consequences

by Matthew R. Halley

Received 28 October 2025; revised 14 March 2026; published 3 June 2026

http://zoobank.org/urn:lsid:zoobank.org:pub:D93A572C-6631-48A2-8873-9ECF266C2865

Summary.—Grey-cheeked Thrush *Catharus minimus* (Lafresnaye, 1848) and Bicknell's Thrush *C. bicknelli* (Ridgway, 1882) are morphologically similar but genetically distinct sister species. Modern checklists recognise the breeding population of *C. minimus* in Newfoundland and eastern Labrador as a subspecies, despite shallow and non-diagnosable genetic divergence, emphasising its browner dorsal plumage. Here, I use specimens to demonstrate that dorsal plumage in both species exhibits a continuous polychromatic gradient with weak geographic structure, invalidating it as a diagnostic character. The gradients are not illustrated or depicted in field guides and are rarely acknowledged in the literature. I propose a taxonomic revision that treats *C. minimus* and *C. bicknelli* as monotypic (yet polychromatic) species and reassess two centuries of nomenclatural history. Because the holotype of *Turdus minimus* Lafresnaye, 1848, is unidentifiable and untraceable, I designate a neotype to stabilise the name. I also resolve ambiguity relative to the *C. bicknelli* type series by designating a lectotype. This is the fifth in a series of papers dealing primarily with long-standing taxonomic and nomenclatural problems in *Catharus*.

The dorsal plumage of Grey-cheeked Thrush *Catharus minimus* (Lafresnaye, 1848) and Bicknell's Thrush *C. bicknelli* (Ridgway, 1882) is polychromatic, showing an unusually wide breadth of intraspecific colour variation in both species. Specimens can be arranged along a continuous gradient between 'grey' (or 'olive') and 'brown' endpoints, which have been variously referred to as 'forms', 'morphs' or 'phases' (Fig. 1). The polychromatism was first noticed by W. E. Clyde Todd (1874–1969), who mistook it for subspecific variation (Todd 1958, 1963), and George J. Wallace (1929–85), who perceived geographic structure but did not consider the differences worthy of formal recognition (Wallace 1939). However, because the pattern is practically impossible to observe in the field—discernible only in curated samples of museum specimens—its existence was largely forgotten by the late 20th century.

The polychromatic gradients are not depicted in any field guide, have never been systematically illustrated, and are rarely acknowledged in literature. Although the gradient endpoints were first discerned a century ago, many living ornithologists are unaware or unconvinced of their existence. To my knowledge, only one photo of *C. minimus* 'colour morphs' is available (fig. 3 *in* Halley 2018) and none is available for *C. bicknelli*. After nine decades, Wallace's (1939) tentative conclusions about the geographic structure of the polymorphism remain unverified. He recognised four 'forms' in the complex (Fig. 1) and suggested that the 'large-sized, brown-backed' phenotype (the so-called 'brown morph' of *C. minimus*) was confined during the breeding season to Newfoundland and eastern Labrador. However, after noting that some Newfoundland and continental specimens were identical, and that the 'forms' of *C. bicknelli* were bridged by intermediates forming

ISSN-2513-9894 (Online)

Figure 1. Polychromatic dorsal plumage in Grey-cheeked Thrush *Catharus minimus* (1, 2, 5, 6) and Bicknell's Thrush *C. bicknelli* (3, 4, 7, 8) adults collected during the breeding season. (1) CM P129365, female collected by A. C. Twomey at Aklavik, Northwest Territories, 29 May 1942; (2) CM P74155, female collected by G. M. Sutton at Curling, Newfoundland, 23 June 1920; (3) NYSM 4001, male topotype collected by W. C. Dilger at Slide Mt., New York, 9 June 1954; (4) MCZ 324734, female collected by A. P. Chadbourne on Mt. Washington, New Hampshire, 11–12 July 1884; (5) CM P110528, female collected by Sutton at Churchill, Manitoba, 11 June 1931; (6) MCZ 190490, male collected by J. C. Cahoon at Cuslett, Newfoundland, 14 June 1890; (7) AMNH 758364, female collected by A. C. Bent on Seal Island, Nova Scotia, 5 July 1904; (8) MCZ 257366, female collected by Bent on Seal Island, 4 July 1904; the 'morphs' are merely endpoints of a continuous polychromatic gradient, which occurs in both species (Matthew R. Halley)

a continuous gradient (Wallace 1939: 233), he declined to assign subspecies rank to the Newfoundland population.

Two decades later, Todd (1958: 160) asserted that the Newfoundland birds were 'easily recognizable by the browner, less olivaceus color of the upperparts and wings externally,' and argued that, if they 'represent a color phase, as Dr. Wallace contends, it is certainly a localized color phase, which is the equivalent of a subspecies.' Following that logic, Phillips (1991) and a wave of recent authors (e.g., Pyle 1997: 395, SSAC 2010, Whitaker *et al*. 2015, 2020, FitzGerald *et al*. 2017, 2020, Robineau-Charette *et al*. 2023) have advocated treating the 'Newfoundland Gray-cheek' at subspecies rank, citing the 'browner (less gray)' plumage as a diagnostic character (but see Pyle 2022, 2025). This treatment has been widely adopted by world checklists (e.g., Clements *et al*. 2023, Gill *et al*. 2024), despite relatively low and non-diagnosable genetic divergence (FitzGerald 2017a, FitzGerald *et al*. 2017, 2020, Halley *et al*. 2025). No study has documented vocal divergence between these putative forms, to my knowledge. The taxonomic status of the 'Newfoundland Grey-cheek' now rests solely on the morphological evidence, which is a focus of the present study.

The last ornithologists to intensively study the specimens that formed the basis of Wallace's (1939: 387–401) and Todd's (1958, 1963) hypotheses—e.g., George M. Sutton (1898–1982), Allan R. Phillips (1914–96), Henri R. Ouellet (1938–99), Kenneth C. Parkes

ISSN-2513-9894
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(1922–2007) and Joseph T. Marshall (1918–2015)—left behind their own rich legacies of specimens, publications and scattered archival sources. I availed myself of these resources during more than a decade of research (2015–26) and re-evaluated the polychromatic gradients in *C. minimus* and *C. bicknelli* with a geographically representative sample of study skins from seven major institutions, to inform a taxonomic revision.

I took digital photos under controlled lighting conditions to document the geographic structure of the colour gradients, with historic and modern study skins, providing unprecedented insight into historical taxonomic determinations. I also compared these specimens to sympatric *Catharus* species that breed and migrate through eastern North America: (1) Veery *C. fuscescens fuscescens* (Stephens, 1817); (2) 'olive-backed' Swainson's Thrush *C.* [*ustulatus*] *swainsoni* (Cabanis *in* Tschudi, 1845); and (3) 'eastern' Hermit Thrush *C.* [*guttatus*] *faxoni* (Bangs & Penard, 1921).[1] Finally, with an expanded understanding of the polychromatic gradient, I reviewed the historical development of *Catharus* taxonomy from 1799 to the present, to identify and address lingering points of nomenclatural instability.

Specimen methods

The origins of this study date from 2015, when I was hired as crew leader of an expedition to Newfoundland and Labrador, arranged by colleagues at the New York State Museum, Albany (NYSM), and Memorial University of Newfoundland, St. John's. Our primary objective was to collect *C. minimus* blood samples and other data for FitzGerald's (2017a) dissertation and subsequent papers (e.g., FitzGerald *et al*. 2017, 2020). I was paid as a technician with no expectation of authorship.

At that time, I had practically no experience with *C. minimus* specimens (or collecting or preparing study skins) but had read about the colour patterns debated by Wallace (1939), Todd (1958) and Marshall (2000), and the disputed taxonomic status of the Newfoundland birds. On 10 June 2015, when J. J. Kirchman (NYSM) and I captured, banded, bled and released our first *C. minimus* on Burgeo Road, south-west Newfoundland, I observed a 'rufescent [brownish] tint in the tail and dorsum' and confidently wrote in my field diary: 'Most definitively C. m. minimus—welcome to Newfoundland!' However, my confidence in the constancy of the character soon eroded, as we sampled birds along Labrador's east coast (22 June–3 July) and on the Great Northern Peninsula, Newfoundland (6–7 July), where the 'rufescent tint' was subtler or practically absent. This observation was the impetus of the present study.

In September 2015, after returning to Philadelphia, I began my graduate studies at the Academy of Natural Sciences of Drexel University (ANSP) and developed an extensive systematic study of *Catharus* (e.g., Halley 2021a, Halley *et al*. 2023, 2025), of which this paper is but one chapter. Over the course of a decade, I studied material in the American Museum of Natural History, New York (AMNH), Carnegie Museum of Natural History, Pittsburgh (CM), Delaware Museum of Nature & Science, Wilmington (DMNH), Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), New York State Museum, Albany (NYSM), and National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Following a standard procedure, I took the following suite of measurements from each study skin, with digital callipers or a metric ruler (as noted) to the nearest 0.01 mm and 1 mm, respectively, unless the body part was damaged: (WG) wing length, measured with a ruler from the carpal joint of the flattened (closed) wing

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[1] In previous papers, I designated neotypes for *C. fuscescens* (Halley 2018) and *C.* [*u.*] *swainsoni* (Halley 2019). I have also advocated treating *C.* [*u.*] *swainsoni* and *C.* [*g.*] *faxoni* at species rank (e.g., Halley 2019, 2021a)—a position I maintain. Herein, to acknowledge the lack of consensus on the ranks of these taxa, I have placed the contested names in brackets.

ISSN-2513-9894 (Online)

to the tip of the longest primary; (TL) tail length, measured with a ruler from the insertion point of the two central rectrices to the tip of the longest rectrix; and (TR) tarsometatarsus length, measured with callipers from the intertarsal joint to the distal end of the final leg scale. I performed statistics and generated figures with the program R Studio (R Core Team 2020).

My primary goals were to demonstrate the existence of the polychromatic gradients, roughly assess their geographic structure, and review the taxonomic history of *Catharus* in the context of polychromatism. Historical authors based taxonomic diagnoses on visual information, by qualitatively comparing specimens to each other, to coloured plates in published works, and/or to published colour standards (e.g., Ridgway 1886). No quantitative method of colour analysis was widely available until the late 20th century, and none is used here. Instead, I aimed to replicate the observational approach of earlier workers, to make the visual evidence that formed the basis of their taxonomic decisions accessible to modern readers, and to expose flaws in their reasoning which impact taxonomy and nomenclature. To accomplish this, I assembled a sample of historic and modern study skins at DMNH, including select specimens on loan from AMNH, ANSP, CM, MCZ, NYSM and USNM, to supplement the extensive DMNH holdings, which include the bulk of the Phillips and Sutton collections. I curated the specimens to illustrate the relevant phenotypic patterns and produced a series of digital reference photos, beneath a bright array of flat-panel LED lights, with an iPhone 12 camera. These photos were not intended to demonstrate the relative frequency of the 'colour morphs' in any given population, but rather to show the breadth of variation and its known geographic limits. Furthermore, in several cases, the photos feature the same specimens that were used to make historical determinations (e.g., Wallace 1939, Todd 1963).

J. J. Kirchman (NYSM) enriched the study by loaning the largest available collection of recent (21st century) breeding *C. bicknelli* specimens. This included material he collected in south-east New York near the type locality (2010–12); that he and J. R. Ralston collected in the Adirondacks of northern New York (2009–11); and specimens collected by C. C. Rimmer in Vermont (2004–09) and New Hampshire (2010). These specimens were compared directly to historic topotypes (Slide Mt.) and examples from now-extirpated breeding populations on the north shore of the Gulf of St. Lawrence (Todd 1963), Seal Island, Nova Scotia (Langille 1884) and other sea-level island sites in the region.[2]

The photographed sample of *C. minimus* specimens was also geographically representative and historically significant, including breeding specimens from Newfoundland and Labrador collected by Todd and Sutton (Todd 1958, 1963) and Burleigh & Peters (1948), which were examined by Wallace (1939), Phillips (1991) and/or Marshall (2000); and from breeding localities in western and interior North America including Alaska, Alberta, British Columbia, Manitoba, Nunavut and Yukon.

Polychromatism in *C. bicknelli*

C. bicknelli exhibits polychromatism across the sampled breeding range (Fig. 2). The colour gradient was evident in a topotypical series ($n = 3$) collected on Slide Mt. during the 1953–54 breeding season: NYSM 4001 is darker brown and more saturated than CM P133715 and DMNH 49481 (Fig. 2: 1–3). Three recent specimens (2010–12) from nearby

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[2] Standardised proper names of mountains in the United States are consistently inconsistent with respect to the placement of the word 'mount' (Mt.) or 'mountain', before or after the name of said mountain. Here, for example, I refer to 'Slide Mt.' (New York) and 'Mt. Mansfield' (Vermont), to retain the continuity of the standardised names as they have been used in more than a century of scientific literature (e.g., Wallace 1939: 253–256, Marshall 2000: 49–51).

ISSN-2513-9894 (Online)

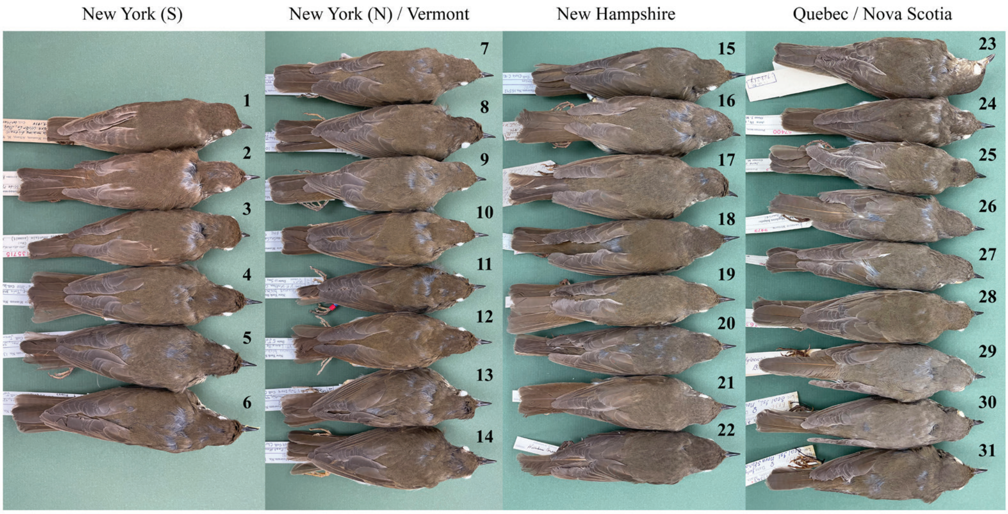

Figure 2. Intraspecific colour variation in Bicknell's Thrush *Catharus bicknelli* adults in breeding plumage, arranged geographically from south to north: <u>southern New York (Catskills)</u>: (1) NYSM 4001, collected by W. C. Dilger on Slide Mt., 9 June 1954; (2) CM P133715, collected by K. C. Parkes on Slide Mt., 6 June 1953; (3) DMNH 49481, collected by R. E. Goodwin on Slide Mt., 13 July 1953; (4) NYSM 11138, male collected by J. J. Kirchman on Twin Mt., 30 June 2010; (5) NYSM 13331, female collected by Kirchman on Blackdome Mt., 27 June 2012; (6) NYSM 11235,[1] male collected by Kirchman on Blackhead Mt., 7 June 2011; <u>northern New York (Adirondacks)</u>: (7) NYSM 10982, male collected by J. R. Ralston on Phelps Mt., 6 June 2009; (8) NYSM 10930, male collected by Kirchman on Cascade Mt., 3 June 2009; (9) NYSM 10926, male collected by Kirchman on Cascade Mt., 2 June 2009; (10) NYSM 11253, male collected by Kirchman on Cascade Mt., 14 June 2011; <u>Vermont</u>: (11) NYSM 15341, male collected by C. C. Rimmer on Mt. Stratton, 10 June 2004; (12) NYSM 15344, female collected by Rimmer on Mt. Mansfield, 5 July 2009; (13) NYSM 14313, female collected on East Mt., 1 July 2004; (14) NYSM 14312,[2] male collected on East Mt., 25 June 2004; <u>New Hampshire</u>: (15) NYSM 15342, male collected by Rimmer on Mt. Jefferson, 12 July 2010; (16) ANSP 37860, male collected by A. B. Vanderwieler on Carter's Dome, 2 July 1896; (17) ANSP 37859, male collected by Vanderwieler on Carter's Dome, 1 July 1896; (18) MCZ 324734, female collected on Mt. Washington, 1 July 1884; (19) MCZ 297176,[3] collected on Mt. Washington, 11 July 1884; (20) MCZ 207389, collected on Mt. Washington, 20 July 1882; (21) MCZ 209323, collected on Mt. Washington, 12 July 1884; (22) MCZ 209324, collected on Mt. Washington, 12 July 1884; <u>Maritime Canada (Gulf of St. Lawrence)</u>: (23) AMNH 758369, male collected by L. C. Sanford at Matapédia, New Brunswick, 15 June 1946; (24) CM P57400, male collected by O. J. Murie at Grand Portage, Québec, 14 June 1917; (25) CM P102637, male collected by G. M. Sutton at Little Mecatina River, Québec, 27 June 1928; (26) CM P102539, male collected by Sutton at Pointe-Natashquan, Québec, 2 June 1928; (27) CM P9479, male collected by W. E. C. Todd on Gross-île, Magdalen Islands, Québec, 27 June 1901; (28) CM P9480, male collected by Todd on Gross-île, 28 June 1901; (29) AMNH 758364, female collected by A. C. Bent on Seal Island, Nova Scotia, 5 July 1904; (30) MCZ 257366, female collected by Bent on Seal Island, 4 July 1904; (31) MCZ 257367, female collected by Bent on Seal Island, 4 July 1904 (Matthew R. Halley)

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[1] Tissue sampled for UCE sequencing by Halley (2021a) and Halley *et al*. (2025).

[2] Tissue sampled for UCE sequencing by Halley (2021a) and Halley *et al*. (2025).

[3] Wallace (1939: 230) wrote: '[This specimen], taken July 11, and sexed as a female, has wing lengths of 100 and 101 mm. This is so far above the maximum for Bicknell's thrush of either sex that to make use of such an extreme measurement would ruin criteria for separating [*C. minimus*] from [*C. bicknelli*]. It is a brown-phased specimen, but the possibility of its being a stray Newfoundland bird seems rather remote. In other measurable features this bird is entirely within the size limits of the smaller form and it seems best to regard it as an extreme variant in wing length.'

mountains (*c*.26–33 km from Slide Mt) trend toward the darker end of the gradient (Fig. 2: 4–6). Specimens from the Adirondack Mountains of northern New York were on the brighter (warmer) side of the spectrum (Fig. 2: 7–10). Specimens from Vermont were polychromatic: a specimen from Mt. Mansfield (NYSM 15344) was brighter than specimens from Stratton Mt. and East Mt. (Fig. 2: 11–14). Specimens from New Hampshire exhibited an impressive

ISSN-2513-9894
(Online)

polychromatic spectrum of olives and browns of varying brightness and saturation (Fig. 2: 15–22). Specimens from extirpated populations in the Gulf of St. Lawrence, and along the north shore, also exhibited polychromatism (*contra* Wallace 1939: 392, who scored them all as 'olive'). Three breeding specimens from Seal Island, collected by A. C. Bent on 3–4 July 1904, provide an informative example: MCZ 257367 is darker than the other two (Fig. 2: 29–31). Specimens from the north shore of the Gulf are likewise polychromatic: CM P57400 is darker than the other four (Fig. 2: 24–28).

Polychromatism in *C. minimus*

C. minimus also exhibits polychromatism across the sampled breeding range (Fig. 3). Some birds at the brown end of the gradient were collected in interior and western North America (e.g., Alberta, Yukon). That phenotype was not confined to Newfoundland and eastern Labrador, as suggested by Wallace (1939) and assumed by Todd (1958). Therefore, 'brown (not grey)' plumage loses its value as a diagnostic (taxonomic) character. The polychromatism is not a product of wear and fade (*contra* Marshall 2000: 5, 8)—it persists during all states of plumage wear. Specimens collected in fresh autumn plumage, after the first cycle preformative (FPF) or definitive cycle prebasic (DPB) moults, also exhibit a polychromatic gradient, which implies that the pattern has a genetic basis (Fig. 4). During autumn migration, the endpoints of the *C. minimus* colour gradient are so wide that they practically encompass the phenotype of *C.* [*u.*] *swainsoni* (Fig. 4).[3]

Remember that Wallace (1939: 228) merely '[assumed that] the large-sized, brown-backed thrushes taken in spring and autumn [were] migrants from Newfoundland, [because] this form migrates southward in late September and October along the [Atlantic] coast.' However, he was unable to test this hypothesis because he lacked freshly moulted (autumn) specimens from Newfoundland. Marshall (2000: xii–xv) claimed to have resolved this problem with specimens in the USNM collection, and 'confirmed' that the fresh plumages were relatively uniform within each geographic region (i.e., no polychromatic pattern):

> 'In museums I tried to find molting birds still on the breeding ground for a look at the fresh fall feather colors. These and a large series of fall migrant Newfoundland Gray-cheeked Thrushes and Bicknell's Thrushes (Smithsonian Institution) do not show the color phases claimed with considerable misgivings by Wallace (1939). I merely confirm what is already known from Wallace (1939) and Ouellet (1993b) that the Alaska to Québec *aliciae* is olive gray, Newfoundland *minimus* olive-brown, and New England *bicknelli* is a deeper, richer brown. In fresh plumage all three have reddish [tails], but redder in the same order that the backs are browner … The northern populations (*aliciae* and *minimus*) are not identifiable in the field and are only barely distinguishable by color in the fresh fall plumage in the museum.'

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[3] This offers a novel and elegant (biological) solution to Kaufman's (2024: 90–91) puzzle: '[How did] no one [recognise *C. minimus* and *C.* [*u.*] *swainsoni*] as part of the eastern [USA] avifauna until [the 1840s–50s?] … That these two common thrushes managed to evade detection by scientists for such a long time makes for one of the more bizarre and tangled tales in the history of ornithology.' P. Pyle (*in litt.* 2025) recalled, when he and Chandler Robbins (1918–2017) were banding in Maryland in the 1970s, they encountered *C. minimus* that resembled *C.* [*u.*] *swainsoni* and resorted to 'relying (correctly or not) on the presence or absence of [an] emargination of [the 6th primary] to separate the species.' Marshall (2000: 9) attributed this method to R. C. Laybourne (1910–2003), who proposed that the sixth primary is emarginated in *C. f. fuscescens*, Newfoundland 'graycheek' and Bicknell's Thrush; but not emarginated in the western *C. f. salicicola*, interior and western 'graycheeks' and *C. ustulatus* (*sensu lato*). However, this pattern is not consistent or diagnostic in a larger polychromatic series (pers. obs.) and the 'colour morphs' used to diagnose the groups show weak geographic structure.

ISSN-2513-9894 (Online)

Figure 3. Intraspecific colour variation in Grey-cheeked Thrush *Catharus minimus* adults in breeding plumage, arranged in two geographic groups. The 'continental' series includes specimens from Alaska (AK), Alberta (AB), British Columbia (BC), Manitoba (MB), Nunavut (NU), Yukon (YT); and the 'Newfoundland+' series includes specimens from Newfoundland and coastal eastern Labrador (NL). *Continental*: (1) MCZ 194748, male collected by W. H. Osgood at Coal Creek, YT, 6 August 1904; (2) USNM 193036, female collected by A. E. Preble at Athabasca Landing, AB, 12 September 1903; (3) CM P129365, female collected by A. C. Twomey at Aklavik, NT, 29 May 1942; (4) CM P129364, male collected by Twomey at Aklavik, 29 May 1942; (5) MCZ 229024, male collected by Preble near Telegraph Creek, BC, 25 July 1910; (6) CM P110503, male collected by G. M. Sutton at Churchill, MB, 8 June 1931; (7) AMNH 376893, male collected by J. Dwight at Nome, AK, 17 June 1909; (8) AMNH 758357, male collected by R. H. Beck on Kodiak Island, AK, 8 July 1919; (9) CM P110528, female collected by Sutton at Churchill, MB, 11 June 1931; (10) USNM 448056, female collected by F. Schweder at Nueltin Lake, NU, 22 July 1947; *Newfoundland+*: (11) USNM 382007, male collected by H. S. Peters & T. D. Burleigh at Glenwood, NL, 18 June 1942; (12) USNM 382023, female collected by Peters & Burleigh at Glenwood, 24 June 1945; (13) MCZ 190492, male collected by J. C. Cahoon at Cuslett, NL, 14 June 1890; (14) MCZ 190494, male collected by Cahoon at Cuslett, 16 June 1890; (15) CM P74155, female collected by Sutton at Curling, NL, 23 June 1920; (16) MCZ 190486, unsexed collected by Cahoon at Cuslett, NL, 12 June 1890; (17) MCZ 190495, male collected by Cahoon at Cuslett, NL, 23 June 1890; (18) MCZ 190490, male collected by Cahoon at Cuslett, NL, 14 June 1890; (19) USNM 382025, male collected by Peters & Burleigh at Fogo Island, NL, 2 July 1945; (20) CM P74188, female collected by Sutton at St. Mary's River, NL, 10 July 1920 (Matthew R. Halley)

This widely read passage appeared in Marshall's (2000: xii) preface, but he later conceded that he had examined 'only one' moulting specimen from Newfoundland (i.e., precluding detection of the gradient) and neglected to provide its catalogue number (Marshall 2000: 78). In an Appendix, he listed only the *C. bicknelli* (not *C. minimus*) specimens that he examined (Marshall 2000: 93–100), which has made it difficult to retrace his work. I am not familiar with any moulting *C. minimus* from Newfoundland in the

ISSN-2513-9894 (Online)

Figure 4. Interspecific colour gradient in sympatric *Catharus* species in eastern North America, illustrated by southbound migrants in fresh plumage, collected in Delaware (DE), Pennsylvania (PA), Virginia (VA) and West Virginia (WV): (1) DMNH 85914, female Grey-cheeked Thrush *C. minimus* salvaged in early October 2024 in Pottstown, PA; (2) DMNH 85915, male *C. minimus* salvaged on 1 October 2024 in Kennett Square, PA; (3) DMNH 85573, male *C.* [*u.*] *swainsoni* salvaged on 17 October 2018 in Middletown, DE; (4) DMNH 85678, female *C.* [*u.*] *swainsoni* salvaged on 10 October 2019 in Wilmington, DE; (5) DMNH 46104, female *C. minimus* collected by T. D. Burleigh on 4 October 1959 on Mt. Vernon, VA; (6) DMNH 49483, male *C. minimus* collected by G. M. Sutton on 17 September 1936 in Bethany, WV; (7) DMNH 85576, female Hermit Thrush *C.* [*g.*] *faxoni* salvaged on 20 October 2014 in Wilmington, DE; (8) DMNH 85677, salvaged on 7 October 2007 at Montchanin, DE; (9) DMNH 85916, male *C. fuscescens* collected by M. R. Halley on 22 September 2024 at Stoffa Cabin, Drums, PA; (10) DMNH 85574, male Veery *C. fuscescens* salvaged on 23 August 2021 in Hockessin, DE (Matthew R. Halley)

USNM collection, but there is a juvenile undergoing preformative moult at CM, which Sutton collected on 30 August 1920, within the breeding range of the 'Newfoundland Gray-cheek' in eastern Labrador (CM P74267). Its replaced formative feathers are dark olive and indistinguishable from the dark end of the polychromatic gradient (Fig. 5), *contra* Wallace (1939) and Marshall (2000). Marshall (2000: 94) presumably examined this specimen when he visited the CM collection in 1989, but he did not mention it in his book—nor did he mention that he had directly observed moulting *C. minimus* in Newfoundland and found evidence that contradicted his later claims.

Marshall (2000: 37–41) reported many behavioural observations from Table Mountain in south-west Newfoundland, where he camped from 31 July to 4 August 1981, but neglected to mention that he also captured (with mist-nets) and crudely marked five *C. minimus* individuals, by cutting notches into their flight feathers. His unpublished 'netting catalog' (USNM Bird Division) reveals that two of the three *C. minimus* adults he captured, and both juveniles, were moulting into a 'very peculiar color, dark olive-gray' (Appendix 1). For unknown reasons, Marshall (2000: xii) suppressed this information and argued on the basis of scant evidence that the Newfoundland breeding population was uniformly 'olive-brown' and '[does] not show the color phases' (Marshall 2000: xii, *contra* Wallace 1939, Peters & Burleigh 1951, Phillips 1991)—but this hypothesis is not supported by the primary evidence.

ISSN-2513-9894 (Online)

Figure 5. (left trio) A moulting juvenile male from eastern Labrador (2: CM P74267, collected by G. M. Sutton at Nain, 30 August 1920) compared to the endpoints of the Grey-cheeked Thrush *Catharus minimus* colour gradient (1: DMNH 85914, female salvaged by H. Yorgey in Pottstown, Pennsylvania, early October 2024; 3: DMNH 49483, collected by Sutton at Bethany, West Virginia, 17 September 1936); (right trio) an unusually saturated 'brown morph' *C. minimus* (5: ANSP 191610, salvaged by D. Mizrahi in Cape May Courthouse, New Jersey, 13 October 2002) compared to the endpoints of the *C. minimus* colour gradient (4: DMNH 85777, male salvaged by B. Alexander at Kennett Square, Pennsylvania, 20 September 2022; 6: DMNH 49484, collected by Sutton at Bethany, West Virginia, 16 September 1937) (Matthew R. Halley)

Archival methods

Having established the existence and geographic breadth of polychromatism in *C. minimus* and *C. bicknelli*, I now apply that knowledge to the historical record. My goal is to reassess how scientific concepts of these taxa developed over time, and to show how misinterpretations of plumage variation—caused by ignorance of the polychromatic gradient—shaped taxonomic and nomenclatural outcomes. To reconstruct the relevant historical context, I examined a wide range of archival materials housed in the same institutions that preserve the study skins, including unpublished manuscripts, field notes, diaries, correspondence, etc. When an archival source is cited with a collection number, it indicates that I consulted and transcribed the original document. Quoted passages drawn from such sources are taken from my own transcript, even when published transcripts were available. My editorial comments and additions are placed in brackets within quoted passages.

The rest of the paper adopts a semi-chronological narrative structure, beginning with the earliest references to specimens of *C. minimus* and/or *C. bicknelli*, then tracing the gradual accumulation of knowledge across two centuries. To maintain continuity, relevant analyses including morphometric statistics, specimen comparisons, critical commentary, etc., are integrated directly into the narrative. This structure makes it easier to follow the sequential discovery of facts, the context in which key ideas took shape, and the sources from which they were drawn. It also reveals how historical misunderstandings continue to influence modern taxonomy and conceptual frameworks. For foundational background on the proto-Linnaean name *Turdus minimus* (Catesby 1731), the composite origin of *T. minor* J. F. Gmelin, 1789, and other ambiguous references from the 18th and early 19th centuries, readers are referred to my previous papers (Halley 2018, 2019, 2021a,b, 2025).

ISSN-2513-9894
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Peale and the composite 'Little Thrush'

Charles Willson Peale (1741–1827) was an American polymath who, in 1786, developed an arsenic-based taxidermy technique and used it to assemble one of the first scientific bird collections in the Americas (Miller 1983, 1988, Halley 2026a,b). He displayed these specimens in semi-public venues in Philadelphia—first in Philosophical Hall (1794–1800), then the Pennsylvania State House (now Independence Hall), where his establishment became widely known as 'Peale's Museum' or the 'Philadelphia Museum' (Halley 2022, 2026a,b).

Like his contemporaries, William Bartram (1739–1823) and Benjamin Smith Barton (1766–1815),[4] Peale recognised only one species of spotted, forest-dwelling thrush in the USA: the composite *Turdus minor* J. F. Gmelin, 1789, known colloquially by various names including 'Wood Robin', 'Wood Thrush', and 'Little Thrush'. He did not distinguish the larger-bodied *Hylocichla mustelina* (Gmelin), now sole bearer of the name 'Wood Thrush', from the smaller *Catharus* species. In his 31st lecture (*c*.1799), he described male and female specimens that best match *C. minimus* or *C. bicknelli*, treating them under the composite name 'Little Thrush … *Turdus minor*' (Halley 2026a):

> 'No. 1288. Little Thrush. this American bird is described by Edwards [1760] from a specimen sent to him by Mr. Wm. Bartram, who'es [*sic*] attention to subjects of natural history have very much aided naturalists in the discoverey [*sic*] of many subjects belonging to America [for historical context, see Halley 2018]. The Head & all the upper parts are brown of an olive cast, the throat breast & underparts a dingy white beautifully spotted with brown black. Feet flesh colour. White line round the eye. *Turdus minor* Linn. Grivette d'Amerique Buff. Little Thrush Edwards, Penn; Latham & Catesby. No. 1289. Female, is so much like the male as not to be distinguished by the external appearance, when preserving I have recourse to desection, which enables me to rectify the errors of several authors, who have wrote on the American birds. They are generally found in the retired places of our woods, and very often on the ground. common throughout the United States. No. 1290. A Variety of the same, the only difference, these are smaller. No. 1291. Female.' (ANSP Archives, coll. 40)

What were the identities of Peale's specimens? He made no mention of a rusty tail, which allows us to eliminate the taxa with the most extreme expression of this character—*C.* [*g.*] *faxoni* and *C. fuscescens* (Fig. 4). He likewise did not describe a buffy suffusion to the breast and face, or bold buffy eye-rings and lores, which are characters of *C.* [*u.*] *swainsoni* (Halley 2019: 253). By deduction, the only olive-backed species in which these characters are weakly expressed are *C. minimus* and *C. bicknelli*, and these also match Peale's description of a 'White line round the eye' and a 'dingy white [throat and breast] beautifully spotted with brown black' (Halley 2026a). Peale may have had one species, or two specimens of each, or three of one and one of the other. However, because of the tragic fate of Peale's collection, the composition of his *Catharus* series will probably never be resolved (Halley 2026b).

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[4] Barton wrote in a diary while traveling in New York: 'In our ride through the woods today, we heard, as imagined, the note of the charming little wood-thrush, the *Turdus minor* of Gmelin [1789]. It is not often that the traveler enjoys the melody of birds in the forests of the unsettled parts of our country. A vast silence (to use the expression of the historian) often pervades them.' (Historical Society of Pennsylvania, HSP coll. 34).

ISSN-2513-9894
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Vieillot splits the Wood Thrush from the composite *T. minor*

Louis Pierre Vieillot (1748–1830) lived in New Jersey for several years (1793–98) and visited Peale's collection during that time. After returning to France, Vieillot (1809) applied the name *T. mustelinus* J. F. Gmelin, 1789 ('La Grive Tannée') to the species now known as Wood Thrush *Hylocichla mustelina* (Gmelin), distinguishing it from the smaller *T. minor* J. F. Gmelin, 1789, which he called 'La Grive Solitaire' (Hermit or Solitary Thrush). He reasoned incorrectly that variation in plumage colour was attributable to age, and treated all *Catharus* specimens as belonging to a single (composite) species:

> 'Son plumage varie avec l'âge: certaines ont une couleur brune nuancée d'olivâtre sur les parties supérieures, d'autres ont la poitrine ombrée de jaunâtre ou de roux, et d'autres encore ont des taches plus ou moins allongées. Cependant, toutes ces grives appartiennent à la même espèce.'
>
> English translation: 'Its plumage varies with age: some have a brown colour tinged with olive on the upperparts, others have a chest shaded with yellowish or red, and still others have more or less elongated spots. However, all of these thrushes belong to the same species.'

Wilson splits the composite *T. minor* into two composites

Wilson (1808, 1812), like Vieillot (1809), recognised the Wood Thrush as distinct, but went further by subdividing the composite *T. minor* into two species—both of which were themselves composite (Halley 2018, 2025). His original drawing of *T. solitarius* was evidently based on a specimen of *C.* [*g.*] *faxoni*, yet the published plates (prints) were coloured using a *C.* [*u.*] *swainsoni* or 'grey morph' *C. minimus* for reference. The result was a literal composite, reflecting the limits of Wilson's taxonomic understanding (Halley 2025). Thus, Wilson's *T. solitarius* was not 'the same bird we know as the Hermit Thrush today' (*contra* Kaufman 2024: 97).

Wilson's (1812: 95) anecdote about finding a nest of *T. solitarius* on 12 May 1810 in the Mississippi lowlands warrants close scrutiny, as no *Catharus* species has ever been known to nest in that region or habitat. He wrote: 'In the cane swamps of the Chactaw nation … on the twelfth of [May] I examined one of their nests on a horizontal branch immediately over the path. The female was sitting, and left it with great reluctance, so that I had nearly laid my hand on her before she flew.' Wilson consistently used the word 'swamp' to describe densely vegetated areas that were seasonally or permanently flooded (Halley 2024). 'Canebrakes' are swampy tracts dominated by *Arundinaria* grasses, which were seasonally inundated (April–June) by the annual flood-pulse of the Mississippi River, at least until the hydrology was altered by 20th century water control structures.

Wilson was travelling on horseback along the Natchez Trace, an ancient road stretching more than 700 km between Nashville, Tennessee, and Natchez, Mississippi. Originally a footpath used by the Choctaw, Chickasaw and Natchez peoples, the Trace was gradually widened by the US government starting in 1801 and had become navigable by wagon by 1809—one year before Wilson's journey (Anon. 1948). According to an itinerary he sent to his engraver, Alexander Lawson (*c.*1772–1846), Wilson passed through 'Chickasaw Bigtown' (modern Tupelo, Mississippi) on 10 May, heading south-west. On 11 May, he rode through 'open woods' past several dwellings and native farms, noting 'great droves of cattle, horses, and hogs,' and he camped 'on the top of a hill, far from water, and suffered

ISSN-2513-9894 (Online)

extremely from thirst' (Hunter 1983: 366–367). Of the day he reportedly found the *T. solitarius* nest, Wilson wrote:

> 'On Saturday [12 May], I passed a number of most execrable swamps. The weather was extremely warm, and I had been attacked by something like the dysentery, which occasioned a constant burning thirst, and weakened me greatly. I stopt this day frequently to wash my head and throat in the water, to allay the burning thirst … [by the end of the day] My complaint increased so much that I could scarcely sit on horseback, and all night my mouth and throat were parched with a burning fever' (Hunter 1983: 367).

In the absence of any other Mississippi breeding record for any *Catharus* species—and given Wilson's dehydrated and feverish state on 12 May 1810—we may reasonably conclude that he either misidentified the bird (e.g., it was merely *Hylocichla mustelina*, a common breeder) or fabricated the account. Regardless of the cause, Wilson (1812) erroneously inferred that *T. solitarius* '[remained] in the southern states during the whole year,' linking his dubious Mississippi observation to an earlier winter encounter with *C.* [*g.*] *faxoni* in South Carolina (1807–08). In fact, no *Catharus* species breeds or resides year-round in the lowlands of the south-eastern USA. This mistake had downstream effects, reinforcing the composite identity of *T. solitarius* and delaying recognition of multiple migratory *Catharus* taxa.

Latham eschews the Linnaean system

John Latham (1740–1837) described two *Catharus* specimens that John Abbot (1751–*c.*1840) collected in Georgia and sent to John Francillon (1744–1816), a London silversmith and natural history dealer (Allen 1942). Latham (1822: 141) distinguished *Hylocichla mustelina* under the name 'Tawny Thrush' and correctly cited *T. mustelinus* J. F. Gmelin, 1789. Then, he described two smaller species called 'Tawny-throated Thrush' (insufficient to distinguish between *C. fuscescens* and 'brown morph' *C. minimus*/*bicknelli*) and 'Catesby's Thrush' (insufficient to distinguish among *C.* [*u.*] *swainsoni* and 'grey morph' *C. minimus*/*bicknelli*). In any case, Latham's (1822) inability to disentangle the composites is not consequential for nomenclature, because he eschewed the Linnaean system.

Nuttall perpetuates the composites

Thomas Nuttall (1786–1859) travelled extensively in the USA and, although primarily a botanist, published an original book on American birds in two editions (Graustein 1967). His accounts contained some original observations but, after separating the 'Wood Thrush' (*Hylocichla mustelina*), both of his smaller (*Catharus*) species were composites (Kaufman 2024: 100). The first species, 'Little or Hermit Thrush' (Nuttall 1832: 346, 1840: 393), contained citations to *T. minor* J. F. Gmelin, 1789 (Halley 2018) and/or *T. solitarius* Wilson, 1812 (Halley 2025). The second species, 'Wilson's Thrush, or Veery' (Nuttall 1832: 349, 1840: 396), contained a citation to the composite *T. mustelinus* Wilson, 1812 (Halley 2018).

Re-interpreting Audubon

In an extant journal, John James Audubon (1786–1851) recorded the following entry on 14 October 1820, near Cincinnati, Ohio: 'We returned to our Boat with … a Hermit Thrush which was too much torn to make a drawing of it[.] this was the first time I had met with this Bird and felt particularly Mortified at the Situation' (Fig. 6.1). The next day, he wrote

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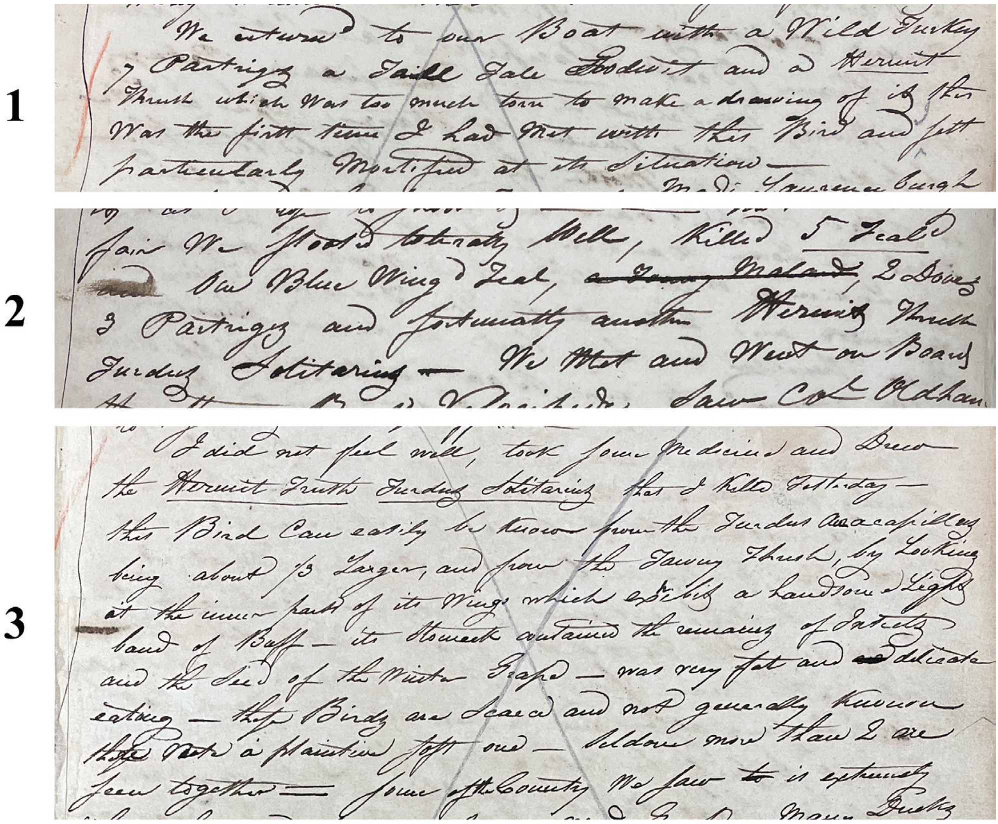

We returned to our Boat with a Wild Turkey
7 Partridges a Small Tale Godwit and a <u>Hermit</u>
Thrush which Was too much torn to make a drawing of it this
Was the first time I had Met with this Bird and felt
particularly Mortified at the Situation—

fair We Shoot tolerably Well, killed 5 Teal
one Blue Wing'd Teal, ~~a Tawny Malard~~, 2 Doves
3 Partridges and fortunately another Hermit Thrush
Turdus Solitarius — We Met and Went on Board

I did not feel well, took some Medicine and Drew
the <u>Hermit Thrush</u> <u>Turdus Solitarius</u> that I killed Yesterday—
this Bird Can easily be known from the Turdus Aurocapillus
being about 1/3 Larger, and from the Tawny Thrush, by Looking
at the inner parts of its Wings which exhibit a handsome Light
band of Buff — its Stomack contained the remains of Insects
and the Seed of the Winter Grape — was very fat and ~~an~~ delicate
eating — these Birds are Scarce and not generally known
their note a plaintive soft one — Seldom more than 2 are
Seen together — Some of the County We saw ~~to~~ is extremely

Figure 6. Select entries in the 1820 diary of John James Audubon (1786–1851), which refer to specimens of 'Hermit Thrush Turdus solitarius' that he collected and/or painted during autumn migration in 1820, on 15 October (1), 16 October (2) and 17 October (3). Reproduced courtesy of the Special Collections, Ernst Mayr Library, Harvard University (coll. MCZ F117).

(italics mine): '[I] killed … fortunately another Hermit Thrush *Turdus solitarius*' (Fig. 6.2, Corning 1929: 5–6). On 16 October, he added:

> 'I did not feel well, took some Medicine and drew the <u>Hermit Thrush</u> <u>Turdus solitarius</u> that I killed yesterday—this Bird can easily be known from the *Turdus Aurocapillus* [Ovenbird *Seiurus aurocapilla* (Linnaeus, 1766)] being about 1/3 Larger, and from the Tawny Thrush [composite *Catharus* sp., see Halley 2018, 2025], by Looking at the inner parts of its Wings which exhibit a handsome light Band of Buff—its stomack [*sic*] contained the remains of Insects and the Seed of the Winter Grape—was very fat and delicate eating—these Birds are scarce and not generally known [their] note a plaintive soft one—Seldom more than 2 are seen together' (Fig. 6.3, Corning 1929: 6–7).

This is primary evidence that Audubon's first encounter with any of the olive-backed *Catharus* species occurred in October 1820. It also seems unlikely that he collected a 'Tawny Thrush' before that date because all migratory *Catharus* species have the 'handsome light Band of Buff' on the underwing—a character Wilson (1812) had simply failed to mention in his original description of *T. mustelinus*. Audubon (1839a: 204) later corrected this error, noting: 'I am [now] of the opinion that no distinctive character can be obtained from the

ISSN-2513-9894
(Online)

colouring of the inner webs of the quills as seen from beneath, those parts being more or less yellowish or buffy in all the species.'

Audubon (1831: 303) asserted that *T. solitarius* was 'a constant resident … found in considerable numbers during spring and summer,' implying that he had personal knowledge of its breeding habits in the southern USA. He further suggested that the species nested in canebrakes along the Mississippi River and retreated to higher ground during the seasonal floods (Audubon 1831: 304):

> 'Except during winter, this Thrush prefers the darkest, most swampy, and secluded cane-brakes along the margins of the Mississippi [River], where it breeds and spends the summer, retiring to higher lands during the period when the alluvial grounds are covered with the water which, during freshets, generally inundates these low cane-brakes and swampy retreats.'

This might sound plausible to unknowing readers, but the seasonal floods occurred from April to June—squarely within the supposed breeding season of *T. solitarius*—not after summer, as Audubon (1831: 304) claimed. Kaufman (2024: 94) noted that Audubon 'wrote about [the nests of *T. solitarius*] as if he had found several,' and expressed broader scepticism about his claims: 'Unless he made up all these details—which is possible, given his history—Audubon must have found nests of other species and assumed them to be those of Hermit Thrushes.' Or, perhaps Audubon (1831) simply copied and embellished Wilson's (1812: 95) erroneous breeding record from lowland Mississippi (see above), just like he falsely claimed to have 'followed [Wilson's] track' at the 'Great Pine Swamp' (Halley 2024).

Audubon's admitted ignorance of *Catharus* species in his 1820 diary provides critical context for interpreting his later published accounts. He spent the summers of 1821–23 and 1825 in southern Mississippi—a region with no legitimate *Catharus* breeding records—and the summer of 1824 near Philadelphia, where no *Catharus* species bred until *C. fuscescens* expanded its range in the mid-20th century (Heckscher 2004). Thus, Audubon probably never observed any *Catharus* species on its breeding grounds before 1826, when he relocated to Europe and began publishing *The birds of America* (1827–38) and *Ornithological biography* (1831–39). By the time he published his text account of the 'Hermit Thrush' (Audubon 1831: 303) under the composite name '*Turdus minor* Gmel.' (i.e., treating *T. solitarius* as a junior synonym), despite his confident assertions about its natural history, his first-hand experience with *Catharus* appears to have been limited to a few migratory specimens and wintering *C.* [*g.*] *faxoni*.

Audubon initially labelled his original drawing of *C.* [*g.*] *faxoni* as 'tawny thrush' (New-York Historical Society [N-YHS] no. 1863.17.58, see fig. 6 *in* Halley 2018) and his later text account of the 'Tawny Thrush' (Audubon 1834) indicates that he conflated the taxa now known as *C. fuscescens*, *C. minimus*/*bicknelli*, *C.* [*g.*] *faxoni* and *C.* [*u.*] *swainsoni* (Halley 2019). Audubon (1834: 362) later claimed to have heard a 'tawny thrush' singing in South Carolina in March 1834, within the exclusive non-breeding range of *C.* [*g.*] *faxoni*. Consequently, most references to 'tawny thrush' in Audubon's writings must be regarded as composite and unidentifiable. For example, the 'tawny thrushes' he reported during his expedition to the north shore of the Gulf of St. Lawrence were probably *C.* [*g.*] *faxoni* (Halley 2019: 88), *contra* Todd (1963), who suspected they were a now-extirpated breeding population of *C. bicknelli*.

Audubon's undated mixed-media painting—later engraved for Pl. 164 of *The birds of America* (1833)—was said to be based on a specimen 'procured and drawn in the State of

ISSN-2513-9894 (Online)

Maine' in 1832.[5] The painting depicts a particularly grey bird, most consistent with 'grey morph' *C. minimus* or *C. bicknelli* (Halley 2018). However, the bird that appears in the published Pl. 164 is markedly browner, which suggests that the colourists used Wilson's plate or a different specimen as their reference—possibly *C. fuscescens* or 'brown morph' *C. minimus/bicknelli* (see fig. 5 *in* Halley 2018). If so, the result was a composite figure, caused by copying details from multiple specimens at different stages of the intaglio printing process (e.g., Halley 2025). 'Nowhere in [Audubon's] works—not even in the revised, more compact edition he released in the 1840s—was there any delineation of the abundant Swainson's Thrush or the common Gray-cheeked Thrush; they were still obscured behind the general concept of a Tawny/Wilson's Thrush' (Kaufman 2024: 100).

Franklin Expedition specimens

In May 1827, while Audubon's work was in production, the expedition party of John Franklin (1786–1847) and John Richardson (1787–1865) reached Carlton House, Saskatchewan, where they collected several *Catharus* later described by Swainson & Richardson (1831). However, they 'failed to clarify the thrush situation' (Kaufman 2024: 102). Their first species was 'Little Tawny Thrush' *Merula minor* Swainson & Richardson, 1831, based on a migratory specimen from Carlton House with 'tawny, or *reddish*-brown plumage,' and a new circumscription of the composite *T. minor* J. F. Gmelin, 1789, 'omitting [all] synonymes' except the 'Little Thrush' of Edwards (1760), which was itself a composite (Halley 2018). The dorsal coloration in their illustration suggests either *C. fuscescens* or a 'brown morph' *C. minimus* (Fig. 7), yet the bird has pale cheeks and white flanks, contradicting their text description ('the cheeks [have] a faint tinge of wood-brown … The sides of the breast, flanks, and linings of the wings are smoke-grey'). The Carlton House specimen is apparently not extant among the remnants of Swainson's collection at

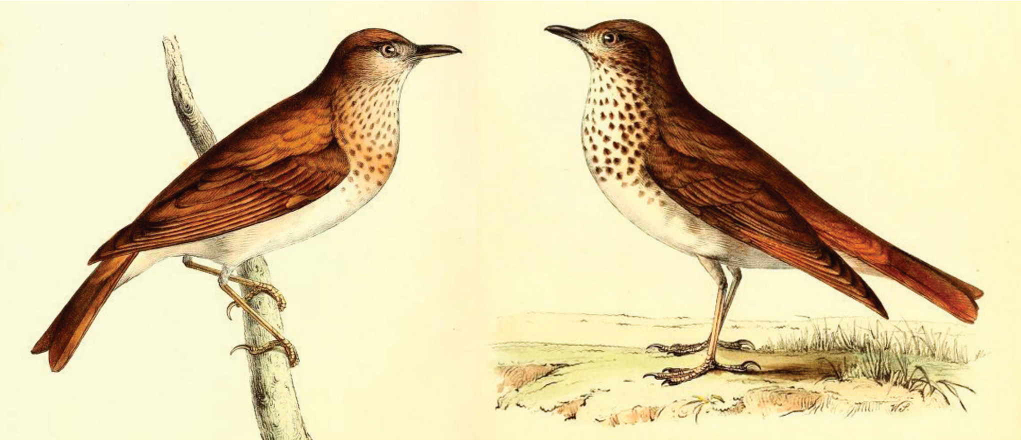

Figure 7. (left) Pl. 36 in Swainson & Richardson (1831), which depicts '*Merula minor*. (*Turdus minor* Gm.)'; (right) Pl. 37 from the same work, which depicts '*Merula solitaria*'.

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[5] Some authors have proposed that a 'tawny thrush' found in August 1832 near Boston, Massachusetts, which was mentioned in a letter to Edward Harris (1799–1863), served as the model for the bird depicted in Pl. 164, and that this specimen was *C. fuscescens* (e.g., Fries 2006: 68, Logan 2016: 538, note 266). However, this interpretation is not supported by either the original artwork or Audubon's (1834: 364) published account. The more plausible conclusion is that the model for his painting was collected during the autumn migration of 1832, when the Audubon family was travelling along the Maine coast.

ISSN-2513-9894 (Online)

the University Museum of Zoology, Cambridge, UK (UMZC), and the taxon is therefore unidentifiable.[6]

Their second species was 'Wilson's Thrush' *Merula Wilsonii* Swainson & Richardson, 1831, to which they applied Bonaparte's (1828) replacement name (*T. Wilsonii*) for Wilson's tawny-backed composite (*T. mustelinus*). As with *M. minor*, they included a description of an original specimen collected at Carlton House in May 1827 (Swainson & Richardson 1831: 182), but it was too vague to distinguish among similar taxa—specifically *C.* [*u.*] *swainsoni* and 'grey phase' *C. minimus*. In earlier work, after demonstrating that the Carlton House material was lost and untraceable, I designated a neotype (ANSP 207077) for *T. swainsoni* Cabanis *in* Tschudi, 1845, which was a replacement name for the preoccupied *M. Wilsonii* Swainson & Richardson, 1831 (Halley 2019).

The third species was 'Hermit Thrush' *Merula solitaria* Swainson & Richardson, 1831, based on the composite material they circumscribed under *T. solitarius* Wilson, 1812, together with a 'specimen, killed at Penetanguishene [Ontario], on the north shore of Lake Huron', which they described and figured (Fig. 7, right). The published illustration shows a bird with a rusty tail and bright uppertail-coverts, suggestive of *C.* [*g.*] *faxoni*, but the flanks are greyish olive (contradicting their description of 'a pure hair-brown tint') and the long primary projection suggests 'brown morph' *C. minimus* or *C. bicknelli* (which also have rusty tails). Thus, the identity of *M. solitaria* Swainson & Richardson, 1831, is also ambiguous.

The final species was 'Silent Thrush' *Merula silens* Swainson & Richardson, 1831, presented without synonyms, although Swainson (1827: 369) had already introduced the name in reference to a specimen with 'hair-brown, inclining to oil-green' dorsal plumage, collected 'five leagues to the west of Mexico' (= Temascaltepec, México). Among the remnants of Swainson's collection at UMZC is an extant specimen of *C. g. auduboni* (Baird, 1864), collected by Bullock in Mexico, bearing a label with the name 'Merula silens' (UMZC 27/Tur/6/f/11). This may be Swainson's type, but there is no indication of such status. Swainson & Richardson (1831: 186) characterised *M. silens* as 'intermediate between [their] *M. solitaria* and *M. Wilsonii*, having the rufous tail of the first, and the greyish olive-brown plumage of the second.' Later, Baird *et al.* (1858: 208) identified a specimen from 'Mexico' (USNM A7950) with the name '*Turdus silens*?' and noted that it was 'larger and more olivaceous on the back, with the same contrast of color on the tail' as *C.* [*guttatus*]. Yet Baird *et al.* (1858) were 'not prepared to say whether [it was] more than an extreme case of [*C. guttatus*],' and the identity is now impossible to determine because the specimen was destroyed in September 1880, according to a USNM ledger.

Baird collects *C. minimus* but overlooks its novelty

Spencer Fullerton Baird (1823–87) began collecting specimens near his home in Carlisle, Pennsylvania, in 1839, and assumed—quite reasonably, given the available literature—that Wilson had already described all the spotted thrushes in the eastern USA. In his early field catalogue, Baird used the name '*Turdus mustelinus*' for *Hylocichla mustelina* (Gmelin), used Bonaparte's (1828) replacement name '*T. wilsoni*' for Wilson's (1812) tawny-backed composite, and reserved '*T. solitarius*' for the olive-backed composite (Table 1, orig. nos. 90–93). However, from 1841, he began to have doubts about this taxonomy after collecting four '*Turdus*' specimens that he struggled to identify to species (Fig. 8, Smithsonian Institution Archives [SIA], coll. 7002). At least one of these specimens survives: ANSP 16089 (orig. no. 423), a *C. minimus* collected on 26 May 1841 (Fig. 9). In Baird's field catalogue it

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[6] An online search for *Catharus* specimens in the UMZC bird collection database yielded 35 results, but none has data that matches the Carlton House specimen. https://www.museum.zoo.cam.ac.uk/ (accessed 2 March 2026).

ISSN-2513-9894 (Online)

TABLE 1

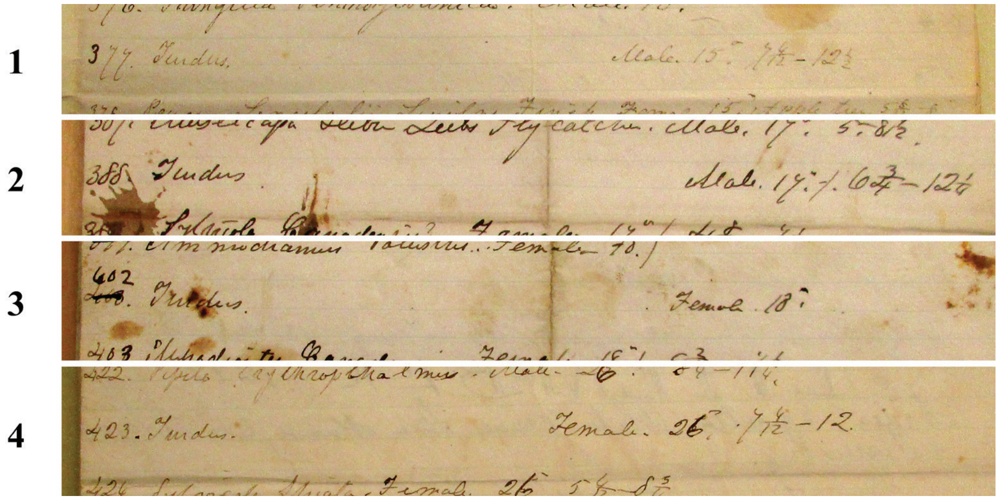
Exhaustive inventory of *Catharus* specimens in the collection of Spencer F. Baird, from its inception in 1839, through the summer of 1847 (SFB nos. 1–2,631), arranged chronologically according to date of collection. Sex is denoted as follows: male (M), female (F), undetermined (U). The 'SFB.id' column provides the taxonomic identity of each specimen, as recorded verbatim by Baird in his field catalogue. Modern identifications are also provided (MRH.id) based on extant specimens, or presumed based on dates of collection (e.g., specimens collected before 20 April were presumed to be *C.* [*g.*] *faxoni*), in which case they are enclosed in brackets.

Year	Date	SFB	sex	SFB.id	Baird (1858)	MRH.id	Modern location
1840	10 Apr	93	M	'*Turdus solitarius*'	'*T. pallasii*'	[*C.* [*g.*] *faxoni*]	
	16 Apr	91	F	'*Turdus solitarius*'		[*C.* [*g.*] *faxoni*]	
	18 Apr	92	M	'*Turdus solitarius*'		[*C.* [*g.*] *faxoni*]	
	11 May	90	M	'*Turdus wilsoni*'	'*T. fuscescens*'	*C. fuscescens*	
1841	15 May	377	M	'*Turdus*'			ANSP 16086?
	17 May	388	M	'*Turdus*'	'*T. swainsonii*'		ANSP 16086?
	18 May	402	F	'*Turdus*'			ANSP 16086?
	26 May	423	F	'*Turdus*'		*C. minimus*	ANSP 16089
1842	11 May	656	U	'*Turdus wilsoni*'			
	13 May	666	M	'*Turdus*'	'*T. swainsonii*'		ANSP 16086?
1843	26 Apr	927	F	'*Turdus solitarius*'		[*C.* [*g.*] *faxoni*]	UMZC 27/Tur/6/f/1
	18 May	980	M	'*Turdus* (*minor* Gm.)'	'*T. swainsonii*'		
	18 May	981	F	'*Turdus* (*minor* Gm.)'	'*T. swainsonii*'		
	18 May	982	M	'*Turdus* (*minor* Gm.)'			
	19 May	989	F	'*Turdus wilsonii*'	'*T. fuscescens*'		
1844	13 Apr	1352	F	'*Turdus solitarius*'		[*C.* [*g.*] *faxoni*]	
	20 Apr	1375	F	'*Turdus solitarius*'	'*T. pallasii*'		
	29 Apr	1401	F	'*Turdus solitarius*'		[*C.* [*g.*] *faxoni*]	
	22 May	1567	M	'*Turdus minor*'			
1845	12 Apr	2092	U	'*Turdus solitarius*'	'*T. pallasii*'	[*C.* [*g.*] *faxoni*]	
	26 Apr	2145		'*Turdus wilsonii*'	'*T. fuscescens*'	*C. fuscescens*	USNM A2145
	26 Apr	2146	F	'*Turdus solitarius*'	'*T. pallasii*'	[*C.* [*g.*] *faxoni*]	
	3 May	2206	M	'*Turdus olivaceus* Giraud'	'*T. swainsonii*'		MCZ 336597?
	3 May	2207	M	'*Turdus wilsonii*'			UMZC 27/Tur/6/d/2?[1]
	16 May	2263	M	'*Turdus olivaceus* Giraud'	'*T. swainsonii*'		MCZ 336597?
1846	30 Apr	2530	M	'*Turdus* (*olivaceus*)'			
	4 May	2543	F	'*Turdus solitarius*'		[*C.* [*g.*] *faxoni*]	
	8 May	2601	M?	'*Turdus olivaceus*?'		*C. minimus*	AMNH 834640?
	12 May	2638	M	'*Turdus* (*olivaceus*)'			UMZC 27/Tur/6/j/4?
	12 May	2639	M	'*Turdus* (*olivaceus*)'	'*T. swainsonii*'		
	12 May	2640	M	'*Turdus* (*olivaceus*)'			

[1] This specimen is listed as '5 May 1845' in the Vertnet.org database. The original data have not been verified.

appears as '423. *Turdus* [blank]. Female. [May] 26. 7 4/12–12.' (SIA, coll. 7002). A second *C. minimus* specimen from Carlisle (ANSP 16086), now lacking a collecting date and original number, was probably another of these unidentified '*Turdus*' specimens (Fig. 9).

ISSN-2513-9894
(Online)



1 377. Turdus. Male. 15. $7\frac{4}{12}$–$12\frac{1}{2}$

2 388. Turdus Male. 17. /. $6\frac{3}{4}$–$12\frac{1}{4}$

3 ~~400~~ 402. Turdus. Femal 18.

4 423. Turdus. Femal. 26. $7\frac{4}{12}$–12.

Figure 8. Field catalogue entries for four unidentified ‘*Turdus*’ specimens collected by Spencer F. Baird (1823–87) in May 1841 at Carlisle, Pennsylvania: (1) SFB no. 377, a male collected on 15 May 1841, now unlocated; (2) SFB no. 388, a male collected on 17 May 1841, now unlocated, was identified as ‘*T. swainsoni*’ by Baird *et al*. (1858); (3) SFB no. 402, a female collected on 18 May 1841, now unlocated; and (4) SFB no. 423, a female *C. minimus* collected on 26 May 1841 (now ANSP 16089). Courtesy of the Smithsonian Institution Archives (SIA coll. 7002).

Baird sent one of his unidentified ‘*Turdus*’ specimens to Audubon with a letter dated 21 June 1841 (‘The thrush I sent you, was also quite common in the mountains around here’), to which Audubon replied on 29 July: ‘As to the Thrush which I have of yours it is … only a Bird of 12 months old of the [tawny-backed] *Turdus mustelinus* of Wilson’ (Deane 1906). Audubon therefore failed to recognise the novelty of Baird’s specimen, although Baird was evidently unconvinced by his explanation. When he later entered ANSP 16089 into a more formal catalogue, he changed the identification to ‘423. *Turdus minor*? Gm.’ (i.e., Audubon’s name for the olive-backed composite, not *T. mustelinus*).

Baird’s confusion was not resolved by the time he described *Turdus aliciae* Baird *et al*., 1858 (see below for full discussion), because he later admitted: ‘During the many years I collected birds about Carlisle, [Pennsylvania,] and in the course of which I killed large numbers of *T. swainsonii*, I never saw an *aliciae*, although I observed the same variations in shade and color of [*C.* [*u.*] *swainsoni*] referred to by Mr. [Joel Asaph] Allen’ (Baird 1864: 22)—see below for Allen’s rebuttals. This statement confirms that Baird, like Audubon before him, failed to disentangle Wilson’s composites, despite having *C. minimus* specimens in his own possession. After Baird’s death, Witmer Stone (1866–1939) entered the *C. minimus* specimens from Carlisle into the ANSP ledger under the name ‘*T. ustulatus swainsoni*’ (*c*.1888–89), reflecting his own ignorance of the polychromatic gradient. The specimens remained misclassified under that name until the 20th century, when an unknown ANSP worker (‘MFT’) re-examined the material and corrected the identifications. The following annotation now appears on the label of ANSP 16089: ‘=*Catharus m. minimus* / MFT’ (Fig. 9).

Giraud splits *C.* [*u.*] *swainsoni* from the composite *T. solitarius*

Henry Casimir de Rham, Jr. (*c*.1818–40), an ornithologist and son of the Swiss-American diplomat and merchant of that name, announced at a meeting of the Lyceum of Natural History of New York in December 1839 that ‘he had detected a confusion existing among the North American [thrushes] … but not having had an opportunity fully to investigate

ISSN-2513-9894 (Online)

Figure 9. Two *Catharus minimus* specimens collected by Baird at Carlisle, Pennsylvania, which pre-date the description of *T. minimus* Lafresnaye, 1848, and *T. aliciae* Baird *et al*., 1858: (1) ANSP 16089, collected by Baird on 26 May 1841 (orig. [SFB] no. = 423), bears an original (green) label; (2) ANSP 16086, a data-deficient *C. minimus*, is likely one of the unidentified 'Turdus' specimens collected in 1841, which are now 'unlocated' (Table 1). Both specimens were misidentified as 'Turdus ustulatus swainsoni' in the original ANSP catalogue, prepared *c*.1888–99 by Witmer Stone (1866–1939) (Matthew R. Halley)

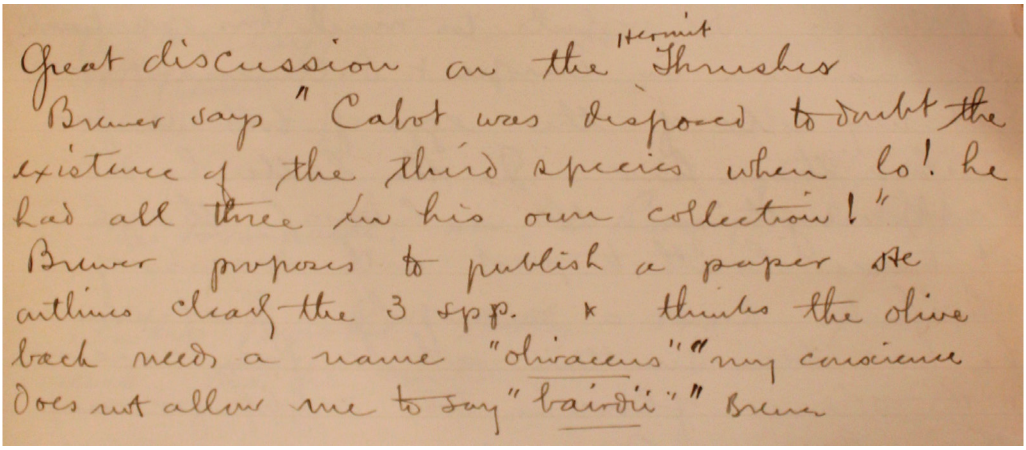
the subject, he was not at that moment prepared to unravel it' (Giraud 1844: 91). However, de Rham soon 'fell victim to a disease' and died in 1840 without resolving the issue. His untimely death created an opening for Jacob Post Giraud, Jr. (1811–70), a New York City merchant and amateur ornithologist, who subsequently disentangled the species now known as *C.* [*u.*] *swainsoni* from Wilson's composite *T. solitarius* (Giraud 1844). According to Stone (1919: 465), '[Giraud] did not skin birds, and everything in the way of taxidermy was done for him by John G. Bell (1812–99). He was [also] careless in examining bird skins, and generally they left his hands with the feathers disarranged.' Despite these limitations, Giraud's (1844: 91–92) 'careful investigation [was reportedly] made by comparisons with specimens in [his] possession, as well as those in the extensive collections' of George N. Lawrence (1806–95) and Bell.

Giraud (1844: 91) distinguished '*Turdus olivaceus* / Olive-backed Thrush' from the composite '*Turdus minor* / Hermit Thrush' by emphasising its 'uniform dark brownish-olive' upperparts, 'duller' tail, and 'line from the bill to the eye, circle around the eye, and sides of the neck [which are] rufous; [and also the] throat [is] cream color, inclining to rufous'. These characters, especially the buffy spectacles and lores, are diagnostic of *C.* [*u.*] *swainsoni* in modern treatments (Halley 2019, 2021b, Pyle 2022). Giraud (1844) assumed that his olive-backed species corresponded to *T. Wilsonii* Swainson & Richardson, 1831 (now unidentifiable, see above), but found that name preoccupied by *T. Wilsonii* Bonaparte, 1828, which applied to Wilson's tawny-backed composite, *T. mustelinus* (Halley 2018). His own name, *T. olivaceus* Giraud, 1844, was likewise preoccupied by Olive Thrush *T. olivaceus* Linnaeus, 1766 (an unrelated African species) and ultimately declared a synonym of *T. swainsoni* Cabanis *in* Tschudi 1845, which name I stabilised by designating a neotype (Halley 2019).

Brewer splits *C.* [*u.*] *swainsoni* from the composite

In Boston, just as Giraud's (1844) publication was going to press, Thomas Mayo Brewer (1814–80) independently disentangled *C.* [*u.*] *swainsoni* from the *T. solitarius* composite, apparently after discussing the matter with Baird. According to Stone's partial transcript of a June 1844 letter from Brewer to Baird, now preserved in the American Philosophical Society Library, Philadelphia (APS), Brewer '[proposed] to publish a paper [that] outlines clearly the 3 [species]' noting that the 'olive-back needs a name' and that he intended to call it *olivaceus*—the same preoccupied name Giraud had independently chosen. With characteristic humour, Brewer added that his 'conscience does not allow [him] to say [*bairdii*]' (Fig. 10). Brewer also remarked that Samuel Cabot (1815–85), newly appointed

ISSN-2513-9894 (Online)



Great discussion on the "Hermit Thrushes
Brewer says "Cabot was disposed to doubt the
existence of the third species when lo! he
had all three in his own collection!"
Brewer proposes to publish a paper &c
outlines clearly the 3 spp. & thinks the olive
back needs a name "olivaceus" "my conscience
Does not allow me to say "bairdii"" Brewer

Figure 10. Unpublished memorandum written by Witmer Stone (1866–1939) upon reading an unpublished letter from Thomas M. Brewer (1814–80) to Spencer F. Baird (1823–87), which contained a 'great discussion on the Hermit Thrushes'. The original letter may be preserved among Baird's papers (SIA coll. 7002), but was not located or examined by MRH.

curator at the Boston Society of Natural History (BSNH), 'was disposed to doubt the existence of the third species when lo! He had all three in his own collection!'

As promised, at a BSNH meeting on 17 July 1844, 'Dr Brewer called the attention of the [attendees] to some facts tending to clear up the confusion and errors in the history of the Hermit Thrush (*Turdus solitarius*, Wilson),' unaware of Giraud's (1844) recently published paper. Brewer (1844: 190) wrote:

> 'There are three distinct species which, by different authors, have been strangely mixed up. Wilson described one as *Turdus mustelinus*, tawny thrush [a composite, Halley 2018]. This is common, and is now known as *T. Wilsonii*. The second is described by Wilson under the name *T. solitarius*, hermit thrush; but under the same name he has also given a figure of a third species, every way distinct [also composite, Halley 2025]. This last is not described in either of the works of Audubon. Swainson recognizes three species, but has confounded them in a most remarkable manner. The first, he describes as a new species, *Merula minor*; the second he describes as *Merula solitaria*, but accompanies it with a plate of the third species; while he confounds the third with *T. Wilsonii*.'

The original description of *Merula olivacea* Brewer, 1844, was insufficient to distinguish between *C.* [*u.*] *swainsoni* and the grey endpoint of the *C. minimus/bicknelli* gradient—whereas Giraud's (1844) description, though simple, can be considered diagnostic. Neither species is 'most abundant in Pennsylvania and to the south,' as Brewer (1844: 191) claimed, which suggests that he was misled by Wilson's (1812) and Audubon's (1831) dubious breeding records from lowland Mississippi. The following year, Baird privately recognised the priority of Giraud's (1844) description in his field catalogue by applying the name '*Turdus olivaceus* Giraud' to specimens collected on 3 and 16 May, respectively (Table 1). MCZ 336597, a *C.* [*u.*] *swainsoni* collected in Carlisle in 'May 1845', is perhaps one of those specimens, although it lacks an original label.

ISSN-2513-9894 (Online)

Trade skins from Bogotá

In the late 1830s, a French collector called 'M. Rieffer' (presumably Monsieur Rieffer) living near Bogotá, Colombia (then República de la Nueva Granada), began sending study skins to Auguste Boissonneau (1802–83), a French naturalist. Rieffer's identity has long been uncertain. In June 2021, in an online discussion thread at BirdForum.net, a tentative consensus emerged around a man named 'Etienne Rieffer' who was listed as a French 'Naturalist' on a 'Certificate of Arrival' issued at the Port of London in 1843, although this identification is not confirmed (BirdForum 2021). By that time, Boissonneau had been selling bird specimens in Europe for several years—at least since 1837—acting as an intermediary between foreign collectors and members of the French aristocracy. One of his regular buyers was Nöel Frédéric Armand André, Baron de Lafresnaye (1783–1861), who maintained a private collection of several thousand mounted birds in his château at Falaise, Normandy, roughly 180 km west of Paris (Penard 1945: 230).

Lafresnaye published 14 papers during 1840–48, describing new taxa based on material acquired from Bogotá through the Rieffer/Boissonneau network (Sclater 1855: 37). The last of these contained the original description of *Turdus minimus* Lafresnaye, 1848, based on a holotype from 'Bogotam, in Nova-Grenada.' For more than a century, ornithologists have recognised this as the original description of *C. minimus* (e.g., Clements *et al*. 2023, Gill *et al*. 2024, HBW 2024). However, the name fell into obscurity soon after publication and was not revived until Bangs & Penard (1919) examined a specimen from Lafresnaye's collection, which they problematically argued was the *T. minimus* holotype (see below). Later, I discuss the disposition of Lafresnaye's collection and the original description of *T. minimus* in detail. For now, to retain chronological momentum, the narrative must shift to Bonaparte.

Bonaparte synonymises *T. minimus* with the composite *T. swainsoni*

Charles Lucien Bonaparte (1803–57), who lived in Philadelphia early in his career (1824–27), credited Wilson as 'the first [author] to distinguish the three closely allied species of North American thrushes from each other, by decided characters' (Bonaparte 1824: 33), by which he meant *Hylocichla mustelina* and Wilson's composite *T. solitarius* and *T. mustelinus* (Halley 2018, 2025). Thirty years later, Bonaparte (1854: 26), persuaded by Giraud's (1844) description of the 'olive-backed thrush' (which Bonaparte interpreted as *T. minor* Gmelin; see below), but still unaware that *T. solitarius* and *T. mustelinus* were themselves composites (see Bonaparte 1828: 76), concluded that *T. minimus* Lafresnaye was a junior synonym of *T. minor*. Bonaparte (1854: 26) wrote:

> '12. *T. solitarius*, Wils. (*minor*, Gambel, nec Bp.), don't un exemplaire, tue en Suisse, est depose au Museum de Strasbourg; nouvelle prevue que les differentes petites especes americaines prises constamment les unes pour les autres, et don't Swainson n'a pas toujours figure et decrit la meme sous des noms identiques, se montrent accidentellement en Europe.'
>
> 12. *T. solitarius*, Wils. (*minor*, Gambel, nec Bp.), of which an example, killed in Switzerland, is deposited in the Strasbourg Museum; it is apparent that the different small American species [that are] constantly mistaken for each other, and that Swainson does not always figure and describe the same under identical names, are accidentally shown in Europe.

ISSN-2513-9894 (Online)

> '13. *T. minor* Gm., et an tout cas, Bp. ex Gm., aux nombreux synonymes duquel il faut ajouter, d'apres un exemplaire de l'Amerique meridionale, *Turdus minimus*, du respectable doyen de l'ornithologie francaise. C'est l'espece trouvee par M. Deby dans les Ardennes, en 1847, dont l'exemplaire fait maintenant partie du Musee de Selys; et tres-certainement aussi la *Muscicapa guttata* de Pallas, quoique ce ne soit pas le *Turdus pallasi* de Cabanis, qui l'a nomme *Turdus swainsoni*!'
>
> 13. *T. minor* Gm., and in any case, Bp. ex Gm., with numerous synonyms to which we must add, based on a specimen from South America, *Turdus minimus*, from the esteemed dean of French ornithology. This is the species discovered by Mr. Deby in the Ardennes [northern France] in 1847, an example that now forms part of the collection of Selys [i.e., Edmond de Sèlys Longchamps (1813–1900)]. And most certainly, it is also the *Muscicapa guttata* of Pallas [now *C. guttatus*], although it is not the *Turdus pallasi* [now a synonym of *C. guttatus*] named by Cabanis, who called it *Turdus swainsoni*!

It is unclear whether Bonaparte (1854) examined the *T. minimus* holotype before conflating several 'olive-backed' *Catharus* species in the passages quoted above. According to Sclater (1858), Bonaparte visited Lafresnaye's collection in Falaise *c*.1856–57, shortly before his own death, but whether this was his only visit is uncertain. Sclater (1858: 64) wrote: 'The Prince informed me (after a visit to M. de Lafresnaye's collection, which he made shortly before his decease) that *Myioturdus fuscater* [Lafresnaye, 1845] belongs to this same genus [*Catharus*]—so that is probably the fourth species known.' This remark refers to the holotype of *C. fuscater* (Lafresnaye, 1845), *sensu stricto* (Halley *et al*. 2023), which was the only other *Catharus* type in Lafresnaye's collection. Bonaparte's visit to Falaise most likely occurred during his residency in Paris from March–May 1856, following his winter travels in Portugal and Spain (Stroud 2000). If he saw the *T. minimus* holotype during that visit, Sclater (1858) did not mention it.

Bonaparte's health was rapidly deteriorating when he left Paris in late May 1856, for an extended tour of the major German, Belgian and Dutch collections—Köthen, Berlin, Brunswick, Leipzig, Dresden, Strasbourg, Frankfurt, Bremen, Leiden, Wiesbaden, Antwerp, Brussels and Ghent. By the time he returned to Paris in January 1857, he was exhausted and suffering from 'terrible edema—probably the result of heart trouble—in his ulcerated legs.' By May he was bedridden, '[yet] he worked on, his bedside table covered with books, bird specimens wrapped in straw, and proofs waiting for correction' (Stroud 2000: 314). He died at home on 27 July 1857, nearly 30 years after he had last set foot in America, without disentangling Wilson's composites, and unaware that the small '*Turdus*' thrushes of the USA would eventually be classified in the genus *Catharus* Bonaparte, 1850.

Hayden's types of *Turdus aliciae* Baird *et al.*, 1858

The taxonomy of the olive-backed *Catharus* species continued to develop in North America, unaffected by *T. minimus* Lafresnaye, 1848, which was all but forgotten among the synonyms of *T. swainsoni*. In May 1856, while Bonaparte was preparing his final tour of the European collections, a unit of the US Army commanded by Gouverneur Kemble Warren (1830–82) was preparing to ascend the northern reaches of the Missouri and Yellowstone Rivers, in what is now North Dakota and eastern Montana. Warren's unit reached Fort Pierre, South Dakota, during the winter of 1855/56, accompanied by Lieutenant Ferdinand Vandeveer Hayden (1829–87), a naturalist recommended by Baird and supported in part by Smithsonian funds. According to Warren's (1858: 646) expedition report, the party remained at Fort Pierre until 28 June 1856: 'Much snow fell here during the winter, and in the spring

ISSN-2513-9894 (Online)

there were heavy showers of rain, so that a more beautiful prairie country could not be found than this, as it appeared in May and June 1856.' Thus, their *Catharus* specimens were likely spring migrants.

Later that year, Warren deposited a series of eight *Catharus* specimens in the USNM, all collected by Hayden, which Baird catalogued in a single series (USNM 4706–4713). Of these, seven were listed under the name '*Turdus swainsoni*' (which by then had supplanted the preoccupied *T. olivaceus* Giraud, 1844) and one was listed under '*Turdus Wilsonii*'. Baird later determined that four of the '*T. swainsoni*' specimens, and two collected by the Kennicotts in spring 1857 (see below), were separable and named them *Turdus aliciae* Baird *et al*., 1858, widely recognised as the name of the northern (continental) subspecies of *C. minimus*, by those who advocate treating the species as polytypic (e.g., Dickinson & Christidis 2014, Gill *et al*. 2024).

Hayden's syntypes of *T. aliciae* were, in the chronological order of their collecting dates: (1) AMNH 39130 (formerly USNM 4712), male collected at 'Vermillion' on 8 May 1856, given to G. N. Lawrence in 1859, and catalogued at AMNH on 23 May 1889; (2) USNM 4711, male collected at 'James River' on 8 May, given to the University of Michigan Museum of Zoology, Ann Arbor (UMMZ 20427); (3) USNM 4708, male with no locality data, collected on 11 May; and (4) USNM 4709, male collected at 'Vermillion' on 18 May 1856 (destroyed in August 1881). The localities called 'Vermillion' and 'James River' (printed as 'Jacques River' by Baird *et al*. 1858: 217) were evidently close to Fort Pierre, where the expedition had established its base camp (Warren 1858: 646). A list of specimens appended to the reprint of Warren's report (Warren 1875: 97), but absent from the original printing (Warren 1858), was almost certainly prepared with Baird's assistance, as it separately enumerated '[*Turdus*] *aliciae*, Baird' (four specimens) and '[*T.*] *swainsonii*, Cab.' (three).

The Kennicotts' types of *Turdus aliciae* Baird *et al*., 1858

Robert Kennicott (1835–66) and his sister Alice Mary Kennicott (1844–1919) grew up on a large property in West Northfield (now Glenview), Illinois, about 8 km north of Chicago. Their father was a travelling physician who transitioned into the horticulture business in 1842, founding 'The Grove Nursery' on the same property. The site soon became known as 'Kennicott's Grove' or simply 'The Grove,' and was designated as a National Historical Landmark in 1973, preserving it from development.

Alice, when 13 years old, collected a greyish *C. minimus* specimen at 'West Northfield' (presumably Kennicott Grove) in the spring of 1857, which would later became a syntype, then the lectotype, of *T. aliciae* Baird *et al*., 1858 (Fig. 11: USNM 10084, Deignan 1961). The other syntypes, including the Hayden series (USNM 4706–4713) and a specimen collected by Robert in southern Illinois (USNM 10083), are now paralectotypes with no name-bearing function (ICZN 1999, Art. 74.1.3). A letter from Robert to Alice, said by Deignan (1961: 432) to be preserved in the 'Deane collection' at the Library of Congress (LOC), but which cannot now be located,[7] contains the following relevant passage (my italics):

> 'Among my birds is one pretty little thrush which is new. The first specimen collected you skinned. Hoy called it *Turdus solitarius* but he is wrong. Prof. Baird names it *T. alicea* [*sic*]. It's a pretty little bird and I was very glad to have Prof. Baird name it for

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[7] I wrote to the LOC on 24 April 2024, requesting a digital scan or photo, and received the following reply from the Reference Librarian of the Prints & Photographs Division (J. Eaker *in litt*. 2024): 'I've searched everything I can think of, but the letter has not turned up … the Manuscript Division, who you originally [sent] your question to, said they were not able to find any letters donated by Deane or any other collections with letters from the Kennicotts.'

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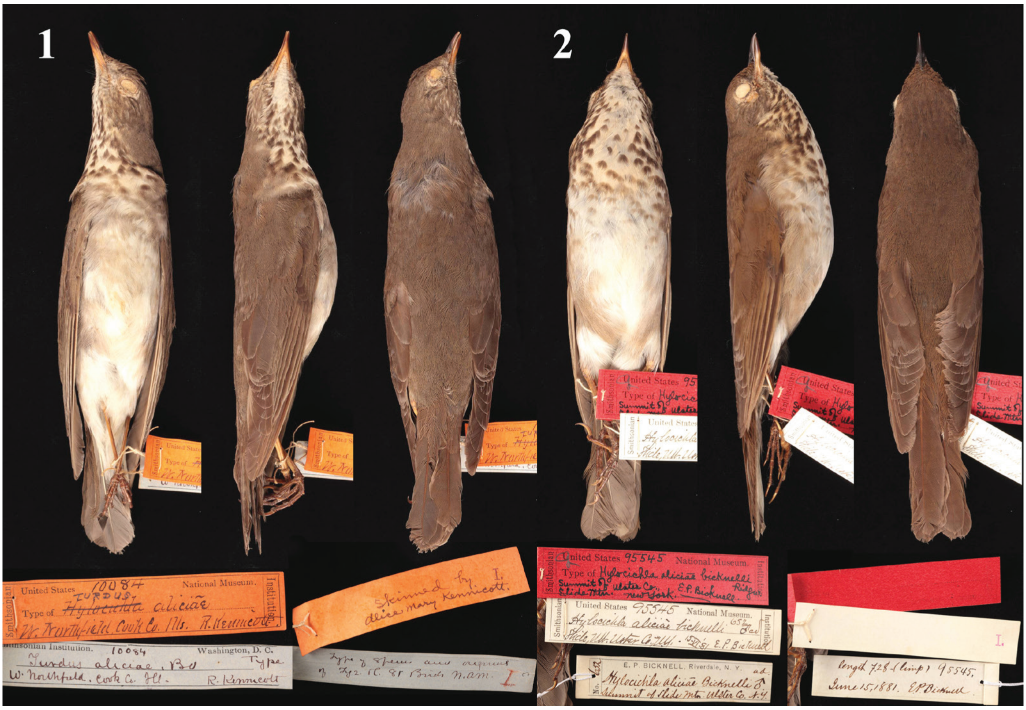

Figure 11. Three views each of (1) USNM 10084, lectotype of *Turdus aliciae* Baird *et al*., 1858 (Deignan 1961: 432); (2) USNM 95545, syntype of *Hylocichla aliciae bicknelli* Ridgway, 1882 (Deignan 1961: 433); reproduced with permission (Matthew R. Halley)

> you. I think it is rather common. It is one of the smallest of the Thrushes and you could probably get a lot about the first of May. Don't neglect work in the house for bird skinning tho'.'

Allen's rebuttals

Joel Asaph Allen (1838–1921) expressed doubt as to the validity of *T. aliciae* on 2 May 1864, at a meeting of the Essex Institute (Salem, MA): 'The "*Turdus aliciae*" of Baird, I have found to be not rare [in Massachusetts]; and from a careful examination of many specimens of both *T. aliciae* and *T. Swainsonii*, have found *aliciae* to be based on faintly colored specimens of *T. Swainsonii*, and not to be a distinct species, as heretofore supposed' (Allen 1866: 48). Allen (1861) had previously recognised three *Catharus* species under the names (1) 'Hermit Thrush' *T. solitarius* Wilson, 1812; (2) 'Olive-backed Thrush' *T. olivaceus* Giraud, 1844; and (3) 'Veery or Wilson's Thrush' *T. Wilsonii* Bonaparte, 1828. Even though he recognised *T. olivaceus*, he did so with hesitation, noting that it 'closely resembles the Hermit Thrush in size, color and general markings, to which it is closely allied' (Allen 1861: 172). In his critique of Baird *et al*. (1858), Allen (1866) maintained his former position, but adopted the replacement name (*T. swainsoni*) for the preoccupied *T. olivaceus* Giraud and treated *T. aliciae* as its junior synonym. Foreshadowing the discovery of the *C. minimus*/*bicknelli* polychromatic gradient, which practically overlaps the 'colour space' of *C.* [*u.*] *swainsoni* (see Fig. 4), Allen (1866: 56) wrote:

> '*Turdus Swainsonii* Cab. (*Turdus Swainsonii* and *T. aliciae* of Baird) … After a critical examination of a very extensive series of specimens, including many fresh ones, I

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> am forced to the conclusion that *Turdus aliciae* and *Turdus swainsonii* form but one species. I have carefully studied the bills, feet, wings, size, and proportions for specific differences, and find that, though there is more or less variation in all these [characters], as there is among individuals of almost every species, there is nothing that approaches to constant specific difference. Indeed, the principal character that has ever been urged as separating them is that of the color. But this I find is not a constant character. I have had specimens before me during the last year exhibiting every gradation in the color of the breast, sides of the neck, eye circle, &c., from the strongly buff-tinted of the true *T. Swainsonii* to the pale gray of the typical *T. "aliciae,"* where the buff was scarcely perceptible or quite obsolete…
>
> Detecting *T. aliciae* among specimens I had collected, and many specimens intermediate in color between this form and strongly marked *T. Swainsonii*, I began to search for some more constant character than color to separate the two forms; and found by extensive measurements that both the largest and the smallest specimens occurred in the form recognized as *T. Swainsonii*, though some *T. aliciae* were larger than the average of the series. On comparing the proportions of the primaries, some *aliciae* agreed with *Swainsonii* while others differed. Comparisons made between the bills, feet, and other characters, gave similar results; while in color the majority of the specimens ranged *between* those having the greatest amount of reddish-yellow and those in which the buff was scarcely appreciable. The difference in color is merely one of intensity, dependent neither upon sex nor season, possibly upon age, and extends throughout the plumage; thus, those that have the breast of the brightest buff, have also more of this tint pervading the whole plumage, the paler specimens being of the purest dark olive above, without the brownish cast observable in the more rufous individuals … even in *T. Swainsonii* the gradations from one extreme to the other are so minute and complete that the state described as *T. aliciae* can now hardly be considered "a very strongly marked" variety.'

The material basis of *C. bicknelli* (Ridgway, 1882)

On 15 June 1881, during the breeding season, Eugene S. Bicknell (1859–1925) collected two specimens on the summit of Slide Mt. in the Catskills Mountains of New York. After returning home and consulting his collection, he identified both as '*Hylocichla aliciae*' (i.e., *C. minimus*). Their presence in the Catskills—far south of the known boreal breeding range of *C. minimus*—prompted a careful examination of '[his] series of seventeen examples [of *C. minimus*] and [he] found them separable into two forms, characterized by slight differences in coloration and a notable difference in size' (Bicknell 1882: 155). Recognising the potential significance of this pattern, Bicknell sent all his material to Robert Ridgway (1850–1929), USNM curator, who published Bicknell's Thrush *Hylocichla aliciae bicknelli* Ridgway, 1882, at subspecies rank.

Ridgway (1882: 378) based the new taxon on seven specimens supplied by Bicknell, 'the only ones [of the new form he had] seen,' and listed each with full data. Although the two Catskills males were the only breeding specimens, Ridgway (1882) 'made [each of the seven specimens] an equivalent cotype' (Deignan 1961: 433). The remaining five syntypes were spring and autumn migrants that Bicknell had collected near his home in Riverdale, now a neighbourhood in the Bronx, New York City. Deignan (1961: 433) stated that Ridgway returned Bicknell's specimens in *c.*1882, and that Bicknell later deposited two of them at USNM in February 1884—one of the Catskills-breeding males (USNM 95545) and one Riverdale migrant (USNM 95546). He further speculated that 'it is probable that the ravages

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of Dermestidae led to [the] destruction [of Bicknell's remaining specimens], with the result that the two in Washington are the only surviving cotypes.' However, this conclusion was premature. Four additional syntypes and one topotype (MCZ 275709) were donated to the MCZ in the 1940s (Marshall 2000: 7).

In chronological order of their collecting dates, the seven syntypes of *C. bicknelli* are: (1) MCZ 275706, migrant male collected on 24 May 1877; (2) MCZ 275707, migrant female collected on 27 September 1878; (3) USNM 95545, breeding male collected on Slide Mt. summit on 15 June 1881; (4) MCZ 275708, another breeding male collected at Slide Mt., 15 June 1881 (Deignan 1961: 433); (5) USNM 95546, migrant female collected on 8 October 1881 (Deignan 1961: 433); (6) MCZ 275711, migrant male collected on 29 September 1881; and (7) MCZ 275783, an unsexed migrant collected in the 'Fall' of 1875.

USNM 95545 was 'singled out by [Charles W.] Richmond [1868–1932] as the type' (as a matter of curatorial routine, not in publication), but Deignan (1961: 433) transcribed a letter from Bicknell to Ridgway suggesting that Bicknell himself may have considered the other breeding male (now MCZ 275708) as 'the best type specimen.' Bicknell wrote on 18 February 1884:

> 'The Catskill example I send [USNM 95545] is less typical than the one I retain [MCZ 275708], which is much browner above, more reddish on the tail, and is the specimen about which you [Ridgway 1882: 378] particularly remarked [on] the *Luscinia* character of [the] bill. This I would have sent, believing that the [USNM] ought to have the best type specimen, but as it shows slight marks of *dermestes*, I send the more perfect one.'

Additional evidence of Bicknell's preference for MCZ 275708 is found in his unpublished correspondence with William Brewster (1851–1919), MCZ curator, in July 1882. By that time, Bicknell had three breeding specimens to hand—the two males from 1881 and a third male collected on 25 June 1882. Soon after Ridgway's (1882) description was published, Bicknell wrote to Brewster on 25 July 1882 (MCZ, Ernst Mayr Library, William Brewster Papers):

> 'Dear Mr. Brewster: Yours of the 22d came to hand this [morning] … Am glad to hear your interesting news about aliciae [*C. minimus*] and shall take pleasure in sending you as many of my examples of bicknelli [*C. bicknelli*] as you may desire.[8] For the present I send two only, for the sake of precaution … Of the three specimens I have from the Catskills, I send the type [MCZ 275708, see below] with the one taken last June [MCZ 275709, collected 25 June 1882]. The one I retain [USNM 95545] is similar to the type except in being less distinctly brownish above, and much less buffy on the breast. The bill is very similar. This year's specimen [MCZ 275709] is in somewhat worn plumage and differs somewhat from the others. The bill especially is different, as you will see, being stouter … The head of this specimen is much like that of T. nanus [*C.* [*g.*] *faxoni*], or, more properly, of a specimen of nanus, in about equally worn plumage, also taken on Slide Mtn. The race, indeed, seems to be somewhat intermediate between swainsoni and nanus with which species it was so intimately associating, and the idea of hybridity has suggested this to me. Obvious considerations, however, tend to make this appear so improbable as to preclude it being entertained, at least for the present.'

---

[8] Brewster evidently wrote to Bicknell on 22 July 1882, two days after collecting two breeding *C. bicknelli* on Mt. Washington, New Hampshire—birds with predominately 'olive' plumage—which he apparently assumed were *C. minimus* not *C. bicknelli*. Wallace (1939: 393), who examined both specimens, noted that the first (now MCZ 207389) was 'olive, with brown wings and tail,' appearing intermediate between the two *C. bicknelli* 'morphs.' That specimen was figured by Forbush (1929) and appears in my reference photo (Fig. 2: 20).

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Therefore, as Deignan (1961: 433) suspected, Bicknell clearly considered the browner specimen (MCZ 275708) to be the type—not USNM 95545. Previously, Wallace (1939: 234) had repeatedly referred to USNM 95545 as 'the Catskill type' and 'the type', a usage that could be interpreted as a lectotype designation under the Code (ICZN 1999, Art. 74.5). However, he did not clearly indicate that he 'was selecting from the type series that particular specimen to serve as the name-bearing type,' as emphasised in the Code (see Areta *et al.* 2024 for a similarly ambiguous case). Marshall (2000: 9) also referred to USNM 95545 as 'the type', while speculating (without evidence) that it had been mislabelled because it 'wears the dark brown colors that most individuals would acquire only by the fall molt', but his comments were published after 1999, precluding a lectotype designation (ICZN 1999, Art. 74.7).

Given that the identities of the migrant syntypes are uncertain (especially MCZ 275706, which has a long wing of 96 mm, and Bicknell's orig. no. 692, which is unlocated), the nomenclature of *C. bicknelli* remains unstable. In such cases, when a syntype series is 'mixed' and multiple syntypes are extant, nomenclature may be stabilised via designation of a lectotype from the syntype series (ICZN 1999, Art. 74.1). Both specimens (USNM 95545, MCZ 275708) are breeding males from the type locality and could reasonably serve as lectotypes. However, given Bicknell's preference, and because having the types of *C. minimus* and *C. bicknelli* in the same institution may have practical advantages, I hereby designate MCZ 275708 as the lectotype. This action 'supersedes any previous restriction of the application of the name' (Art. 74.1.2) and 'permanently deprives all other specimens that were formerly syntypes of that nominal taxon [including USNM 95545] of the status of syntype,' rendering them paralectotypes with no name-bearing function (Art. 74.1.3).

The false holotype of *T. minimus* Lafresnaye, 1848

In 1863, two years after Lafresnaye's death, Jules Verreaux (1807–73), who operated a natural history business in France with his brother, Édouard Verreaux (1810–68), spent three months at the Baron's château at Falaise, cataloguing his collection of 8,656 mounted bird skins (Penard 1945). Verreaux copied information from the specimens' wooden stands into a ledger, and prepared a catalogue that was printed via lithograph in 1865, to advertise the sale of the collection (Fig. 12). Baird annotated his personal copy as follows: 'Catalogue of the collection of birds belonging to the late Baron de La Fresnaye. 1865. On sale by Ed Verreaux / price [50,000 francs] / S. F. Baird' (Smithsonian Libraries).

The same year, 1865, the collection was purchased by Dr Henry Bryant (1820–67) of Boston, who travelled to France to complete the transaction. Bryant imported the collection to the USA and, in 1866, donated it to the BSNH, where the specimens were assigned new BSNH catalogue numbers, cross-referenced with the 'Lafresnaye' numbers in Verreaux's catalogue (Table 2, Fig. 13). Verreaux's catalogue was arranged taxonomically by family, then genus, then species. This suggests that the 'Lafresnaye numbers' were not original identifiers but an artifact of Verreaux's cataloguing process (Ménégaux & Hellmayr 1906). The collecting localities, which do not appear in Verreaux's printed catalogue, were apparently copied into the BSNH ledger from the original labels or wooden mounts, although this is not known for certain. Salvin (1874: 321), who examined the collection at BSNH in early 1874, opined that Verreaux's catalogue 'was somewhat hurriedly executed; and the names were taken, in most instances, from the specimens without being checked by reference to Lafresnaye's papers.'

In 1914, after a fire destroyed a portion of the BSNH collection, the MCZ acquired the remnants of the Lafresnaye collection. Outram Bangs (1863–1932) catalogued the specimens and recorded MCZ 76498 as the '<u>Type</u>' of *T. minimus* in the MCZ ledger (Fig. 14). However,

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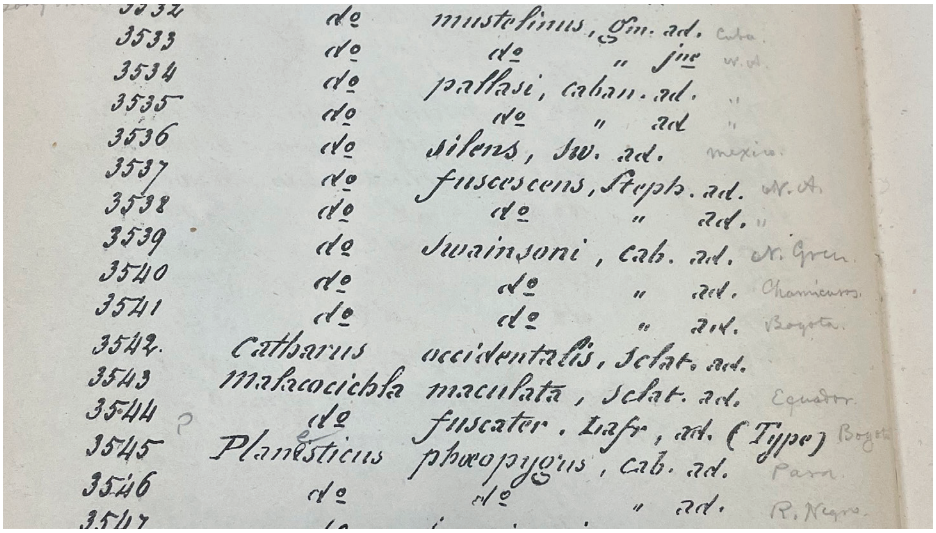

	do	mustelinus, Gm. ad.	Cuba
3533	do	do " jne	N. A.
3534	do	pallasi, caban. ad.	"
3535	do	do " ad	"
3536	do	silens, Sw. ad.	mexico.
3537	do	fuscescens, Steph. ad.	N. A.
3538	do	do " ad.	"
3539	do	swainsoni, cab. ad.	N. Gren.
3540	do	do " ad.	Chamicuros.
3541	do	do " ad.	Bogota.
3542.	Catharus	occidentalis, Sclat. ad.	
3543	Malacocichla	maculata, Sclat. ad.	Equador.
3544	? do	fuscater. Lafr, ad. (Type)	Bogota
3545	Planesticus	phæopygus, cab. ad.	Para.
3546	do	do " ad.	R. Negro.

Figure 12. Digital photo of p. 108 of the *Catalogue des oiseaux de la collection de feu M. le bon. de Lafresnaye de Falaise*, produced by Verreaux *c*.1863, ex. Library of the Boston Society of Natural History, now housed at the Boston Museum of Science. The adult specimen (3541) claimed by Bangs & Penard (1919) to be the type of *T. minimus* was identified as '*T. swainsoni* Cabanis' by Verreaux, and no type status is indicated. The name *T. minimus* does not appear in the catalogue. By contrast, Verreaux clearly indicated the type status of specimen number 3544 (MCZ 76525), which stands as the holotype of *Catharus fuscater* (Lafresnaye, 1845).

TABLE 2

Specimens of *Catharus* in the Lafresnaye collection as listed in Verreaux's catalogue ('Lafr. No.'), the Boston Society of Natural History ledger (BSNH no.) and the Museum of Comparative Zoology ledger (MCZ no.).

Lafr. no.	BSNH no.	MCZ no.	Verreaux.id	Locality	MRH.id
3534	—		[*T.*] *pallasi*	N. America	
3535	—		[*T.*] *pallasi*	N. America	
3536	4563		[*T.*] *silens*	Mexico	
3537	4564		[*T.*] *fuscescens*	N. America	
3538	4565		[*T.*] *fuscescens*	N. America	
3539	4566		[*T.*] *swainsoni*	New Granada	
3540	4567		[*T.*] *swainsoni*	Chamicuros, Brazil	
3541	4568	76498	[*T.*] *swainsoni*	Bogota	*C. minimus*
3542	4569		*Catharus occidentalis*		
3543	4570		*Malacocichla maculata*	Ecuador	
3544	4571	76525	[*Malacocichla*] *fuscater*	Bogotá	*C. fuscater*
8384		89247	*Catharus melpomene*		*C. aurantiirostris*

Verreaux had not listed this specimen as a type in his 1865 catalogue, even though he is alleged to have inflated type counts during appraisals, presumably to raise sale prices at auction (Ménégaux & Hellmayr 1906). In contrast, Verreaux unambiguously marked the 'Type' status of what is now MCZ 76525, the holotype of *C. fuscater* (Lafresnaye, 1845), *sensu stricto* (Halley *et al*. 2023), which was the only other *Catharus* type in Lafresnaye's collection.

Bryant probably hoped to find the *T. minimus* holotype, when he purchased the Lafresnaye collection in 1865, having announced several years earlier that 'specimens in

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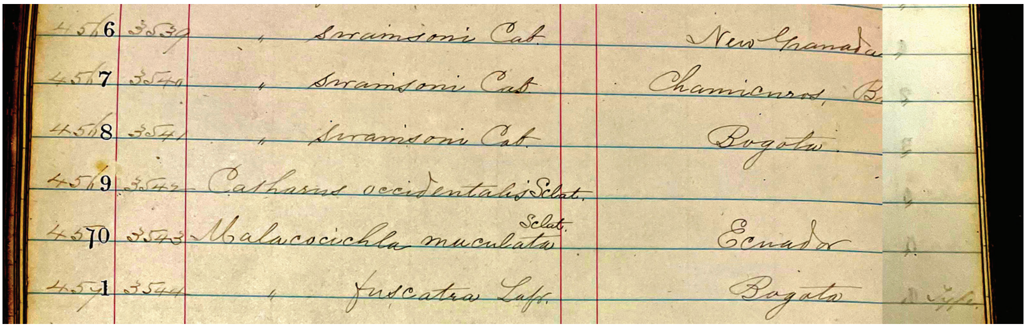
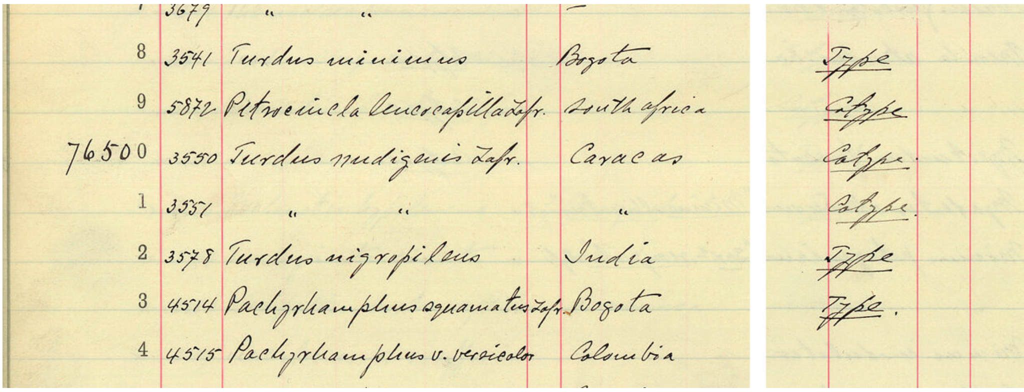


4566	3539	" swainsoni Cab.	New Granada	
4567	3540	" swainsoni Cab.	Chamicuros, B	
4568	3541	" swainsoni Cab.	Bogota.	
4569	3542	Catharus occidentalis Sclat.		
4570	3543	Malacocichla maculata Sclat.	Ecuador	
4571	3544	" fuscatra Lafr.	Bogota	Type

Figure 13. Historic specimen ledger of the Boston Society of Natural History (BSNH), in which the Lafresnaye collection was catalogued in 1866. To improve readability of entries made in faint pencil, the image contrast has been digitally boosted. The first and second columns contain the BSNH and Lafresnaye numbers, respectively, followed by the original identifications and collecting localities of each specimen (i.e., apparently copied from the original labels; see text). The far right of the image contains the final 'type status' column from the adjacent page. 'Type' was recorded for Lafresnaye no. 3544 (MCZ 76525), which is the holotype of *C. fuscater* (Lafresnaye), but not Lafresnaye no. 3541 (MCZ 76498), which Bangs & Penard (1919) claimed was the holotype of *T. minimus* Lafresnaye, 1848 (Matthew R. Halley)



	3679	" "	—	
8	3541	Turdus minimus	Bogota	Type
9	5872	Petrocincla leucocapilla Lafr.	South africa	Cotype
76500	3550	Turdus nudigenis Lafr.	Caracas	Cotype
1	3551	" "	"	Cotype
2	3578	Turdus nigropileus	India	Type
3	4514	Pachyrhamphus squamatus Lafr.	Bogota	Type.
4	4515	Pachyrhamphus v. versicolor	Colombia	

Figure 14. Digital scan of the MCZ specimen ledger, in the handwriting of Outram Bangs (1863–1932), showing that he designated Lafresnaye no. 3541 (second column) as the 'Type' of '*Turdus minimus*'. Courtesy of the MCZ Ornithology Department.

[his own] cabinet [agree] with Lafresnaye's [1848] description [and] are certainly specifically distinct from the North American *T. Swainsonii*' (Bryant 1860). One of these, collected in Bogotá (Bryant no. 92, now lost), was later identified by Baird (1864: 20) as *C.* [*u.*] *swainsoni*.[9] However, there is no indication in the BSNH ledger that Bryant thought MCZ 76498 was the *T. minimus* holotype. Like in Verreaux's catalogue, the specimen was identified as '[Turdus] swainsoni Cab.' with no indication of type status, in contrast to the clearly labelled 'Type' of *C. fuscater*, now MCZ 76525.

Thus, neither Verreaux's catalogue nor the BSNH ledger contains original data linking MCZ 76498 to *T. minimus* Lafresnaye, 1848, nor any mention of its type status. The oldest (and only) primary source where MCZ 76498 is listed as a type is the MCZ ledger. How did Bangs reach this conclusion without provenance? The specimen is 'large and brown' (Fig. 15: 1, Marshall 2000: 4), which contradicts Lafresnaye's (1848) original description

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[9] Baird (1864: 20) '[examined] the specimen from Bogota, which Bryant referred to the species of Lafresnaye (no. 92 of Dr. Bryant's collection), [and was] able to corroborate [his] remarks … however, [he was] not ready to conclude that this specimen is specifically distinct from *Turdus swainsonii*, as North American skins vary a good deal in their characters, some of them approaching it in one direction and some in another.'

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Figure 15. Three views each of (1) MCZ 76498, false holotype of *Turdus minimus* Lafresnaye, 1848 (see text), and (2) MCZ 190495, neotype of *T. minimus* designated herein (see text); reproduced with permission of the Museum of Comparative Zoology, Harvard Univ. (MCZ) (Matthew R. Halley)

(see below). The sole point of agreement is the collecting locality ('Bogotá'), but this alone cannot establish type status. Some 'Bogotá trade skins' imported by Boissonneau were actually collected elsewhere in Colombia, or even in other South American countries (e.g., van Rossem 1934: 389).

Despite the specimen's inadequate provenance, Bangs & Penard (1919: 30) confidently asserted that MCZ 76498 was Lafresnaye's holotype. Subsequent ornithologists including Wallace (1939) were so focused on the taxonomic identity of that specimen, which threatened to overturn the prevailing nomenclature, that they failed to adequately scrutinise its tenuous provenance. The following passage by Bangs & Penard (1919: 30), which elevated the false type, had the unintended effect of destabilising nomenclature and sowing confusion for more than a century:

> '[No] ornithologist of the present generation had examined the type of *Turdus minimus* Lafresnaye, until we recently did so … By common consent the name has [since Bonaparte 1854, see above] appeared in all modern works among the synonyms of *Hylocichla ustulata swainsoni* (Cabanis). We were therefore surprised upon comparing the type to find that not only is it an Alice's [Gray-cheeked] Thrush and not a Swainson's Thrush, but that it is an extreme [=large] example of the southern form of [Gray-cheeked] Thrush, always known as *Hylocichla aliciae bicknelli* Ridgway [=*C. bicknelli*]. If the specimen really came from Bogota as Lafresnaye thought it did, it is also the southernmost record for [*C. bicknelli*], which otherwise has not been found wintering in South America. In order to be certain that our identification might not be questioned, we have submitted the type to the following American ornithologists, Messrs. Batchelder, Brewster, Faxon, Oberholser, and Richmond, who all agree with us.'

ISSN-2513-9894 (Online)

Thus, a cadre of prominent ornithologists took Bangs & Penard's (1919) claim about the provenance of MCZ 76498 without scrutiny, agreed that it was an 'extreme' (unusually large) and geographically disjunct specimen of Bicknell's Thrush, and upended the nomenclature. The name *Hylocichla aliciae bicknelli* Ridgway, 1882, which had been in use for Bicknell's Thrush for half a century, was declared a junior synonym of *Hylocichla minima* (Lafresnaye). This change was implemented in the *Check-list of North American birds* fourth edition, and the non-breeding range of *C. bicknelli*—which winters in the Caribbean, not South America—was expanded to include 'Venezuela' (AOU 1931: 260).

Todd's (1963) 'St. Lawrence Thrush'

W. E. Clyde Todd (1874–1969), working for the Carnegie Museum of Natural History, Pittsburgh (CM), collected five *C. bicknelli* specimens on the north shore of the Gulf of St. Lawrence during expeditions in 1901–28 (Fig. 16). These specimens were the first to clearly show the polychromatic pattern in *C. bicknelli*, and they would have an enduring impact. The first two were males (CM P9479, P9480) collected by Todd on Grosse-Île, Québec, a small island in the Gulf (Fig. 16: 1–2). There had been substantiated reports of *C. bicknelli* breeding on Seal Island, Nova Scotia (Langille 1884), and Todd began to suspect that its breeding range also extended along the Gulf's north shore—a hypothesis he later confirmed

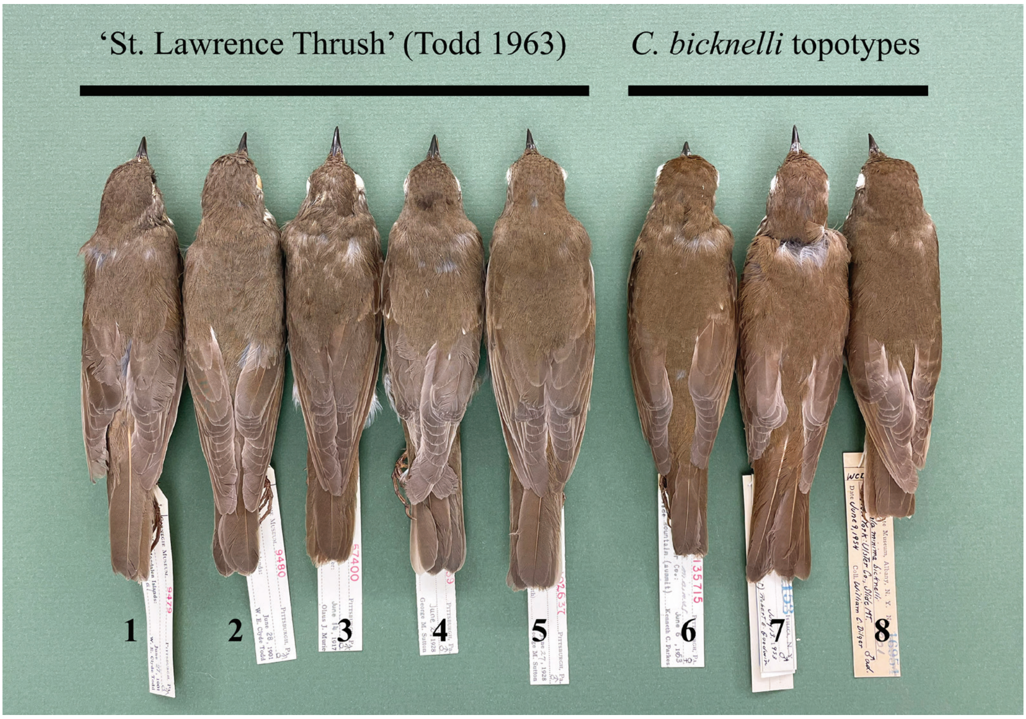

Figure 16. Five specimens mentioned in the description of the 'St. Lawrence Thrush' (Todd 1963) compared to three Bicknell's Thrush *Catharus bicknelli* topotypes: (1) CM P9479, male collected by W. E. C. Todd at Fauriel, Gross-île, Québec, 27 June 1901; (2) CM P9450, male collected by Todd at Fauriel, 28 June 1901; (3) CM 57400, male collected by O. J. Murie at 'Grand Portage (head)', Québec, 14 June 1917; (4) CM P102539, male collected by G. M. Sutton at Pointe-Natashquan, Québec, 2 June 1928; (5) CM P102637, male collected by Sutton at the mouth of the Little Mecatina River, Québec, 27 June 1928; (6) CM P135715, female collected by K. C. Parkes on the summit of Slide Mt., New York, 6 June 1952; (7) DMNH 49481, male collected by R. E. Goodwin at Slide Mt., 13 July 1953; (8) NYSM 4001, male collected by W. C. Dilger at Slide Mt., 9 June 1954 (Matthew R. Halley)

ISSN-2513-9894
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(Todd 1963). Marshall (2000: 3) erred when he stated that 'No field notes for [the CM] expeditions, [in] 1917 and 1928, are found at the Carnegie Museum.' On 14 June 1917, while encamped on the north shore of the Gulf near the mouth of the Sainte-Marguerite River, Todd wrote (CM Bird Division):

> 'In the evening we again heard the note of the Gray-cheeked Thrush from above the camp; and [O. J.] Murie went up and succeeded in bringing down the bird [CM P57400, Fig. 16: 3], which was singing on the top of a tall dead-tree. It is unquestionably a Bicknell's Thrush, and raises an interesting question of range.'

One month later, on 28 July 1917, Todd collected three *C. minimus* at 'Middle Menihek Lake' in western Labrador: an adult female (CMNH P57225) and two juveniles (CM P57223, P57224). All three were noticeably larger than his *C. bicknelli* male from 14 June. Todd's diary entry from 28 July records the encounter: 'In a little grove of spruce and tameracks we ran into several Gray-cheeked Thrushes, and shot a female and a young in juvenal dress, fully grown … Later on, shot a male Gray-cheeked with a small beetle and a wasp in its bill' (CM Bird Division).

Three years later, Todd and George M. Sutton (1898–1982) went to Newfoundland from 21–28 June 1920, where Sutton collected a breeding *C. minimus* female on 23 June (CM P74155, Fig. 3: 15). They crossed the Strait of Belle Isle and continued north along the Labrador coast—the same route we travelled in 2015—where they collected two adult *C. minimus* females at St. Mary's River on 10 July 1920 (CM P74007, P74188, Fig. 3: 20). On 30 August, Sutton also collected a hatch-year *C. minimus* male at Nain (east-central Labrador), which had nearly completed its first-cycle preformative moult (Fig. 5: 2, CM P74267). After these, only one more *C. minimus* specimen from Newfoundland and Labrador was added to the CM collection, and not until mid-century: an adult female from Redmond Lake (western Labrador) collected by R. C. Clement on 21 June 1957 (CM P137622). However, Sutton collected two more *C. bicknelli* males on the north shore of the Gulf of St. Lawrence—one on 2 June 1928 at Natashquan Point (CM P102539, Fig. 16: 4) and another on 27 June 1928 at Little Mecatina River (CM P102637, Fig. 16: 5)—which would become the focus of much debate.

By the late 1920s, with these specimens in hand, Todd began to suspect that there was an undescribed form of Bicknell's Thrush, confined to the north shore of the Gulf of St. Lawrence, but he was unable to test this hypothesis without *C. bicknelli* topotypes for comparison. On 28 May 1931, 'Not knowing who [was] in charge of the museum collection' at Vassar College (VC) in Poughkeepsie, NY, where he believed (incorrectly) that Bicknell's collection had been deposited, Todd wrote to the VC President, Henry Noble MacCracken (1880–1970), hoping to secure a loan of 'all his skins of Bicknell Thrush (*Hylocichla aliciae bicknelli*) from Slide Mountain and other places in the Catskills, for the purpose [of] comparison' (CM Bird Division).

The letter was forwarded to Aaron L. Treadwell (1866–1947), VC curator, who replied on 2 June, informing Todd 'that the Bicknell collection of birds [was] not in the Vassar Museum' (CM Bird Division). Todd had inadvertently conflated VC with the similarly named Vassar Institute (VI), about 3.7 km to the north-west, where Bicknell's specimens had in fact been accessioned. By November 1931, Todd realised his error and, 'at the suggestion of Mr. Ludlow Griscom' (1890–1959), corresponded with Allen Frost (1877–1946), VI curator, who approved the loan.

In January 1932, Todd received the 'six [VI topotype] specimens of Bicknell Thrush' on loan and forwarded them to the MCZ, together with the CM specimens of his proposed

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'St. Lawrence form.' The timing proved fortuitous: Josselyn Van Tyne (1902–57), UMMZ curator, happened to be visiting Harvard College—his alma mater (Mayfield 1957: 323)—when the skins arrived at MCZ. Taking interest in the matter, Van Tyne wrote to Todd on 5 March 1932 (CM Bird Division):

> 'Dear Mr. Todd,
>
> I have compared the type of Turdus minimus Lafresnaye [MCZ 76498] with the bicknelli [topotypes] and Gulf of St. Lawrence form you sent on here and I conclude that the type belongs with your St. Lawrence series. In spite of its age the type is practically as gray above as your recently collected birds. Also it seems to be white and unclouded below like your St. Lawrence birds. The type is really in quite fair condition. The only thing that bothers me is that all of the "bicknelli" specimens we have seen are old ones. What is the fresh skin like? There are more in the MCZ, though I believe Peters has some in his private collection at home (But he is now in bed, quite sick).
>
> Mr. Bangs has gone over these birds with me and agrees with the above. He adds that since the type of minima was taken at the extreme southern limit of the winter range of the species we should expect [it] to have come from the northern part of the breeding range of the species.[10]
>
> Sincerely, Josselyn Van Tyne'

Todd was satisfied and returned the VI loan on 29 March 1932, informing Frost that the skins were 'exactly what [he] needed for [his] comparative studies' (CM Bird Division). Todd was now convinced that two forms of Bicknell's Thrush existed: a 'grey' or 'olive' taxon breeding at sea level in the Gulf of St. Lawrence region, and a brown form breeding at high elevations in New York, Vermont and New Hampshire. He had also confirmed that both forms were distinct from the larger-bodied olive form (*C. minimus*) although he was not yet aware of the brown endpoint of the *C. minimus* gradient (see Wallace 1939), which would soon complicate the picture. In any case, Todd did not move immediately to publish, instead reserving the 'St. Lawrence thrush' for his 'forthcoming' (long delayed) report on the Labradorian avifauna (Todd 1963), a project he did not actually begin writing until 1953 (Parkes 1970: 643).

The Wallacean revolution

Todd was caught off-guard when he received a letter dated 7 August 1933 (see Appendix 2 for full transcript) from George J. Wallace (1929–85), then a graduate student at the University of Michigan (Hardy 1987): 'Dear Mr. Todd: Dr. Van Tyne of the [UMMZ] has informed me that for some time you have been making extended studies on the taxonomy of thrushes, and that you have worked out a new form from the St. Lawrence region … Dr. Van Tyne thought you would be willing to inform me of the present status of these thrushes, as you have revised them.' Todd's response was polite but defensive (10 August 1933, full transcript in Appendix 2):

> 'Dear Sir:
>
> Your letter of August 7 is received. I may say quite frankly that I had not intended making my revision of the Hylocichla minima group public until my Labrador-Hudson Bay report comes out, for which I have been saving it. Inasmuch, however, as Dr. Van

---

[10] Despite this speculation, there is no evidence of leapfrog migration in *C. minimus*, to my knowledge, nor is Bogotá, Colombia, at the southern terminus of the species' non-breeding range.

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> Tyne has (perhaps inadvertently) let the matter be known, and you have a special interest in the case, I shall give you the facts, but with the distinct understanding that they are not to be used for publication in advance of my report.'

In his response, Todd confidentially revealed his key conclusion to Wallace, i.e., that the complex consisted of three taxa: (1) '*H. minima bicknelli*' from New York, Vermont and New Hampshire (now 'brown morph' *C. bicknelli*); (2) '*H. minima minima*' from the periphery of the Gulf of St. Lawrence, excluding Newfoundland (now 'grey morph' *C. bicknelli*); and (3) the northern and western form, *H. minima aliciae* (now *C. minimus*). He insisted that Wallace refrain from publishing this information, but Wallace baulked, leaving open the possibility that he might proceed independently: 'it will be a long time before I will be ready to publish [my *Catharus* research]. In the meantime, I trust that your research will be made public' (16 August 1933, Appendix 2).

Wallace visited the CM in January 1935, where Todd showed him the five 'grey morph' *C. bicknelli* specimens (CM P9479, P9480, P57400, P102539, P102637), then returned to Mt. Mansfield for one final field season. Later that year, shortly before the 53rd stated meeting of the American Ornithologists' Union (AOU) in Toronto, Ontario, he informed Todd that he intended to present his findings at the meeting (12 October 1935, Appendix 2). On 15 October 1935, pressed into action, Todd replied that he too was scheduled to present on the same subject and suggested that their papers be read in sequence.

According to Palmer (1936: 59), in his AOU presentation, Todd proposed to 'revive the name *bicknelli* for the form breeding in the USA and reserve *minimus* for the form north of the Gulf of St. Lawrence.' Wallace, in his own presentation, announced the discovery of 'a large Newfoundland race [of *C. minimus*] which he thinks should be recognized' (*contra* Wallace 1939: 239–242). Wallace also contended that MCZ 76498—the false type of *T. minimus* Lafresnaye, 1848, elevated by Bangs & Penard (1919)—was a 'winter specimen of *aliciae*' (*contra* Bangs & Penard 1919). However, he '[suggested] that it be considered unidentifiable' in the interest of nomenclatural stability (Palmer 1936: 69). Wallace's dissertation, published in 1939, contained many novel observations about *C. bicknelli* and *C. minimus*, but he 'evidently never studied [them] again after 1935' (Marshall 2000: 6).

Campaigns for recognition

Twenty years later, Todd (1958: 160), after '[examining] the [MCZ] specimens from Newfoundland which Dr. Wallace handled' (i.e., the former Batchelder collection), wrote: 'I submit that there are three rather than two races of the Gray-cheeked Thrush: *minimus* of Newfoundland; *aliciae* of the mainland, Labrador to Alaska and Siberia; and *bicknelli*.' When his book finally appeared, Todd (1963: 559) argued that the Newfoundland population should be considered a subspecies because it was 'easily recognizable by the browner, less olivaceous color of the upperparts and wings externally.' This implied that intraspecific variation was minimal, but how he reached this conclusion is difficult to say, given that he had examined 'a series of twenty-six adult specimens collected in [Newfoundland]' (Todd 1963: 559), referring to breeding material collected by Peters & Burleigh (1951) from 1942–45 (USNM 382006–382033), which clearly show the polychromatism of the Newfoundland population ('One is grayer on the upper parts while the other tends to be browner', Peters & Burleigh 1951: 324).

In any case, Todd's (1958, 1963) proposals were not adopted by the AOU's North American Checklist Committee (NACC). In 1973, when the NACC reduced *Hylocichla* to a monotypic genus for the Wood Thrush *H. mustelina* (Gmelin) and moved the remaining '*Hylocichla*' species to *Catharus*, following Ripley (1952, 1964) and Dilger (1956a), they

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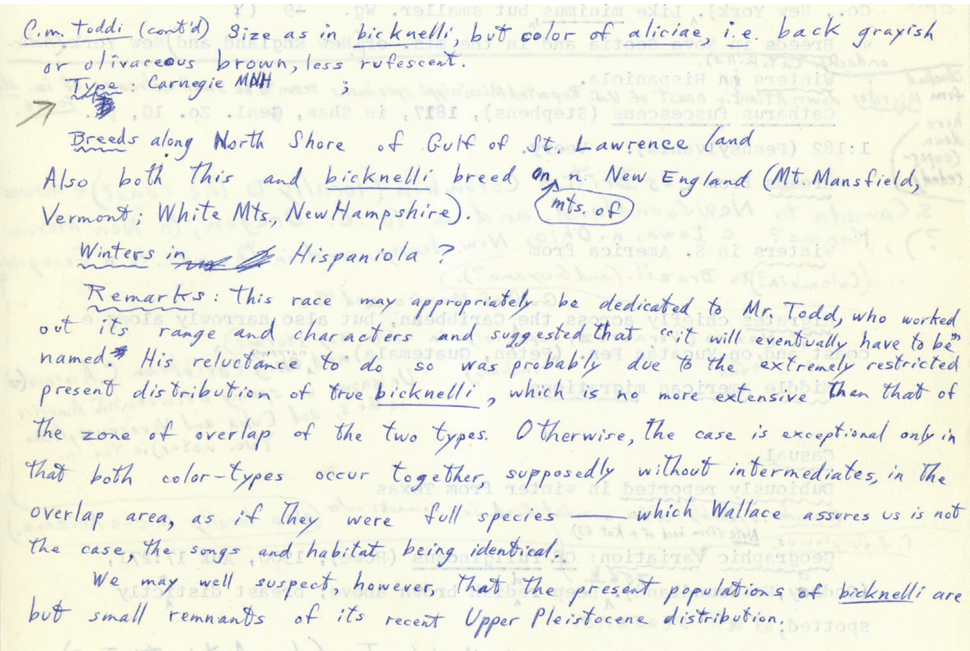
continued to treat Bicknell's Thrush as a subspecies of *C. minimus* and offered no opinion on the taxonomic status of the Newfoundland population (Eisenmann *et al*. 1973: 416). Then, subspecies were omitted from the sixth edition of the *Check-list* (AOU 1983: 555), after which Phillips (1991) elevated *C. bicknelli* to species rank in a self-published book, basing the nomenclature on Wallace's determination of MCZ 76498, and recognised the Newfoundland population at subspecies rank ('*C. m. minimus*'). Phillips (1991: 95, my edits in brackets) apparently did not consider the possibility that MCZ 76498 was not actually Lafresnaye's type, when he wrote:

> 'Supposition of Bangs and Penard, Batchelder, Brewster, Faxon, Oberholser, and Richmond that type of *minimus* "is an extreme example of the southern form [*bicknelli*]" was, rather, an example of how foxing changes thrushes' colors and of widespread carelessness in measuring wings … One wing of the type has broken primaries … As stated by Burleigh and Peters [Peters & Burleigh 1951], Newfoundland birds in half-useful plumage (of which they took few) show 2 color phases [see Figs. 1, 3]. But even the grayer phase is less grayish than *aliciae* [i.e., the continental subspecies].'

Phillips (1991: 96) also wrote: '[Todd 1963] suggested that [northern] *bicknelli* may be separable, as duller brown. But some foxing, wear, and color-phases may be involved. I have not evaluated this suggestion.' This last comment was evidently not true, as Phillips had drafted an original description of the putative taxon, with a novel eponymous name: 'Catharus minimus toddi, subsp. nov.' (Fig. 17). However, he ultimately decided to exclude this description from Phillips (1991).

Henri R. Ouellet (1938–99), a member of the NACC, undertook a biochemical analysis and marshalled evidence in favour of elevating *C. bicknelli* to species rank and recognising two subspecies of *C. minimus*. Based on Wallace's determination of MCZ 76498, he applied



C.m. toddi (cont'd) Size as in bicknelli, but color of aliciae, i.e. back grayish or olivaceous brown, less rufescent.

Type: Carnegie MNH ;

Breeds along North Shore of Gulf of St. Lawrence (and

Also both this and bicknelli breed on mts. of n. New England (Mt. Mansfield, Vermont; White Mts., New Hampshire).

Winters in Hispaniola ?

Remarks: this race may appropriately be dedicated to Mr. Todd, who worked out its range and characters and suggested that "it will eventually have to be" named.* His reluctance to do so was probably due to the extremely restricted present distribution of true bicknelli, which is no more extensive than that of the zone of overlap of the two types. Otherwise, the case is exceptional only in that both color-types occur together, supposedly without intermediates, in the overlap area, as if they were full species — which Wallace assures us is not the case, the songs and habitat being identical.

We may well suspect, however, that the present populations of bicknelli are but small remnants of its recent Upper Pleistocene distribution.

Figure 17. Draft account of 'Catharus minimus toddi, subsp. nov.' in the hand of Allan R. Phillips (1914–96), prepared for but excluded from Phillips (1991). Reproduced courtesy of the Delaware Museum of Nature & Science (DMNH).

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the name *C. m. aliciae* for the populations from western Labrador to Russia, and *C. m. minimus* for those from Newfoundland and eastern Labrador (Ouellet 1993a: 568, 1993b). However, two years later, when the NACC voted to elevate *C. bicknelli* to species rank, they treated *C. minimus* as monotypic and again refrained from considering the status of the putative Newfoundland subspecies (Monroe *et al*. 1995: 824). Nevertheless, by recognising the name *C. bicknelli* (Ridgway) for Bicknell's Thrush, they implicitly accepted Wallace's (1939) reidentification of MCZ 76498, thereby rejecting the hypothesis that it was a Bicknell's Thrush (*contra* Bangs & Penard 1919).

However, ornithologists did not unanimously fall in line with the NACC decision. Clement (2000: 309–310) recognised *C. bicknelli* at species rank but, *contra* Monroe *et al*. (1995), treated *C. minimus* as polytypic. Marshall (2000: xiv), by contrast, treated Bicknell's Thrush as a subspecies (*C. m. bicknelli*), *contra* Monroe *et al*. (1995), but refused to recognise the Newfoundland population as distinct. Thus, at the turn of the 21st century, several critical puzzles remained unresolved: the existence and taxonomic value of the polychromatic gradient, the provenance and application of the false holotype (MCZ 76498), the taxonomic status of Bicknell's Thrush, and the validity of the putative *C. minimus* subspecies from Newfoundland and eastern Labrador (e.g., Phillips 1991: 94, Clement 2000: 309, Marshall 2000: xiv).

Genetic studies

Building on early biochemical work by Seutin and Ouellet (*in* Ouellet 1993a), the genetic diagnosability and distinctiveness of *C. minimus* (*sensu lato*) and *C. bicknelli* has now been demonstrated with a variety of methods including single-gene and concatenation approaches (e.g., Outlaw *et al*. 2003, Voelker *et al*. 2013), next-generation sequence capture (e.g., genotype-by-sequencing [GBS]: FitzGerald *et al*. 2020; ultra-conserved elements [UCEs]: Everson *et al*. 2019, Halley 2021a, Halley *et al*. 2025), and whole-genome approaches (e.g., Termignoni-Garcia *et al*. 2021). This has bolstered the case for species rank for *C. bicknelli* (*contra* Marshall 2000).

However, the evidence for the genetic diagnosability of the 'Newfoundland Gray-cheek' has been less convincing. FitzGerald *et al*. (2017) studied mitochondrial (ND2) and nuclear intron (ADAM-TS 6, FIB7) sequences from a geographic sample of *C. minimus* ($n = 44$), including samples collected by myself and colleagues, and found 'no genetic breaks across the putative [*C. minimus*] subspecies boundary in Labrador, or across the Strait of Belle Isle that separates Newfoundland from Labrador.' The putative subspecies were not reciprocally monophyletic in the ND2 dataset, exhibiting low divergence (pairwise distances averaged 0.3%) and shared haplotypes. In a phylogenetic analysis of UCE-derived sequences, Halley *et al*. (2025) found that two samples from western Labrador, within the supposed range of the 'continental' subspecies (see map in FitzGerald *et al*. 2017), were more similar to two Newfoundland samples than to samples from Alaska ($n = 5$) and eastern Russia ($n = 2$). This pattern probably reflects isolation by distance not a 'genetic break' west of Labrador. FitzGerald *et al*. (2020) found the same pattern with a GBS dataset and concluded 'that genetic differentiation between the subspecies is slight and probably only detectable at quickly evolving loci.'

Taxonomy and the identity of *Turdus minimus* Lafresnaye, 1848

Given that (1) the brown phenotype of MCZ 76498, which lacks a valid claim to type status, is not diagnostic of the Newfoundland population of *C. minimus* (Figs. 1, 3) as Wallace (1939) hypothesised, and (2) the Newfoundland population is not genetically

ISSN-2513-9894 (Online)

diagnosable (FitzGerald *et al*. 2020, Halley 2021a, Halley *et al*. 2025), the question of nomenclature arises. Without consistent plumage or vocal differences, the only evidence of its distinctiveness lies in slight shifts in the geographic means of clinal morphometric traits (e.g., extent of pale colour on the mandible; FitzGerald *et al*. 2017), which alone are insufficient to confer subspecies rank, following delimitation criteria set forth in our recent revision of the *C.* [*fuscater*] clade (Halley *et al*. 2023). Rather, the preponderance of evidence indicates that *C. minimus* is a monotypic (yet polychromatic) species and the undiagnosable 'Newfoundland Grey-cheek' is not a valid taxon (*contra* FitzGerald *et al*. 2017). In *C. bicknelli*, the polychromatism exhibits a similarly weak geographic structure, insufficient to justify the recognition of the greyer end of the gradient at subspecies rank (Figs. 2, 16)—in other words, *C. bicknelli* is monotypic like *C. minimus*.

What then becomes of nomenclature, if the polychromatic *C. minimus* and *C. bicknelli* are treated as monotypic sister species? MCZ 76498, the purported *T. minimus* holotype (Bangs & Penard 1919), lacks any legitimate provenance of type status and does not even exhibit the morphological characters described by Lafresnaye (1848). Therefore, to identify the taxon, we must scrutinise the original description of the holotype, which was composed of two short sections, in Latin and French; although he did not explicitly mention any specimen, the singular measurement values (vs. a range of values) imply a holotype. Lafresnaye (1848: 5) wrote:

> 'T. supra obscure olivaceo-fumigatus unicolor, subtus albus, gutture collo antico et laterali pectoreque maculis late triangularibus nigro-fuscis obtectis, hypochondriis grisescentibus; ventre anoque mediis et subcaudalibus niveis; rostro parvo, nigricante, subtus basi albicante pedibus elongatis lividis.'
>
> > 'Above [dorsal] dark smoky-olive monochromatic; below [ventral] white; throat, neck, and front and sides of the breast covered with broad, triangular, dark-black spots; upper abdomen greyish; belly, anus […] and below the tail snow-white; bill small, blackish, below whitening at the base; feet slender and lead grey.'
>
> 'Cette espèce, très-remarquable par sa petite taille, puisqu'elle atteint à peine 6 pouces anglais, tandis que la plus petite de toutes celles de l'Amérique septentrionale, décrite par Audubon sous le nom de *Turdus nanus* (Aud.), a, selon cet auteur, 6 pouces anglais 9 lignes 1/2 de longueur, ne l'est pas moins par sa coloration supérieure d'un gris-olive obscur ou enfumé, et ne présentant aucune nuance de roux ou brun roux comme le *Turdus nanus*, entre autres, soit sur le croupion, les suscaudales et la queue, soit sur les parties inférieures.'
>
> > 'This species, remarkable for its small size, barely reaches 6 English inches. In comparison, the smallest of all North American birds, described by Audubon under the name *Turdus nanus* [Audubon, 1839a], has a length of 6 English inches and 9½ lines, according to the same author. However, what sets it apart is its upper coloration, which is a dark olive-gray or smoky hue, devoid of any reddish or chestnut tones found in *Turdus nanus*, particularly on the rump, undertail-coverts, and tail, as well as on the underparts.'
>
> 'C'est avec le *Seiurus aquaticus* (*Turdus aquaticus* Wilson [1812: 23]) qu'elle offre une analogie véritable de coloration supérieure; mais le des sous, la forme de ses pattes et de son bec en font un veritable *Turdus*, voisin de ces petites espèces de l'Amérique du

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Nord, *T. mustelinus*, *Wilsoni*, *solitarius*, *minor*, *silens* (Swainson) et *nanus* (Audubon) avec lesquelles ou avec les descriptions desquelles nous l'avons minutieusement comparée, sans trouver qu'elle pût convenir à aucune d'elles. (De la Nouvelle-Grenade.)'

> 'It is with the [genus *Parkesia* Sangster, 2008] that it offers a true analogy in terms of upper coloration [Fig. 18]. However, its undersides, leg shape, and bill form make it a true *Turdus*, akin to the small species of North America such as *T. mustelinus*, *T. Wilsoni*, *T. solitarius*, *T. minor*, *T. silens* (Swainson), and *T. nanus* (Audubon). We meticulously compared it with their descriptions but found that it did not fit any of them. (From New Granada.)'

As noted above, MCZ 76498 is 'large and brown' (Fig. 15: 1, Marshall 2000: 4) and does not match Lafresnaye's (1848) description of a very small bird with dark or smoky grey-olive dorsal plumage ('gris-olive obscur ou enfume') and without any hint of russet or reddish brown ('ne presentant aucune nuance de roux ou brun roux'). This discrepancy cannot be explained as a product of foxing without weakening Wallace's (1939: 241) own diagnosis of MCZ 76498 as 'a Newfoundland bird', which was based in part on its brown coloration. The length of Lafresnaye's holotype ('Longitud. tota 5 cent.') was evidently a typographical error; the intended value was probably 15 cm, which would match Lafresnaye's (1848) subsequent remark in French ('puisqu'elle attaint à peine 6 pouces [inches] anglaise'). In any case, body length measurements taken from dried specimens are generally unreliable because different preparators may shorten or lengthen the body to meet stylistic preferences.

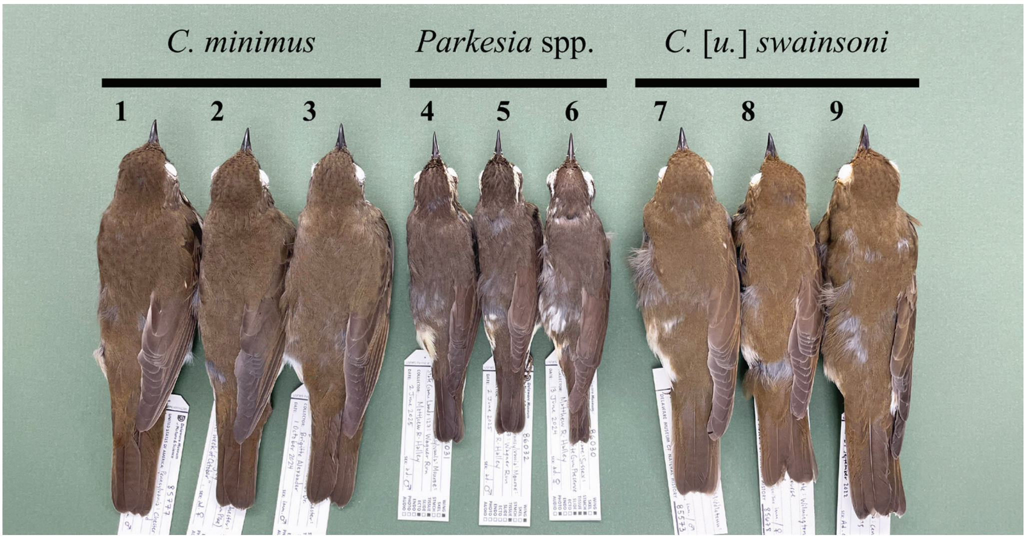

Figure 18. Comparison of the darker 'morph' of Grey-cheeked Thrush *Catharus minimus* (1–3), *Parkesia* spp. (4–6) and Swainson's Thrush *C.* [*u.*] *swainsoni*: (1) DMNH 85777, male salvaged in Kennett Square, Pennsylvania (PA), 20 September 2022; (2) DMNH 85914, female salvaged by H. Yorgey in Pottstown, PA, early October 2024; (3) DMNH 85915, male salvaged in Kennett Square, PA, 1 October 2024; (4) DMNH 86031, male Northern Waterthrush *P. noveboracensis* collected by M. R. Halley at State Game Lands (SGL) 127, PA, 2 June 2025; (5) DMNH 86032, male *P. noveboracensis* collected by Halley at SGL 127, PA, 2 June 2025; (6) DMNH 85032, male Louisiana Waterthrush *P. motacilla* collected by Halley at Nanticoke Wildlife Management Area, Delaware (DE), 13 June 2024; (7) DMNH 85573, male salvaged in Middletown, DE, 17 October 2018; (8) DMNH 85678, female salvaged in Wilmington, DE, 10 October 2019; (9) DMNH 85896, male salvaged in University Park, PA, 27 September 2022 (Matthew R. Halley)

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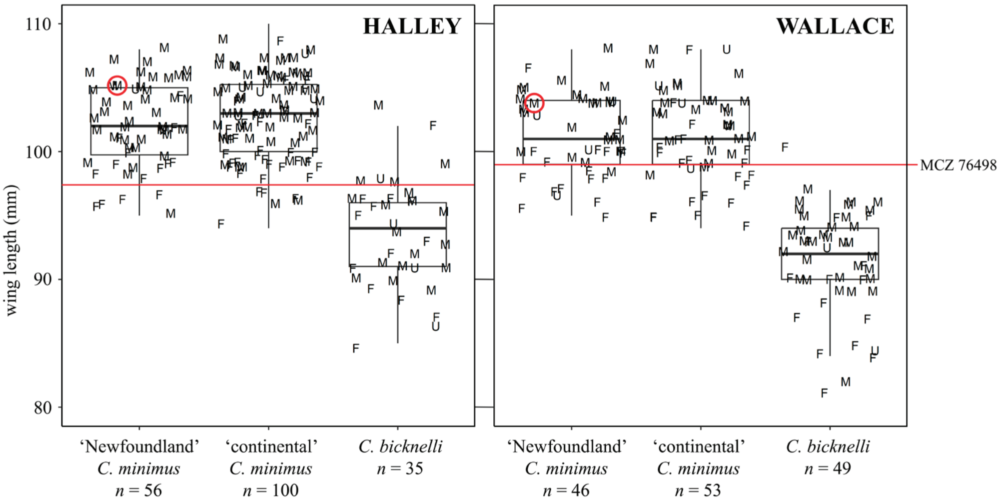

Figure 19. Wing length variation among the three putative *Catharus* taxa (Turdidae), based on datasets generated independently by the author (Halley) and Wallace (1939), who measured 'wing length' as the unflattened wing chord. The sex class of each specimen is shown (F = female, M = male, U = unknown). Horizontal red lines denote our respective measurements of MCZ 76498, which Bangs & Penard (1919) claimed was the holotype of *Turdus minimus* Lafresnaye, 1848. Red circles denote measurements of the Grey-cheeked Thrush *C. minimus* neotype, MCZ 190495 (see text).

Lafresnaye (1848) did not provide a wing length measurement, which can be valuable for distinguishing between *C. bicknelli* and *C. minimus* when specimens have relatively long or short wings, although it is less useful for specimens with intermediate values like MCZ 76498 (Fig. 19). He did, however, give tail and tarsometatarsus lengths, which prove informative. I evaluated his measurements with two independent morphometric datasets: Wallace's (1939) and my own. The tail of Lafresnaye's (1848) holotype ('caudae 6 cent.' = 60 mm) was much shorter than that of MCZ 76498 (Fig. 20; 68 mm in my dataset, 69 mm in Wallace 1939: 240); and it also has a shorter tarsometatarsus ('tarsi 2 cent. ¾' = 27.5 mm) than MCZ 76498 (Fig. 21; 29.53 mm in mine; 30 mm in Wallace 1939: 240). Notably, the measurements of Lafresnaye's (1848) holotype fall outside the range of variation of the 'Newfoundland Gray-cheek' in both datasets (Figs. 20–21).

Neotypification of *Turdus minimus* Lafresnaye, 1848

Neotypification is reserved for circumstances in which no type material is extant or identifiable and 'an author considers that a name-bearing type is necessary to define the nominal taxon objectively' (ICZN 1999, Art. 75.1). The identity of *T. minimus* Lafresnaye, 1848, is ambiguous because the *Catharus* species that best matches the morphological characters given in the original description is *C. bicknelli*, which does not occur in South America, where the holotype was supposed to have been collected. The holotype is also untraceable: MCZ 76498, which Bangs & Penard (1919) claimed to be Lafresnaye's type, lacks sufficient provenance to establish its type status and does not match the characters described by Lafresnaye (1848).

Therefore, to fix the taxonomic identity of *T. minimus* in accordance with prevailing usage, so that the name applies exclusively to the Grey-cheeked Thrush *C. minimus* (Lafresnaye), here considered monotypic, I hereby designate an adult male (MCZ 190495) in the collection of the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA, as its neotype (Figs. 3: 17, 15: 2). This action stabilises traditional nomenclature and prevents

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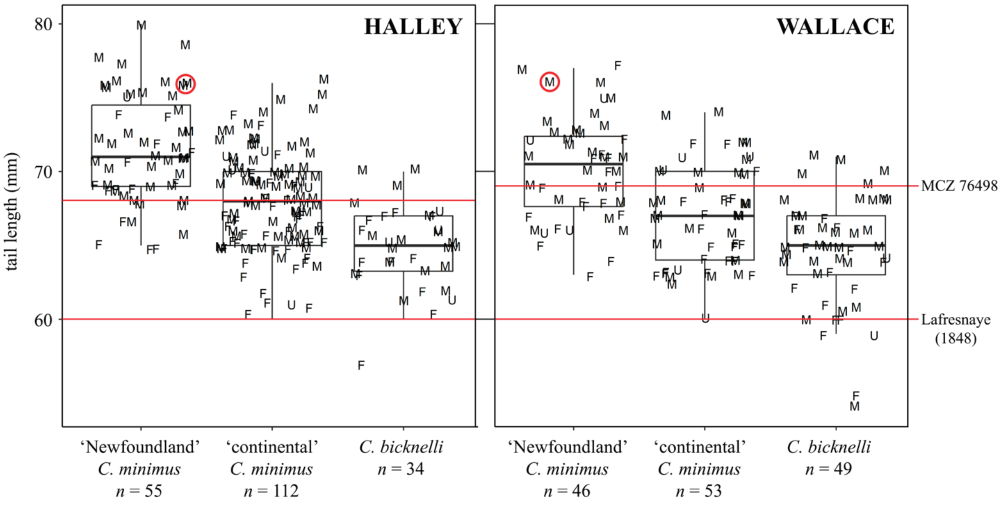

Figure 20. Tail length variation among the three putative *Catharus* taxa (Turdidae), based on datasets generated independently by the author (Halley) and Wallace (1939). The sex class of each specimen is shown (F = female, M = male, U = unknown). Horizontal red lines denote our respective measurements of MCZ 76498, which Bangs & Penard (1919) claimed was the holotype of *Turdus minimus* Lafresnaye, 1848, and the value given by Lafresnaye (1848) in the original description. Red circles denote measurements of the Grey-cheeked Thrush *C. minimus* neotype, MCZ 190495 (see text).

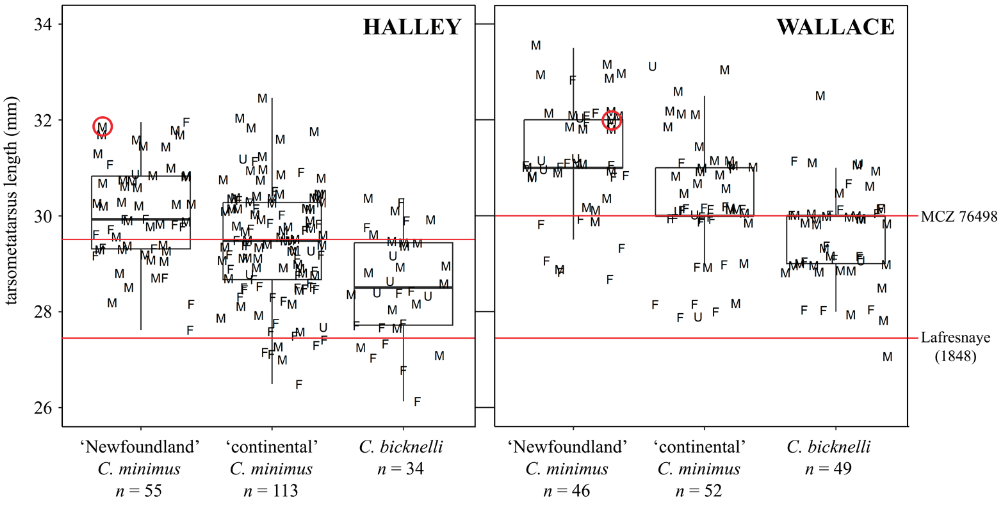

Figure 21. Tarsometatarsus length variation among the three putative *Catharus* taxa (Turdidae), based on datasets generated independently by the author (Halley) and Wallace (1939). Notably, Wallace (1939) measured 'tarsal length' from the intertarsal joint 'to the junction of the tarsus with the toes' (vs. to the final leg scale). The sex class of each specimen is shown (F = female, M = male, U = unknown). Horizontal red lines denote our respective measurements of MCZ 76498, which Bangs & Penard (1919) claimed was the holotype of *Turdus minimus* Lafresnaye, 1848, and the values given by Lafresnaye (1848) in the original description. Red circles denote measurements of the Grey-cheeked Thrush *C. minimus* neotype, MCZ 190495 (see text).

confusion arising from alternative identifications. It satisfies the requirements for neotype designation in the Code (ICZN 1999) by clarifying the taxonomic application of the name, as explained above (Art. 75.3.1) and at length by Halley (2021a), describing, illustrating and referencing the defining characters of *C. minimus* and its neotype (Art. 75.3.2), providing

ISSN-2513-9894 (Online)

TABLE 3

Summary statistics of sex-specific morphological variation in the breeding populations of Grey-cheeked Thrush *Catharus minimus* in Newfoundland and eastern Labrador (NL) and continental interior from western Labrador to Alaska (CON), and Bicknell's Thrush *C. bicknelli*, based on study skin measurements taken by the author (see text).

		WG			**TR**			**TL**		
Taxon	**Sex**	***n***	**mean ± SD**	**range**	***n***	**mean ± SD**	**range**	***n***	**mean ± SD**	**range**
C. minimus (NL)	M	41	103.1 ± 2.8	95–108	40	30.2 ± 1.0	28.2–31.9	40	72.3 ± 3.6	66–80
C. minimus (CON)		61	103.8 ± 3.0	96–110	68	29.8 ± 1.1	27.0–32.5	69	69.0 ± 2.9	64–76
C. bicknelli		15	94.9 ± 4.1	89–104	15	29.0 ± 1.0	27.1–30.4	15	65.0 ± 2.4	61–70
C. minimus (NL)	F	6	98.7 ± 1.8	96–101	6	29.7 ± 1.4	27.6–32.0	6	69.8 ± 1.8	67–72
C. minimus (CON)		14	100.7 ± 3.7	94–109	21	29.1 ± 1.1	27.1–30.9	18	66.3 ± 3.1	61–74
C. bicknelli		10	92.4 ± 5.2	85–102	10	28.0 ± 1.7	24.9–30.3	9	63.3 ± 3.3	57–67

data sufficient to ensure recognition of the designated specimen (Art. 75.3.3), providing grounds for believing that all original type material has been lost and is untraceable (Art. 75.3.4), showing that traits of the neotype are included in the original description (Art. 75.3.5), choosing a neotype collected during the breeding season in Newfoundland, for the sake of stability (Art. 75.3.6), and recording that the neotype is preserved in a recognised scientific institution (Art. 75.3.7).

MCZ 190495 is an adult male (study skin) collected by John Cyrus Cahoon (1863–91) on 23 June 1890, at 'Custlett' (= Cuslett), Newfoundland and Labrador, Canada (*c*.46°57'28.62"N, -54°9'38.97"W). I took the following measurements on 9 November 2023: flattened wing length (105 mm), length of tenth primary from the carpal joint (41 mm), tail length (76 mm), tarsometatarsus length (31.79 mm), bill length from the anterior edge of the naris to the tip (9.37 mm), bill width at the anterior edge of the nares (3.86 mm).

Diagnosis.—*C. minimus* is distinguished from its sister species *C. bicknelli* 'with caution' by its larger size, especially wing length (Pyle 2022: 419–421), but plumage characters emphasised by Pyle (2022: 419) and other authors are confounded by polychromatic gradients and (to a lesser extent) by seasonal effects of wear and fade. From other sympatric species, *C. minimus* can be separated by a suite of plumage characters (Fig. 4). From *C.* [*u.*] *swainsoni*, which has bold buffy eye-rings and lores, *C. minimus* is distinguished by relatively thin eye-rings and reduced or absent buff in the face, irrespective of the individual's position on the polychromatic gradient. From *C.* [*g.*] *faxoni*, which has a reddish tail and uppertail-coverts, contrasting with an olive-brown back, *C. minimus* individuals from the 'grey' end of the gradient are distinguished by their uniform olive-grey upperparts; and individuals from the 'brown' end are distinguished by a reduction (but not absence) of the rusty coloration in the tail and uppertail-coverts (Fig. 4). The reduction of the bright rusty wash in *C. minimus* is even more pronounced when compared to *C. fuscescens* (Fig. 4), which also has fainter spots on the upper breast and throat.

Acknowledgements

I am grateful to P. Pyle, J. J. Kirchman, C. M. Heckscher and G. Kirwan for reviewing the manuscript. An embryonic version appeared in Halley (2021a), which was reviewed by N. H. Rice, J. D. Weckstein, J. A. Russell, R. M. McCourt and G. Rosenberg. For critical specimens that rounded out the geographic sample, I am in debt to Kirchman (NYSM), B. T. Smith, P. Sweet (AMNH), Weckstein, Rice (ANSP), S. Edwards, J. Trimble (MCZ), C. Milensky (USNM) and S. S. Brady (CM). I also thank C. C. Rimmer for depositing *C. bicknelli* specimens from long-term study sites in Vermont and New Hampshire in the NYSM, and Kirchman for loaning the material, which considerably improved the geographic breadth of the reference photo series.

ISSN-2513-9894
(Online)

Thanks to R. Young (MCZ) for providing access to Audubon's 1820 diary. Enduring thanks to L. Welsh, R. Boardman, A. M. FitzGerald and D. M. Whitaker for comradery and hospitality in Newfoundland and Labrador and Nova Scotia. Modern specimens were collected or salvaged by the author (MRH) under US Fish & Wildlife Service (USFWS) Migratory Bird permit nos. MBPER0036206, MB019575-1; PA Game Commission special use permit no. 55967; and DE Division of Fish & Wildlife permit no. 2022-WSC-037. T. Yorgey gave permission to collect specimens at Stoffa Cabin. H. Yorgey and B. Alexander salvaged *C. minimus* specimens that were useful for this study. Finally, I acknowledge the collectors, preparators, curators, managers, archivists, librarians and volunteers who have contributed to the long-term care and storage of the primary sources upon which this research was based.

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Appendix 1

Mensural data and physical descriptions of five individuals of Grey-cheeked Thrush *Catharus minimus* trapped, marked and released by Joe T. Marshall at his field site 'beneath Table Mountain', south-western Newfoundland, from 31 July–4 August 1981. Marshall cut small notches into the flight feathers of each bird, upon initial capture, then used the marks to identify recaptured individuals in lieu of leg bands. He also recorded body weight, presumably with a Pesola spring scale, by subtracting the weight of the bag from the combined weight of the bag and bird, and used callipers and a metric ruler to record wing chord (WC), tarsometatarsus length (TR), tail length (TL) and (presumably exposed) culmen (CL). These data are provided here, followed by Marshall's notes about each bird (USNM Division of Birds):

Individual	WT	WC	TR	TL	CL
Adult male #1	33	96	28.5	71	12.5
Adult male #2	33.7	99	33	72	13
Adult female #1	33	97	31	70	–
Juvenile #1	32.5	94.5	29.5	68	12
Juvenile #2	33.7	96.6	31.5	69	11

Adult male #1

<u>1 August: dusk: net #2:</u> 'I heard one *minimus* [give a] high call from the [cloth] bags … adult ♂ … no brood patch, no cloacal [protuberance], lores all grayish.' [*drawing*: rectrix with three triangular notches cut out on the left side, and the phrase '3 notch'].

Adult male #2

<u>2 August: net #2:</u> 'molting inner [primaries] and greater [secondary] coverts … 3 [primaries] incised[11] … belly rather bare, looks like cloacal [protuberance]. Yellow droppings. The new wing feathers, ½ grown, are a dark olive gray with narrow fuscous leading edge.'

Adult female #1

<u>31 July: 1300: net #2:</u> ' ♀ old brood patch near smooth, couple feathers of lateral tract coming in. Molting greater secondary coverts, rest [of the] plumage is old. Appears to have a very large tail. Very olive-gray bird. Mark: outer [right] rectrix 1 cutout inner web + ink mark.'

<u>1 August: morning: net #3:</u> 'caught again going uphill. Has buff on chest … very large eye.'

<u>4 August: misty afternoon, slight drizzle: net #5, near junction with #4:</u> 'recaptured [at the place] where all these birds incl. [*C. fuscescens* #1] go back & forth uphill & avoid a log jam of fallen firs. [*drawing*: rectrix outline with a chunk of barbs removed from left side] cut rectrix is like this, not like picture of [tail made

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[11] Marshall (2000: 9, *fide* R. Laybourne) assumed the shape of the sixth primary was diagnostic, but this was refuted by his own netting data (see juvenile #2); also see footnote 2.

ISSN-2513-9894 (Online)

during] first capture. Ink barely discern[able], bare smooth old brood patch. 3 outer [primaries] definitely incised on inner web. Eyering incomplete on ~~one~~ right side, fairly well defined all around on the left [side] but not the clear circle of [*C.*] *ustulatus*. Greater [secondary] coverts coming in new, also a group of outer left secondaries; also pin feathers can be seen along back, rump, & ventral tract. When I pulled [the] net over its head, it gave harsh squawks and amid its outburst I thought I recognized a call or at least characteristic tone of the buzzy *minimus* voice ("bzze").'

Juvenile #1

1 August: 1200: net #2: 'low going downhill … Tail feathers still have blue bases = still growing perhaps, although all [are] very even & pointed; still coming in with underwing coverts, but crown is starting [the] fall molt in [a] very peculiar color, dark olive-gray. Has buff at sides of the [juvenile] ventral streaks.'

Juvenile #2

2 August: uphill net #1: '2 primaries incised, 5 notches on inner web out of rectrix. The juvenile lores are gray and the eyering is incomplete (on top). Inner scapulars are coming in olive-gray. Some ½ grown breast feathers are buff with [spots].'

Appendix 2

Unpublished correspondence of George J. Wallace (1929–85) and W. E. Clyde Todd (1874–1969), relevant to the systematics of Grey-cheeked Thrush *Catharus minimus* and Bicknell's Thrush *C. bicknelli*, transcribed by MRH from the original letters (CM Bird Division).

Wallace to Todd, 7 August 1933:

Dear Mr. Todd:

Dr. [Josselyn] Van Tyne of the University of Michigan Museum has informed me that for some time you have been making extended studies on the taxonomy of thrushes, and that you have worked out a new form from the St. Lawrence region. This summer I have attempted to conduct a purely field problem on the life history of Bicknell's thrush (H. minima minima) for a doctorate degree. I'm wondering if the position of H. minima minima in the taxonomic series has been changed and what the correct systematic relationships of the Hylocichla group are. I am also of course interested in the new St. Lawrence form. Dr. Van Tyne thought you would be willing to inform me of the present status of these thrushes, as you have revised them. Of course I am particularly interested in Bicknell's Thrush, but would like to know of others whose taxonomic status has been changed. I would indeed feel grateful to you if you will send me the desired information.

Very sincerely, George Wallace

Todd to Wallace, 10 August 1933:

Dear Sir:

Your letter of August 7 is received. I may say quite frankly that I had not intended making my revision of the Hylocichla minima group public until my Labrador-Hudson Bay report comes out, for which I have been saving it. Inasmuch, however, as Dr. Van Tyne has (perhaps inadvertently) let the matter be known, and you have a special interest in the case, I shall give you the facts, but with the distinct understanding that they are not to be used for publication in advance of my report. Hylocichla minima minima is the name for the race that breeds in the region of the Gulf of St. Lawrence (except in Newfoundland). The bird of the Catskills, Adirondacks, White Mountains, and Green Mountains is recognizably different, and will stand as H. minima bicknelli. H. minima aliciae is the northern (Hudsonian Zone) race.

If you are dealing with the bird of Mt. Mansfield in print you had better continue to call it minima for the present, to comply with my request. By the way, if you have any skins of this form to dispose of we should like to acquire them for our collection. I am sure that such a study as you are making of this bird will be interesting and valuable. I shall be pleased to hear from you further.

Very truly yours, [W.E.C. Todd]

Wallace to Todd, 16 August 1933:

Dear Mr. Todd,

Thank you for the kind letter disclosing the information of the taxonomy of the thrushes in which I'm interested. I have gone about as far as I can go for this summer on my life history problem and will have to continue next summer and perhaps the following summer. So it will be a long time before I will be ready to publish. In the meantime, I trust that your research will be made public. It certainly will be good fortune for me to have the taxonomy of the Hylocichla group straightened out before I finish my work on them, since my problem is not a systematic one and I can only draw on ornithological literature for those relationships. But it is indeed a help to know what the taxonomic position of this race of thrushes is destined to be. In all

ISSN-2513-9894 (Online)

probability I will not be dealing with Bicknell's Thrush in print for sometime, but in case I do, I am perfectly willing to call it H. minima to comply with your request.'

[George Wallace]

Wallace to Todd, 12 October 1935:

Dear Mr. Todd,

Since visiting the Carnegie Museum last spring my continued study of Thrushes of the Hylocichla minima group has brought to light a number of interesting facts, some of which may possibly have some bearing on the new race you proposed to describe. Inasmuch as you have so freely disclosed the information you have relating to specimens in the St. Lawrence region I feel obliged to consult you again before considering any nomenclatural changes.

The first disturbing fact pertains to the type specimen which I believe you (arbitrarily?) decided agreed with your St. Lawrence form. Since the identity of Lafresnaye's bird has been verified by so many competent and experienced ornithologists it may be imprudent of me to raise any objections now, but I have measurements on nearly two hundred specimens of H. minima and see no valid reasons why Lafresnaye's bird should be called Bicknell's Thrush of either race. One wing, frayed off at the tip, measured 97 mm., and the other, entire, measured fully 100 mm. which according to my long list of measurements of breeding birds of both the larger and smaller forms is really an aliciae wing. The tail, the next best measurement in dealing with birds of this group, is also nearer aliciae than Bicknell's. Neither could I find anything in the color pattern that would bar it from being simply a winter specimen of aliciae. Mr. Peters kindly checked my measurements.

It appears that birds from the Gulf region may average somewhat larger than New England specimens, but even then it seems doubtful to me if Lafresnaye's bird can rightfully be considered as a typical representative of the Gulf subspecies. If you have carefully compared the type with your specimens and are firm in the conviction that they are identical, I am sorry for introducing this disturbing question; but I believe you said you had not seen the type specimen.

Perhaps you remember my being puzzled by occasionally finding birds of the brown phase that measured aliciae. At last I think I have traced them to their breeding grounds, finding them to be a distinctly separate race.

It seems to me that there is really more than one method of settling this nomenclatural problem, and that ornithologists ought to agree as to the method chosen. If Lafresnaye's bird is really aliciae it would necessitate an inconvenient overthrow of the old names. Or if Lafresnaye's bird could be arbitrarily designated as the St. Lawrence type the present names could be retained as you propose. A third method would be to reject the type and go back to Ridgway's terms aliciae, and aliciae bicknelli with new names for your Gulf bird and the large brown aliciae specimens.

I intend to present some of these problems at the A.O.U. meeting in Toronto, but if you still prefer to have the matter kept silent, I can withdraw from the program. I may not be able to go anyway. I would be very glad to hear from you regarding the nomenclatural changes you deem most advisable in this matter, and hope that you will not resent my suggestions. I hope you will be able to reply before I go to Toronto.

Very sincerely, and hastily, George J. Wallace.

Todd to Wallace, 15 October 1935:

Dear Mr. Wallace:

Your letter of October 12, with reference to the case of the Gray-cheeked Thrush, interests me very much. I had already decided to present my findings at the A.O.U. meeting in Toronto, in a ten-minute talk. Perhaps the Secretary will place your paper and mine one after the other, if you decide to go — in any case, comments will be in order.

The identification of the type of minima with the Gulf race was made by Mr. Bangs and Dr. Van Tyne, with material transmitted by me for that purpose. Later I took occasion to examine this type myself (the next time I went to Cambridge) and was satisfied with their determination, although I did not actually make comparison with the material they had used, but only with specimens from the same region in the Townsend Collection. When Bangs and Penard published their determination of Lafresnaye's type of Turdus minimus they were supported by such good authorities as Batchelder, Brewster, Faxon, Oberholser, and Richmond. Is it likely that all these ornithologists would have been mistaken as between aliciae and the smaller race? Of course they did not know that there were really two smaller races. But I must admit that I did not actually measure the type specimen. It seems to me not unlikely that a winter bird (such as the type is) would have somewhat greater measurements than breeding specimens.

As I told you, I have never seen any brown-backed, large Gray-cheeked Thrushes, and if you have succeeded in working such out as a good race, you have surely accomplished something worthy of record.

Very truly yours, [W.E.C. Todd]

ISSN-2513-9894 (Online)

Appendix 3

Synonyms, taxonomic combinations, and principal citations of Grey-cheeked Thrush *Catharus minimus* (Lafresnaye) and Bicknell's Thrush *C. bicknelli* (Ridgway).

Catharus minimus (Lafresnaye, 1848)
Grey-cheeked Thrush

(?) *Turdus Wilsonii* Audubon 1833, Pl. 163 (in part); 1834: 362 (in part).

Turdus minimus Lafresnaye 1848: 5; Neotype: MCZ 190495 (orig. no. = 943) in Museum of Comparative Zoology, Harvard Univ., Cambridge, MA: Custlett, Newfoundland and Labrador, Canada, 23 June 1890 (see above).

Turdus aliciae Baird *et al*. 1858, xxxi, 210, 217; Baird 1858: xxxi; 1859: 4; Sclater 1859: 326; Coues 1861: 217; Hayden 1863: 159; Dall & Bannister 1869: 275; Ridgway 1869: 128; Baird *et al.* 1874: 11; Salvin & Godman 1879: 12–13; Taczanowski 1884: 484; Palmer 1890: 265; Nehrling 1893: 14; AOU 1895: 317; Dwight 1900: 309; Bigelow 1902: 30; Seebohm & Sharpe 1902: 163; Lectotype: USNM 10084, in National Museum of Natural History, Washington, DC: 'West Northfield, Cook County, Illinois. Not later than Apr. 29, 1857' (Deignan 1961: 432).

Turdus swainsoni aliciae Coues 1872: 73; Stearns 1886: 11.

Hylocichla aliciae aliciae Ridgway 1907: 59; AOU 1910: 360; Thayer & Bangs 1914: 521; Forbush 1929: 393; Chapman 1926: 584.

Hylocichla aliciae Osgood 1909: 43.

Hylocichla minima minima Bangs 1930: 331; Burleigh & Peters 1948: 118; Bent 1949: 188; Peters & Burleigh 1951: 323; AOU 1957: 440; Payne 1961: 384.

Hylocichla minima aliciae Austin 1932: 171; Hellmayr 1934: 458; Wallace 1939: 239.

Hylocichla minima Orr 1948: 224; Stein 1956: 508 (in part); Thompson *et al.* 1999: 316.

Catharus minimus minimus Ripley 1952: 40; Todd 1958: 160; Ripley 1964: 171; Phillips 1991: 94; Ouellet 1993b; Pyle 1997: 395; Clement 2000: 309; Lane & Jaramillo 2000; Marshall 2000: xiv; Pyle 2001: 395; Collar 2005: 702; Dalley *et al.* 2005; Whitaker *et al*. 2015; FitzGerald 2017a: 26; FitzGerald *et al*. 2017; Gómez *et al*. 2018; Whitaker *et al*. 2018; Ralston *et al*. 2019; FitzGerald *et al.* 2020; Whitaker *et al.* 2020; Termignoni-Garcia *et al*. 2021; Clements *et al*. 2023; McDermott *et al*. 2023; Robineau-Charette *et al*. 2023; Gill *et al*. 2024; HBW 2024.

Catharus minimus Dilger 1956a: 176; Vassallo & Rice 1981; AOU 1983: 555; Collier & Wallace 1989; Monroe *et al*. 1995: 824; Hobson *et al*. 2001; Outlaw *et al*. 2003; Winker & Pruett 2006; Frey *et al*. 2008; Topp *et al*. 2013; Voelker *et al*. 2013; Ungvari-Martin *et al*. 2016; FitzGerald 2017a; 2017b; Everson *et al*. 2019; Ralston *et al*. 2019; Starkloff *et al*. 2019; Ralston *et al*. 2021; Pyle 2022: 419.

Catharus minimus aliciae Todd 1958: 160; Phillips 1991: 95; Ouellet 1993b; Pyle 1997: 395; Clement 2000: 309; Lane & Jaramillo 2000; Pyle 2001: 395; FitzGerald 2017a: 26; FitzGerald *et al*. 2017; FitzGerald *et al*. 2020; Whitaker *et al*. 2020; Clements *et al*. 2023; Gill *et al*. 2024; HBW 2024.

***Catharus minimus* subsp.** Todd 1963: 558.

Catharus bicknelli (Ridgway)
Bicknell's Thrush

Hylocichla aliciae bicknelli Ridgway 1882: 377; Ridgway 1907: 62; AOU 1910: 360 (in part); Forbush 1929: 395; Lectotype: MCZ 275708, male, in Museum of Comparative Zoology, Harvard Univ., Cambridge, MA: Slide Mountain, Ulster County, New York, 15 June 1881 (see above).

Turdus aliciae bicknelli Brewster 1883: 12; Nehrling 1893: 15; AOU 1895: 317; Dwight 1900: 310.

Turdus bicknelli Seebohm & Sharpe 1902: 169.

Hylocichla minima minima Austin 1932: 171.

Catharus minimus bicknelli Ripley 1952: 40; Dilger 1956b: 331; 1956c: *frontispiece*; Todd 1958: 160; Marshall 2000: xiv.

Catharus minimus Dilger 1956a: 176 (in part); AOU 1983: 555 (in part).

Hylocichla minima Stein 1956: 508 (in part).

Catharus bicknelli Phillips 1991: 95; Ouellet 1993b; Evans 1994; Monroe *et al*. 1995: 824; Atwood *et al*. 1996; Clement 2000: 310; Ellison 2001; Outlaw *et al*. 2003; Winker & Pruett 2006; Frey *et al*. 2008; FitzGerald 2017b; Ball 2000; Connolly 2000; Lane & Jaramillo 2000; Hobson *et al*. 2001; Goetz *et al*. 2003; Townsend *et al*. 2011; Voelker *et al*. 2013; FitzGerald 2017a; 2017b; FitzGerald *et al*. 2017; Everson *et al*. 2019; FitzGerald *et al*. 2020; Townsend *et al*. 2020; Ralston *et al*. 2021; Clements *et al*. 2023; Gill *et al*. 2024; Rimmer *et al*. 2024.

ISSN-2513-9894
(Online)

Another Night Parrot *Pezoporus occidentalis*? The putative specimen in the collection of Charles Greener

by Alexander L. Bond & Lukas Large

Received 21 November 2025; revised 4 March 2026; published 3 June 2026

http://zoobank.org/urn:lsid:zoobank.org:pub:CF77E5BE-F551-4D28-9142-13CB8409A79E

Summary.—There is a putative record of a Night Parrot *Pezoporus occidentalis* from the collection of Charles Greener, a gunsmith in Birmingham, UK, from his visits to Australia around the turn of the 20th century. Though not mentioned in previous summaries of Night Parrot specimens, ongoing digitisation of museum specimens makes this an important error to correct pre-emptively. The record is almost certainly erroneous, and we believe no such specimen existed.

Night Parrot *Pezoporus occidentalis* is an enigmatic Australian endemic that was long thought to be extinct until its rediscovery in the late 20th century. Sightings and specimens are currently confined to inland areas of western and central Australia, although the species was probably more widespread historically (Leseberg *et al.* 2021). With a population estimated at just 50–250 individuals (Garnett *et al.* 2011), it is currently treated as Critically Endangered on the IUCN Red List.

Given its scarcity, and recent work focused on elucidating its current distribution, there is a great deal of interest in historical records and museum specimens. Forshaw *et al.* (1976) compiled a list of 22 specimens that was supplemented by Black (2012), who added another six, which together spanned the period 1845–1912, with recent specimens from 1990 (Boles *et al.* 1994), 2006 (McDougall *et al.* 2009) and 2016–22 (Yeap *et al.* 2025), and subsequent live captures of individuals (Murphy *et al.* 2017).

Charles Greener and the Birmingham Museum and Art Gallery

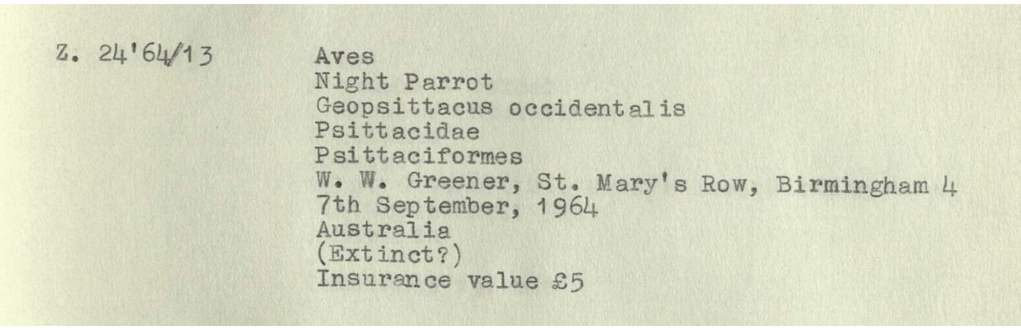
The Birmingham Museum and Art Gallery, England, holds several thousand bird specimens, including *c.*1,200 from outside the UK (Watson 2011). Among these were 104 birds donated by Leyton Greener of the W. W. Greener Company, a Birmingham gunsmith, in 1964, predominantly from Charles Greener's three visits to Tasmania, Victoria and New South Wales during 1896–1907 (Greener 2012, Fforde & Oscar 2020). Charles, alongside his brother Harry, was a partner in the family company in 1890 and its Sales and Marketing Manager, which included establishing and maintaining a large network of potential contributors to the collection, in which he had a great interest (Fforde & Oscar 2020). He assembled mostly bird specimens, but some mammals, notably a Thylacine *Thylacinus cynocephalus* shot in 1903 (Greener 2012), now in the collection of Amgueddfa Cymru—National Museum Wales, Cardiff (J. Galichan *in litt*. 2025).

The putative Night Parrot in Greener's collection

On a typescript inventory produced around the time of acquisition in 1964 is listed a Night Parrot, given the registration number BMAG 1964Z24.13 (Fig. 1). No further information about the specimen is provided.

Periodic (2018–2024 by LL) and extensive (2025 by ALB & LL) searches in the collection failed to locate the specimen. It was also not mentioned by Watson (2011). No catalogue of

ISSN-2513-9894 (Online)



Z. 24'64/13

Aves
Night Parrot
Geopsittacus occidentalis
Psittacidae
Psittaciformes
W. W. Greener, St. Mary's Row, Birmingham 4
7th September, 1964
Australia
(Extinct?)
Insurance value £5

Figure 1. Extract from the typescript inventory of the Greener collection, courtesy of Birmingham Museum and Art Gallery.

(Courtesy of Birmingham Museum and Art Gallery)

262. Night Parrot (Geopsitacus Occidantalis) (Courtesy of Birmingham Museum and Art Gallery)

186

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Figure 2. The photograph of a Puerto Rican Parrot *Amazona vittata* included in place of the Night Parrot *Pezoporus occidentalis* in Greener (2012) also showing the incorrect attribution to the Birmingham Museum and Art Gallery.

the Greener collection exists, although Greener (2012) provided modern images (courtesy of the Birmingham Museum and Art Gallery) of 63 of the 104 bird specimens donated in 1964. The specimen identified as a Night Parrot in the caption is an *Amazona* parrot. Unlike all other photographs of birds in Greener (2012), it lacks a registration number in the caption, despite being attributed to the Birmingham Museum and Art Gallery (Fig. 2). A reverse image search revealed an identical photograph from a blog post, dated 2 October 2007, on the Korean website naver.com of a Puerto Rican Amazon *Amazona vittata* (Fig. 3) (Anon. 2007b), which reports that the images are 'mainly from Google' (Anon. 2007a). Further

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Figure 3. The photograph of a Puerto Rican Amazon *Amazona vittata* in Anon. (2007a); note the similarity with Fig. 2, especially the red branch between the toes.

searches using the tools TinEye and Google Reverse Image Search (Bitirim *et al*. 2020) failed to yield earlier results or an original source. Regardless, the image is not courtesy of the Birmingham Museum and Art Gallery, did not originate from Greener's collection, and is not of a Night Parrot. Why it was included by Greener (2012) is a mystery.

Did Greener's Night Parrot ever exist?

There are three potential explanations for the discrepancies highlighted above. First, there was a Night Parrot in the Greener collection that went missing at some point between 1964 and 2011/12 (when Watson 2011 and Greener 2012 were published). The second possibility is that there was a Night Parrot in the Greener collection and it is still in the museum but has been misplaced. These hypotheses appear doubtful as the collections were moved to the Birmingham Museum Trust's Museum Collection Centre starting in 2001, and no other bird specimens have been reported missing. Occasional searches (LL) and a thorough examination of the parrots (ALB) have not revealed the specimen. It was also not included in the list of non-UK birds in the BMAG collection (Watson 2011). The falsification (deliberate or accidental) of the identity and image attribution by Greener (2012) on the relevant typescript for BMAG 1964Z24.13 further supports the notion that the specimen never existed. As a book written mainly for firearms afficionados, there are several errors and incorrect conventions around the use and capitalisation of English common and scientific names (e.g., capitalised species epithets, 'Bower Bird' [*sic*], misspelt genera). It is conceivable that the image was included with the intent to deceive, thus elevating the

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status of the collection in the eyes of the reader. Equally, it may be deliberate mistake, if the museum could not locate the specimen to provide a photograph, an unattributed one may have been sourced from the internet without due care for its origin. In our online searches, the Puerto Rican Amazon image used is, however, never associated with the term 'Night Parrot'.

Lastly, the most parsimonious explanation is that there was never a Night Parrot in the Greener collection, and that a photograph of *Amazona vittata* was assigned to what was supposed to be a *Pezoporus occidentalis* in a truly spectacular error. *P. occidentalis* is a predominantly green parrot barred black and yellow and *A. vittata* is similarly predominantly green barred black but with no yellow and a red front. The discrepancy in size between Night Parrot and an *Amazona* is so great as to suggest nobody even considered size. It should be noted that all three specimens of *Amazona* parrots in the BMAG collection are present and accounted for, and none originated from Greener (Watson 2011).

Greener's time in Australia (1896–1907) post-dates surviving historical specimens (with collection dates)—all of which were taken before 1890 and mostly pre-1880 (Black 2012), and prior to the species' 'rediscovery' (Boles *et al*. 1994). Without any other archival documentation that the specimen existed (ideally a photo or evidence that the identification had been confirmed), we suspect that when the collection was donated in 1964, staff at the museum took the identifications on the word of the donor or a list of specimens. As with many collections managed by local authorities in the UK, taxonomic expertise may be limited to certain groups, and often one curator is responsible for all zoological or even natural science material, which make misidentifications less likely to be spotted and rectified.

We conclude that there is and probably never was an overlooked Night Parrot specimen in the BMAG collection. Those responsible for museum collections are respectfully advised to engage with taxonomic experts, especially when curating specimens of now extinct or endangered taxa.

Acknowledgements

We thank the British Library for making Greener (2012) available and two anonymous reviewers for improving this manuscript.

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ISSN-2513-9894
(Online)

The former range of Common Buttonquail *Turnix s. sylvaticus* supports its apparent conflation with Common Quail *Coturnix coturnix* in the Egyptian phonogram G-43

by Arturo Valledor de Lozoya & Nigel J. Collar

Received 27 November 2025; revised 17 April 2026; published 3 June 2026

http://zoobank.org/urn:lsid:zoobank.org:pub:F3289E47-2606-4487-A4E8-CCDB1A795FA5

Summary.—Ancient Egyptians made much use of birds in their hieroglyphic characters. One such character or phonogram, G-43 of Gardiner´s *Egyptian grammar*, has the appearance of a Common Quail *Coturnix coturnix* chick and represents the phoneme 'U' or 'W' (hence we refer to it here as the 'U-bird'). However, the Common Quail produces no sound approximating to 'U'. We speculate that the sound value of the glyph may derive from the Common Buttonquail *Turnix sylvaticus*, which closely resembles a small Common Quail and whose *huuu huuu huuu* call clearly reflects the phoneme 'U'. Even so, while migrant Common Quails were superabundant in ancient Egypt and remain heavily exploited for food today, the nominate subspecies of Common Buttonquail, although recorded in the western and central Mediterranean basin, has been thought absent from Egypt in both the distant and recent past. Nevertheless, an overlooked record from east of the Nile Delta in 1855 implies that within the past 200 years the species ranged across all North Africa. Moreover, Pliny the Elder's convincing record from Arles (France) 2,000 years ago equally implies a wider former range, probably related to wetter conditions throughout the Mediterranean basin in the past five millennia. Its year-round presence and extended breeding (hence calling) period could have made the species as familiar to ancient Egyptians as the seasonally abundant Common Quail, and we hypothesise that the two species are conflated in G-43. That *Turnix sylvaticus sylvaticus* may have provided a foundational element of the ancient Egyptians' system of communication adds to the case for preserving its last, near-extinct population, in a tiny coastal strip of central-western Morocco.

The importance of birds to ancient Egyptians is apparent from the fact that, in addition to the well-known deities Horus (a falcon), Thoth (an ibis) and Nekhbet (a vulture), no fewer than 211 avian species have been identified in artefacts of all kinds dating from the 44 centuries between the years 4000 BC and 395 AD (Wyatt 2012). Such evidence not only provides data on the distribution that some species had in the past but also indicates the extent of the reverence which ancient Egyptians showed towards birds (Houlihan 1986, Ikram 2005, Scalf 2012).

Unsurprisingly, then, birds served as an important source for hieroglyphic characters. Wallis Budge (1920) listed 96 glyphs of birds and 18 that represent parts of them. Gardiner (1957) reduced this list to 54 and eight respectively (Fig. 1). The most frequently used of Gardiner's 54 are G-1, G-17 and G-43. G-1, figured by an Egyptian Vulture *Neophron percnopterus*, represents the phoneme 'Ah', possibly associated with the high, open-vowelled calls emitted by some birds of prey. G-17 represents the phoneme 'M', based on the upper border of the facial disc of a Barn Owl *Tyto alba*. G-43 represents the phoneme 'U' or 'W' through a figure that we here term 'the U-bird' (Figs. 2–3). The ornithologist Brehm (1855), who visited Egypt in 1847, thought this figure represented the Egyptian Plover *Pluvianus*

ISSN-2513-9894 (Online)

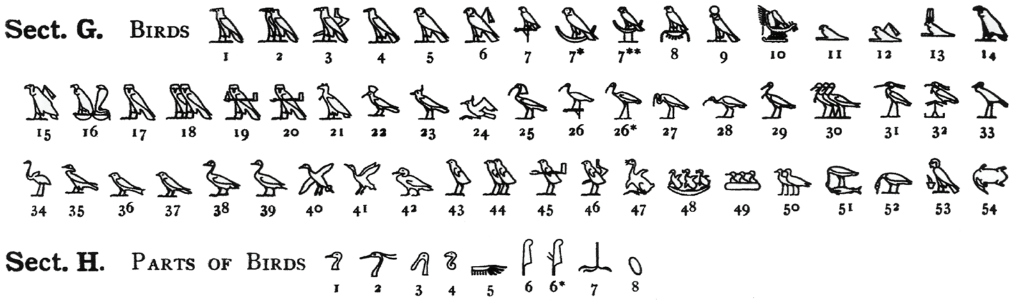

Figure 1. Glyphs representing birds or parts of them according to Gardiner's *Egyptian grammar*, with the U-bird at number 43.

Figure 2 (left). Cartouche of Pharaoh Khufu, the builder of the Great Pyramid, better known by his Greek name Cheops. Read from right to left it consists of the glyphs placenta (the circle, 'kh'), U-bird ('u'), horned viper ('f') and U-bird ('u') again. False door of the mastaba of Khufu-Ankh, Giza, Old Kingdom, 2465–2323 BC. Museum of Fine Arts, Boston (Joan Lansberry)

Figure 3 (right). Hieroglyphs including figures of 'U-birds'. Stele of Minnakht, chief scribe of Pharaoh Ay, New Kingdom, 1321 BC. Louvre Museum, Paris (Anon.)

aegyptius, a bird linked to the Nile ever since Herodotus reported that it cleans the mouths of crocodiles (Macaulay 1890). However, the non-ornithologists Wallis Budge (1920) and Gardiner (1957), who probably saw more images of the U-bird than Brehm, recognised the glyph's galliform appearance, the former venturing 'Chicken, quail (?). Phonetic value U', the latter noting: 'G-43: Quail chick. For unknown reason, phon. w.' Houlihan (1986) reported that during the Early Dynastic Period (3150–2700 BC) this glyph is recognisably a flightless bird, but that only around the start of the Fourth Dynasty in 2613 BC were images clear enough to establish its identity as the chick of the Common Quail *Coturnix coturnix* (Figs. 4–5).

Common Quails in Egypt

Ancient Egyptians considered Common Quails a delicacy for both the living and the departed. *The book of the dead* refers to quail among the food provisions for the afterlife (Wallis Budge 1898), and the *Papyrus Harris I* cites 21,700 quails among the offerings made by Ramesses III to the temple of Ammon at Karnak (Bailleul-LeSuer 2012). Herodotus, who visited Egypt around 460 BC, wrote that salted quails and small birds were a favourite food for Egyptians (Macaulay 1890). On migration quails appeared in unimaginable numbers: in spring they were hunted with nets on growing crops (Duell 1938; Fig. 6; also Parkinson

ISSN-2513-9894
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Figure 4 (left). Glyphs of quail-like chicks and other animals in a mural hieroglyph from the tomb of Pharaoh Sarenput II, Aswan, Middle Kingdom, 1990–1786 BC (Daniel Csörföly)

Figure 5 (right). Enlarged detail from Fig. 4 of a glyph G-43. The dorsal striping of the chick is stylised, as is the hind-toe, the latter suggesting Common Quail *Coturnix coturnix* over Common Buttonquail *Turnix sylvaticus* (Daniel Csörföly)

Figure 6. Bas-relief representing quail hunting with nets during the harvest. Mastaba of Mereruka, Sakkarah, Old Kingdom, 2305 BC. Plate from Duell (1938).

2008), and in autumn they were killed with sticks or caught by hand when flocks arrived exhausted after crossing the Mediterranean. The latter phenomenon was memorably reported both in the Bible, when a strong wind produced a wreck that left the birds piled 'two cubits [90 cm] deep' (Numbers 11.31), and by Pliny the Elder, when winds forced flocks to settle on the rigging and decks of ships in such quantities that the smaller vessels sank (Bostock & Riley 1855).

Nothing so dramatic has been documented since, although the numbers of birds taken for food appear little changed in 25 centuries. Whymper (1909) reported that the entire north coast of Egypt was full of nets for hunting quails and that in 1901 the country supplied five million of them to the English market alone. The wall of nets is still there, with two million quails being taken on the north coast of Sinai each year during 2002–11 and, by broadcasting calls of the species all night, 3.4 million in 2012 (Eason *et al*. 2016)—this latter number being higher than the lower estimate for the total number of birds breeding in western Russia (Burfield & von Bommel 2004). Thus, despite major changes in the terrestrial environment of Egypt since Pharaonic times, the economic and dietary importance of the species to Egyptians, ancient and modern, has remained remarkably stable. To recognise this is not to acquiesce in the continuing massive offtake of quails, which can no longer be justified as a matter of human subsistence and is now the subject of intense concern in Europe (Brochet *et al*. 2016, Elhalawani 2016); but it is to admit the enduring centrality of the species to Egyptian tradition.

Nevertheless, despite the quail's evident cultural importance in ancient Egypt, and the fact that most hieroglyphic illustrations show what resemble chicks of the species,

ISSN-2513-9894 (Online)

none of its calls resembles the phoneme 'U' or 'W'. Neither its well-known trisyllabic self-advertisement song, *whit-whitwit* (e.g. https://xeno-canto.org/245639)[1], nor its quieter guttural disyllabic *wra-wra*, which sometimes precedes the song but is considered a 'nocturnal flight call' (e.g. https://xeno-canto.org/730758), bears any likeness to that sound, and clearly flightless chicks will not produce it—hence, doubtless, the puzzlement ('for unknown reason') of Wallis Budge and Gardiner.

Common Buttonquails in the Mediterranean basin

A potential solution to this difficulty exists in the form of the Common Buttonquail (often called Andalusian Hemipode) *Turnix sylvaticus* (Valledor de Lozoya 2023a,b; Fig. 7), a species with a wide sub-Saharan and tropical Asian range but whose nominate subspecies occupies, or occupied, mainly coastal regions in the western and central Mediterranean basin (Taylor 1986, Debus 1996). Although belonging to a different order of birds (Charadriiformes vs. Galliformes), this species is an overall match not only for the Common Quail in size, appearance (except in lacking the hind-toe), habitat choice and secretive behaviour, but also for the U-bird, as its springtime song is a low, slow *huuu, huuu, huuu*…, similar to the sound

Figure 7. Common Buttonquail *Turnix sylvaticus* (above) and Common Quail *Coturnix coturnix* (below), subspecies of both uncertain (captive birds, Spain). A strong distinction between them, hard to see in the field, is the iris colour (Miguel Ángel Quevedo)

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[1] Two days after the revision of this paper was submitted, we were informed of the publication of a broad study of the evolution of writing (Morenz 2026) in which the song of the Common Quail is reported, by sources advertising or synopsising the book, to be the origin of the glyph's phonetic identity (e.g. Carvajal 2026). We are gratified to find this support for our tentative view that a connection might exist between the sound a glyph represents and the sound the animal depicted makes, but on the particular attribution we respectfully demur, simply owing to the extreme dissimilarity between the high whistling tone of the quail's song and the obvious sonority of the phoneme *uu*.

ISSN-2513-9894 (Online)

obtained by blowing gently across the neck of an empty glass bottle (e.g. https://xeno-canto.org/379220). The roles of the sexes are reversed in buttonquails (family Turnicidae), and while the males undertake all parental duties it is the larger, brighter-plumaged females that sing and defend the territory, having an enlarged trachea and inflatable oesophagus which allow them, with closed mouths, to produce deep ventriloquial booms, far-carrying yet often barely audible to human ears (Debus 1996).

This is not to seek to transfer the identity of G-43 from Common Quail to Common Buttonquail but rather to share it between them. The sound values of phonograms do not necessarily reflect the calls of the species represented, and establishing any such connection would require further investigation. Moreover, the depictions in phonograms do not necessarily represent one particular species. Indeed, this is our point: what we hypothesise here with G-43—that its typical image, with stub wings suggesting a chick and hindclaw indicating a galliform, involves a conflation of characters with a member of the charadriiform Turnicidae.

Nevertheless, if the problem of the Common Quail's misfit voice is overcome by associating the U-bird with a Common Buttonquail, another arises through the fact that the latter has, according to Gutiérrez-Expósito *et al*. (2011), never been recorded in Egypt. This would indeed constitute a significant difficulty, but it is not in fact quite accurate, as Heuglin (1856, 1873) saw it there, elaborating in the latter publication that (our translation):

> In the spring of 1855 I observed a bird of this species in a half-dry clover field in the province of Sharqia, in Lower Egypt; however, I was unable to get it to fly as it quickly ran into a dense undergrowth of date palms and so managed to escape.

Given Heuglin's (1873: 905–906) extensive familiarity with the Common Quail in Egypt and elsewhere, it is highly improbable that his identification was at fault in this encounter, which has major implications for the likely former range of the buttonquail. Sharqia is east of the Nile Delta, some 1,500 km east of Tripolitania, the easternmost point in the species' historical range as mapped in Gutiérrez-Expósito *et al*. (2011), and 1,000 km east of the Jebel Akhdar peninsula in Cyrenaica, mapped in Gutiérrez-Expósito *et al*. (2020b) based on their later reconsideration of Libyan records. One of those records may have been Heuglin's (1856) otherwise overlooked reference to buttonquails being 'frequently collected' in the Benghazi area.

Gutiérrez-Expósito *et al*. (2011) cited sources indicating that the species was also common in the mid-19th century on the coastal plains of northern Tunisia ('no fear of… becoming extinct': Whitaker 1905) and northern Algeria, as well as southern Sicily, where Doderlein (1869) could hunt 10–15 birds a day in the 1860s and Whitaker (1896) found it 'fairly plentiful' up to 1880. For Algeria Gutiérrez-Expósito *et al*. (2011) could also have cited Desfontaines (1789), who found the species 'rather common' near Algiers, and Malherbe (1843) and Loche (1858), who referred to the many specimens they respectively saw from and collected in that country. It was resident across northern Morocco (Vaucher & Vaucher 1915); near Tangiers it was reported to be (a) 'much less common' than the ('very abundant on passage') Common Quail (Irby 1895), and (b), probably in an interpretation of Irby, 'quite common' there (Hartert & Jourdain 1923). From these reports it can reasonably be speculated that 170 years ago the buttonquail had populations, not necessarily continuous but reasonably strong, distributed across all of North Africa.

The survival of these populations into at least the 19th century only increases the probability that their ancestors were far more widespread in the same region 25 centuries

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earlier. There is a single piece of evidence to support this supposition, provided by Pliny the Elder (Bostock & Riley 1855), who reported:

> There is a bird, found in the territory of *Arelate*, that imitates the lowing of oxen, from which circumstance it has received the name of *taurus*, although in other respects it is small in size.

This description fits the buttonquail, which is known to this day in Spanish by the name *torillo*, 'little bull' (del Hoyo & Collar 2014). Pliny's emphasis on its size excludes the Eurasian Bittern *Botaurus stellatus*, known in Spain as *avetoro*, 'bull bird' (see also Kinzelbach 1995). Incidentally, it seems quite likely that Pliny's information came from personal experience, since, in addition to other political and military positions, he had been procurator of *Gallia Narbonensis*, whose second main city in Roman times was *Arelate* (Arles), and, according to his nephew Pliny the Younger (Delaware 1879), it was his uncle's habit to rise long before dawn in order to study and write. Consequently, he could easily have heard the calls of buttonquails at daybreak.

However, Arles, in southern France, is 1,000 km north-east of Andalusia (once the European stronghold of the species), 1,000 km north-west of southern Sicily, and 750 km due north of Algiers (the type locality of the species). So far as is known, Common Buttonquail is sedentary around the Mediterranean basin and either a resident or a relatively short-distance migrant in sub-Saharan Africa, appearing or disappearing in some areas in response to changes in precipitation regimes (Taylor 1986). It is thus unlikely that the birds at Arles 2,000 years ago were isolated by any distance from other populations of the species, but rather were an extension of an Iberia-wide population that penetrated what is now southern France along the Catalan coast, although a connection through the Italian peninsula is also possible. In either case, the point is that the species would have been represented by populations far to the north of the records from which the maps of its 19th-century distribution have been constructed.

Paleoclimatic studies have shown that the Sahara was relatively well vegetated in the African Humid Period, 7000–3500 BC, followed by a steady desiccation into the hyper-arid conditions experienced today (Finné & Holmgren 2010, Brookfield 2011). Until the end of the Old Kingdom, around 4,000 years ago, what are currently deserts were savannas, so that next to the pyramids, which are today surrounded by bare dunes, there were scattered trees and scrub (Baha el Din 2012, Valledor de Lozoya 2023b). In such conditions it is reasonable to assume that the Common Buttonquail would have been widespread and frequent across North Africa throughout the Pharaonic period, mirroring the former distribution and abundance of the Northern Bald Ibis *Geronticus eremita* in Egypt (Janák 2010) and matching its presence in southern France, only 75 km from Arles (Mourer-Chauviré *et al*. 2006). Given that Common Quails for the most part then (as now) simply passed through Egypt in spring and autumn, and were otherwise largely absent, it is entirely plausible that the resident Common Buttonquails would have been as well known to the ancient Egyptians as Common Quails; and indeed, if their behaviour was similar to that described from present-day Morocco, where the breeding season lasts from February to October (Gutiérrez-Expósito *et al*. 2020a), the calls of the species would have been a familiar sound to farmers for three-quarters of the year.

Multiple identities and the fate of *Turnix sylvaticus sylvaticus*

Despite the relatively minor differences in morphology and rather significant ones in vocal and migratory behaviour, the ancient Egyptians apparently conflated the two species

ISSN-2513-9894 (Online)

as a single entity. There is no other glyph that resembles a Common Quail, and the fact that the wings (if shown at all) appear as stubs carries the implication, as Gardiner (1957) and Houlihan (1986) recognised, that the individuals depicted were chicks. Nonetheless, it may be legitimate to speculate that the stubs were simply a device to signal not chick status but *juvenile* status, perhaps then identifying the buttonquail, because it is slighter than the quail, as the latter's offspring.

This tentative interpretation of the glyph is prompted by evidence from nearer times. That buttonquails were thought to be juvenile quails was documented by the man who first obtained specimen material of the former for scientific study. In 1770–71 John White, then chaplain to the British garrison at Gibraltar, procured two skins of the scientifically undescribed three-toed quail, sent them to his brother Gilbert, and later gave one of them to Ashton Lever, founder of the Museum Leverianum (Holt-White 1901, Valledor de Lozoya 2023a). That specimen then became the basis for the description of the 'Gibraltar Quail' by Latham (1783), who 40 years later published information he had received from White about the species: 'The Spaniards often bring it to market, but [are] so ignorant of its true history, that they suppose it to be the young of the Common Quail, from its being a much smaller bird' (Latham 1823). White (1877) said the same in a letter when sending a third specimen in 1772 to Linnaeus, as did Machado y Núñez (1854), who saw specimens of buttonquails being advertised as quails in local food markets. In Morocco in April 2018 the owner of the land where the buttonquail survives, speaking with AVL, apparently believed something slightly different, that the local Common Quails (Arabic *shimana*) were dimorphic, being either light or dark (buttonquails being the paler, as first noted by Shaw 1738), unaware that the two forms were different species; indeed Arabic has no word for buttonquail.

Further confusion arose from the sexual differences in the buttonquail. On the page after his account of the Gibraltar Quail, Latham (1783) described the Andalusian Quail, based on a drawing given him by Thomas Pennant (to whom Gilbert White had sent both of his brother's first two specimens, so the model for the 'Andalusian Quail' was probably the specimen that did not go to Lever) (White 1877, Holt-White 1901). The geographical names Latham used were arbitrary, since the specimens both came from near the Rock, but the morphological distinction he detected between them reflects the difference between the sexes, apparent in the stronger rufous throat and breast of the larger, bolder-marked females (see fig. 3 in Gutiérrez Expósito *et al*. 2011). Thus 'Gibraltar Quail' was evidently a female, having the 'middle' of the breast 'a pale rust colour' while the 'Andalusian Quail' was a male, with just 'a yellow tinge' to this area (Latham 1783, 1823). The understandable but mistaken assumption of two species was then repeated by Gmelin (1789)[2], who, like Latham, called them *Tetrao gibraltaricus* and *Tetrao andalusicus*, and Temminck (1815), who called them *Hemipodius lunatus* and *Hemipodius tachydromus*. Indeed, the confusion persisted independently among Spanish hunters in Andalusia, who 'always declare there are two species' (Irby 1895).

The morphological crypsis and behavioural self-effacement which, alongside the convergent evolution and sexual dimorphism, have fuelled these various misinterpretations may also have contributed to the near-extinction of the subspecies endemic to the Palearctic, nominate *Turnix s. sylvaticus*. As Brehm (1861) observed: 'They live so secretively and are so difficult to see that it cannot be said whether they are scarce or abundant.' Over the course of the 20th century the almost non-existent profile of the species in Europe, as either a study animal or an object of conservation concern, allowed it to slip still further into ornithological

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[2] Gmelin's work, often dated 1788, was published on 20 April 1789 (Dickinson *et al*. 2011). There is no indication when in that year Desfontaines' paper was published, so it is possible that Gmelin's name has priority, but on the principle of prevailing usage it is now in any case a *nomen oblitum*.

ISSN-2513-9894
(Online)

Figure 8. Increasingly intensified agriculture occupied by the last known population of Common Buttonquail *Turnix sylvaticus* in Morocco (and of nominate *sylvaticus* in existence), April 2018 (Arturo Valledor de Lozoya)

oblivion. The alarm was finally sounded near-simultaneously by Violani & Massa (1993), who however offered no opinion on the threats involved, and Urdiales (1994), who judged Europe's population to comprise 'just 5–10 pairs', in Doñana National Park, Spain, blaming the situation on 'modern intensive agriculture, human settlement and the planting of trees, especially *Eucalyptus*'. These same factors, plus overgrazing, have been identified in more recent studies, which also established the species' apparent preference for 'temperate lowlands with a certain degree of humidity, mainly in coastal areas' (Gutiérrez-Expósito *et al*. 2020b). These pressures, perhaps compounded by hunting, have eliminated the species from '99.99%' of its original range, corralling it into a narrow strip of agricultural land (total area 4,675 ha; total population in 2017: 596) on the Atlantic coast of Morocco, itself succumbing to intensification (Gutiérrez-Expósito *et al*. 2019; Fig. 8). It surely only strengthens the case for vigorously and completely protecting this last population that it descends from the birds whose calls could have been one of the building blocks of the ancient Egyptians' extraordinary writing system.

Acknowledgements

We thank Joan Lansberry and Miguel Ángel Quevedo for permission to reproduce their photographs, Murray Bruce and Andy Elliott for comments on the dating of Desfontaines (1789) and Gmelin (1789), and David González for organising the 2018 expedition to the last refuge in Morocco of buttonquails that inspired AVL to propose the hypothesis herein. We express our great appreciation of the courteous and constructive commentaries on the submitted version of this paper by Egyptologists Linda Evans (Macquarie University) and Christopher Stimpson (Bird Group, Natural History Museum), which resulted in a significant reframing of our argument. Robert Prŷs-Jones was (and is) a most attentive and benevolent editor.

ISSN-2513-9894
(Online)

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ISSN-2513-9894
(Online)

A taxonomic revision of the Naked-faced Spiderhunter *Arachnothera clarae*

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Received 3 December 2025; revised 20 March 2026; published 3 June 2026

http://zoobank.org/urn:lsid:zoobank.org:pub:B7FFE631-C958-42B4-B6C7-9C850CBF5386

Summary.—The Naked-faced Spiderhunter *Arachnothera clarae* is endemic to the Philippines, traditionally in four subspecies: *A. c. luzonensis* on Luzon, *A. c. philippinensis* on Samar, Leyte and Biliran, *A. c. malindangensis* in western Mindanao and Basilan, and nominate *A. c. clarae* in eastern Mindanao. Descriptions of *A. c. luzonensis* have largely suggested a minor level of differentiation, but field experience with all taxa and inspection of specimens and photographs of live birds prompt a reconsideration of the evidence. Comparing adult males of *A. c. luzonensis* (*n* = 4), *A. c. philippinensis* (*n* = 11), *A. c. clarae* (*n* = 2) and *A. c. malindangensis* (*n* = 10) in five museums, plus a thorough review of online photographs of living birds, we find that *A.* [*c.*] *luzonensis* differs significantly in six morphological characters: bare bluish-grey lores (vs. mid-grey shading upwards to pinkish yellow in *A.* [*c.*] *philippinensis*, all blackish in *A. c. clarae* and *A. c. malindangensis*), a much shorter pale line along the commissure, softly grey-and-white-mottled (vs. slightly scaled olive-grey) underparts, bold pale upright bars on the median coverts, burnished chestnut (vs. olive-golden) fringes on the closed wing feathers, and a shorter bill. Moreover, *A.* [*c.*] *philippinensis* differs from *A. c. clarae* and *A. c. malindangensis* by the bare pinkish-yellow band extending from the lores over the forehead, paler loral colour, all-whitish (vs. sharply bicoloured) commissure line, and shorter tail. In strength and number these distinctions qualify *A.* [*c.*] *luzonensis* and *A.* [*c.*] *philippinensis* for species rank; and in the absence of any clear difference between specimens (including unmeasured females) *A. c. malindangensis* becomes a synonym of *A. c. clarae*.

The spiderhunters *Arachnothera* Temminck, 1826, are a generally distinctive and rather ancient clade within the sunbird family Nectariniidae, occupying a range in tropical (mainly south-eastern) Asia from India's Western Ghats to the Philippines and Java. They are characterised (relative to sunbirds) by their large size, sturdy physique, long bills and mostly drab plumages with no iridescence or sexual dimorphism. Drab plumage in both sexes may be an evolutionary consequence of biparental incubation, which is apparently autapomorphic in *Arachnothera*, whereas female-only incubation is widespread in the Nectariniidae (Cheke & Mann 2001, 2008, Moyle *et al*. 2011, Campillo *et al*. 2018, but see Rogalla *et al*. 2022).

For many decades following the appearance of the relevant volume of the Peters checklist (Rand 1967), the number of species in *Arachnothera* was stable at ten (e.g., Sibley & Monroe 1990, Inskipp *et al*. 1996, King 1997, Cheke & Mann 2001, 2008, Dickinson 2003, Clements 2007), but the figure rose to 13 following the split of Bornean Spiderhunter *A. everetti* (Sharpe, 1893) from Java's Streaky-breasted Spiderhunter *A. affinis* (Horsfield, 1821); and of Orange-tufted Spiderhunter *A. flammifera* Tweeddale, 1878, and Palawan Spiderhunter *A. dilutior* Sharpe, 1876, respectively, from the widely distributed Little Spiderhunter *A. longirostra* (Latham, 1790) (Moyle *et al*. 2011, AviList Core Team 2025).

ISSN-2513-9894 (Online)

Until those latter two splits, the Naked-faced Spiderhunter *A. clarae* Blasius, 1890, was the only *Arachnothera* species endemic to the Philippines, where it is known from Luzon (subspecies *A. c. luzonensis* Alcasid & Gonzales, 1968), Samar, Leyte and Biliran[1] (*A. c. philippinensis* (Steere, 1890)), Mindanao (nominate *A. c. clarae* in the south-east, and *A. c. malindangensis* Rand & Rabor, 1957, elsewhere) and Basilan (presumed *A. c. malindangensis*) (Dickinson *et al*. 1991, Cheke & Mann 2001, 2008, 2025). The first two taxa in the complex were described almost simultaneously, both at species rank. Blasius (1890) introduced *A. clarae* (on Mindanao) in a newspaper (see Rand 1955)—an unreasonable habit that spurred the creation of the British Ornithologists' Club (Collar 2024)—and, three months later, Steere (1890) described *A. c. philippinensis* (on Samar) as *Philemon philippinensis*. Much later, Rand & Rabor (1957) established *A. c. malindangensis* at subspecies rank (the second taxon on Mindanao), and Alcasid & Gonzales (1968) described *A. c. luzonensis* (Luzon), also at subspecies rank. Two years after the description of *A. c. luzonensis*, Amadon & duPont (1970: 12) corroborated its distinctiveness, reporting on two male specimens (DMNH[2] 3806, 3835) collected on Luzon in 1969, which 'agree with the original description [of *A. c. luzonensis*] and differ from the Mindanao and Negros [evidently a *lapsus* for Samar] birds.'

It appears that *A. clarae* had not been reported on Luzon prior to the collection (in 1965–66) of the material used to describe *A. c. luzonensis* (see Rand 1967: 286–287), and few additional specimens have been acquired in the subsequent decades, suggesting that the species might be uncommon on the island. During an intensive collecting expedition to Mt. Isarog National Park in the late winter and spring of 1988, Goodman & Gonzales (1990: 28) only encountered a single individual, 'at the end of a relatively undisturbed patch of forest at 450 m'. Rabor (1966) apparently overlooked the species during his field work at Mt. Isarog in spring 1961 (see also Rand & Rabor 1967, where Rabor's novelties from that expedition were described).[3] Gonzalez (1995) also failed to detect *A. c. luzonensis* during transect surveys near the type locality in May 1992. A report of the taxon during mist-net surveys at sites on Mt. Palay-Palay and at Indang, General Emilio Aguinaldo, Amadeo and Tagaytay City (Lagat & Causaren 2018), requires confirmation *fide* one of our reviewers, but there are currently photographs on Macaulay Library (www.macaulaylibrary.org) from well-watched localities within Metro Manila, Baras (Rizal) and Mt. Makiling (Laguna) plus, as noted below, many recent records on eBird.

Published descriptions of *A. c. luzonensis* have not suggested that it is particularly distinct. The diagnosis offered by Alcasid & Gonzales (1968) merely stated that it differs from Mindanao birds by 'having the back more brownish and the grey-brown of the breast darker', although in their description of the holotype the authors also mentioned that the breast has 'a mottled appearance'. After acquiring two *A. c. luzonensis* specimens that were collected in 1969 (DMNH 3806, 3835), duPont (1971) noted that the fringes of the flight feathers in *luzonensis* were 'burnt orange', with the 'chin, throat, and breast gray', this latter area being 'ashy olive, washed with olive green' (Steere 1890: 21) in *A. c. philippinensis* and 'olive-gray' (duPont 1971) in *A. c. malindangensis* and *A. c. clarae*. Kennedy *et al*. (2000) followed duPont (1971) in diagnosing *A. c. luzonensis* on its burnt-orange wing fringes and grey breast, describing these areas as respectively 'yellow olive' and 'brownish grey' in the other subspecies. Cheke & Mann (2001, 2025) diagnosed *A. c. luzonensis* by its burnt-orange

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[1] Dickinson *et al*. (1991: 387) expanded the range of *A. c. philippinensis* to Biliran based on a single sight record by the late Robert S. Kennedy (1948–2024). To our knowledge, the Biliran population has not been diagnosed via study skin comparisons.

[2] Museum acronyms are explained under Methods.

[3] There is a single record from Mt. Isarog in the eBird.org database (checklist S24832343) but the species' presence there has apparently not been confirmed with photos or specimens.

ISSN-2513-9894
(Online)

wing fringes and described its underparts as 'green, greyer on throat to breast, with dark centres to feathers giving indistinct streaking', while offering a variety of subtle distinctions (other than the bare forehead in *A. c. philippinensis*) between the other taxa. However, elsewhere (Cheke & Mann 2008) they reverted to duPont's (1971) simple 'burnt-orange edging of remiges, and grey breast' for *A. c. luzonensis*. Allen (2020) made two significant improvements by (1) indicating the mottled breast as a diagnostic character of the taxon, rather than just a feature of the holotype, and (2) pointing out the 'whitish inner [in fact outer] edges to [the] median coverts, appearing as [a] row of spots.' The latter character was inexplicably missed previously—it is present on the specimens duPont used for his description and measurements.

Even so, from personal experience (ROH) and the perusal of study skins and online photographs of living birds (NJC, MRH), we were concerned about the current arrangement of the forms of *A. clarae*. Noting that a molecular sample from Luzon was somewhat divergent from two samples from Mindanao (fig. 2 and Appendix in Moyle *et al*. 2011), we therefore undertook a review of specimen and photographic material in order to establish and articulate the basis for our unease. Hereafter, we use brackets to denote our principal hypotheses about the taxonomic ranks of *A.* [*c.*] *luzonensis* and *A.* [*c.*] *philippinensis*.

Methods

One of us (NJC) examined specimens of *A.* [*clarae*] in five natural history museums, listed here by the size of material represented: American Museum of Natural History (AMNH), New York; Delaware Museum of Natural History (DMNH), Greenville; Peabody Museum (YPM), Yale University, New Haven; Natural History Museum (NHMUK), Tring; and Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), Philadelphia (Table 1). MRH also examined the study skins in ANSP and DMNH and assembled the synonym lists in the Appendix. In addition, because the measurements provided by Alcasid & Gonzales (1968) were taken using different parameters from those in this study, the holotype of *A.* [*c.*] *luzonensis* was kindly measured to our specifications by Rolly C. Urriza at the Philippine National Museum (PNM), Manila. In each case, we used digital callipers to measure (to the nearest 0.01 mm) culmen from tip to front of skull, unflattened wing length (curved) and tail length (point of insertion to tip). Given that all acceptable specimens of *A.* [*c.*] *luzonensis* were male, we restricted our morphometric analysis to males except when comparing *A.* [*c.*] *philippinensis* with Mindanao taxa. This material, as well as the considerable series of images available online at the Macaulay Library (ML), Cornell Lab of Ornithology (www.macaulaylibrary.org), was scrutinised with a particular view to confirming diagnostic characters in the four taxa.

To help decide taxonomic rank under the Biological Species Concept, we employed the system of scoring in Tobias *et al*. (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in

TABLE 1

Tally of *Arachnothera* [*clarae*] study skins used in this study, arranged by sex (M + F) and repository (see Methods for museum acronyms). The measurement of the PNM specimen was provided by Rolly C. Urriza.

Taxon	**AMNH**	**DMNH**	**YPM**	**NHMUK**	**ANSP**	**PNM**	**Total**
A. [*c.*] *luzonensis*	2 + 0	2 + 0				1 + 0	5 + 0
A. [*c.*] *philippinensis*	3 + 2	1 + 1	2 + 2	4 + 1	1 + 1		11 + 7
A. c. clarae	1 + 1	1 + 1					2 + 2
A. c. malindangensis	3 + 3	3 + 2	4 + 4				10 + 9

ISSN-2513-9894 (Online)

body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g., a distinct hue rather than different colour) 2, and minor character (weak difference, e.g., a change in shade) 1; a threshold of 7 is set to allow species status, which cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two non-covarying biometric characters (both these and vocal characters assessed for effect size using Cohen's *d* where 0.2–1.9 is minor, 2.0–4.9 medium, 5.0–9.9 major and 10+ exceptional) and one behavioural or ecological character (allowed 1) may be counted. Notably, given how little is known about reproductive isolating mechanisms in these taxa, we avoided using a threshold based on the level of differentiation in sympatric congeners, or an arbitrary threshold of genetic divergence (Halley *et al*. 2017). In similar cases within *Arachnothera*, the Tobias *et al*. (2010) criteria have yielded strong support for the genetically driven splits of *A. flammifera* and *A. dilutior* from *A. longirostra*, but less so for the split of *A. everetti* from *A. affinis* (see del Hoyo & Collar 2016).

Vocal recordings of the *A.* [*clarae*] complex are few and, given that spiderhunters are oscine passerines, any interpretation would be laden with unrealistic assumptions (e.g., Halley *et al*. 2023, Halley 2025). Therefore, no attempt was (or could be) made to include acoustic characters in this analysis. However, ROH qualitatively reviewed his personal recordings of the taxa and was unable to discern, either by ear or on a sonogram, any difference between their common 'short buzz' calls (which are presumed to be innately acquired).

Results

Using the Tobias *et al*. (2010) criteria, the case for recognising *A.* [*c.*] *luzonensis* at species rank was very strong (Figs. 1–8). The taxon is differentiated from the other three taxa by a series of unique (autapomorphic) characters:

(i) pale bluish-grey lores (plush when viewed at short range) and narrow eye-rings (Figs. 4–8; Tobias score 3);

(ii) an obviously shorter pale line formed on the mandibles at the commissure, with a very short white line on the maxilla below the front of the eye and a longer pinkish line on the mandible beginning under the basal end of the nares and ending under the front edge of the eye, where it abruptly switches to a hard-to-distinguish black that continues under the eye, whereas the other taxa show this feature as a longer, bolder line, whitish (*A. c. philippinensis*) or bicoloured orange-and-whitish (Mindanao taxa) from under the nares to the rear of the eye, where it often has a slight upward angle (Figs. 4 and 6–20; score 2);

(iii) extensive pale grey-on-white mottling that extends from the throat to undertail-coverts, in clear contrast to the darker, more uniform olive-grey underparts of the other taxa, which appear very slightly scaled with fine dark shaft-streaks (Figs. 2 and 4–7; score 2);

(iv) short but bold whitish vertical bars (typically four, one per feather) on the median coverts (Figs. 1, 4–7; score 3);

(v) a strong pale burnished chestnut ('burnt orange'), rather than olive-yellow or -golden, wash to the fringes of the remiges in the folded wing (best seen in Figs. 4–7 vs. Figs. 13–16; score 2);

(vi) mean bill length around 5 mm shorter than (and not even close to an overlap with) means of the other three taxa (34.1 vs. 39.5 [three taxa combined]) (Table 2; despite the small sample [*n* = 4] we judge this striking discontinuity to warrant a score of at least 2).

Observing the rule in Tobias *et al*. (2010) that the scores of only three plumage differences may be counted, we are left with 3+2+3+2 = 10 for the taxonomic assessment of *A.* [*c.*] *luzonensis*, placing it well over the threshold for assigning species rank.

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Figure 1. Top to bottom: lateral view of AMNH specimens representing *Arachnothera* [*clarae*] *luzonensis* (807229), *A.* [*c.*] *philippinensis* (685526) and *A. c. clarae* (783711) (Nigel J. Collar)

Figure 2. Top to bottom: ventral view of same material as in Fig. 1 (Nigel J. Collar)

Figure 3. Top to bottom: dorsal view of same material as in Fig. 1 (Nigel J. Collar)

Figure 4. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *luzonensis*, Palo Alto, Rizal, Luzon, 29 January 2025 (Jeorge V. Lacson)

The morphological case for recognising *A.* [*c.*] *philippinensis* as a species is rather less categorical but still well founded. The taxon is distinguished from Mindanao birds by its (a) bare yellowish to pink frontal band running from the lores across the lower forehead (Figs. 1, 3, 9–14; score 3), (b) overall paler lores (tinged yellowish on the top edge; no score), (c) all-whitish vs. white-based orange commissure line (Figs. 9–20; score 2), (d) possibly slightly paler and less extensively grey-tinged underparts (Fig. 2; no score) and (e) shorter tail (effect size vs. Mindanao taxa [males] −2.03, Table 2; effect size vs. Mindanao taxa [8 vs.

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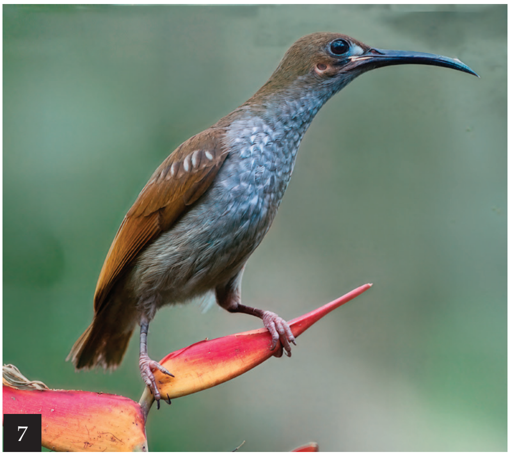

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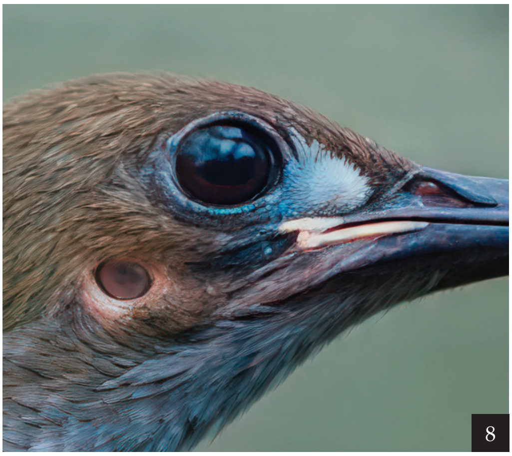

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Figure 5. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *luzonensis*, Palo Alto, Rizal, Luzon, 29 January 2025 (Jeorge V. Lacson; Macaulay Library ML629885229)

Figure 6. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *luzonensis*, Palo Alto, Rizal, Luzon, 14 January 2026 (Robert O. Hutchinson; Macaulay Library ML650870978)

Figure 7. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *luzonensis*, La Mesa Eco Park, Quezon City, Luzon, 26 December 2010 (Luis Limchiu; Macaulay Library ML379372871); see also Fig. 8.

Figure 8. Enlargement of Fig. 7 to show the lore in a 'Plush-lored Spiderhunter', our proposed English name for *Arachnothera* [*clarae*] *luzonensis* (Luis Limchiu; Macaulay Library ML379372871)

11 females] −2.12, score in both cases 2). The frontal band might be unique as a taxonomic character in birds: despite being considered 'barely visible in field' (Allen 2020), this unfeathered patch extends over the upper loral area, producing a very different appearance from the dark-lored *A. c. clarae* and *A. c. malindangensis* (Figs. 15–20). Viewed front-on, it makes such a strong signal in combination with the commissure lines (Fig. 12) that it might qualify as an exceptional difference; but we treat it as major, with medium scores for the commissure line colour and the shorter tail (3+2+2 = 7).

We failed to identify any plumage or morphometric character that distinguishes the Mindanao taxa *A. c. clarae* and *A. c. malindangensis* from each other. In the original description, *A. c. malindangensis* was diagnosed from '*philippinensis*' (*sic* = *A. c. clarae*) based on it 'having upper parts darker and duller green and under parts grayer with less of an

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TABLE 2

Morphometric variation (means and ranges in mm) in adult males of members of the *Arachnothera* [*clarae*] complex (see Table 1). See Methods for measurement techniques.

Taxon	***n***	**Bill length**	***n***	**Wing length**	***n***	**Tail length**
A. [*c.*] *luzonensis*	4	34.1 (32.9–34.6)	5	85 (83–88)	5	40 (35–41)
A. [*c.*] *philippinensis*	9	39.4 (38.7–40.8)	11	85 (81–91)	11	39 (38–41)
A. c. clarae	2	38.9 (38.7–39.1)	2	90 (89–91)	2	45 (42–47)
A. c. malindangensis	8	39.8 (37.1–42.8)	10	87 (84–90)	10	43 (40–47)


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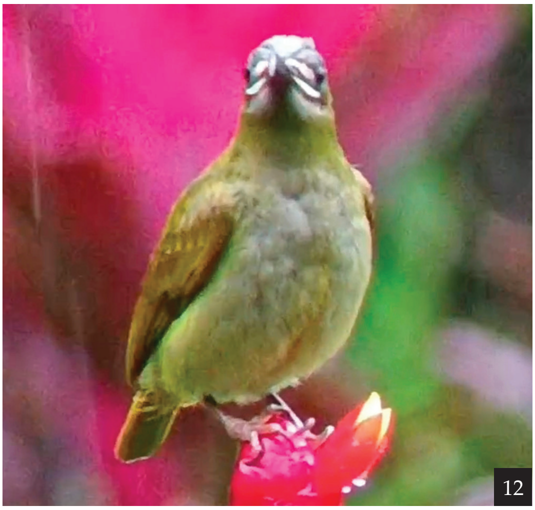
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Figure 9. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *philippinensis*, Leyte, 15 February 2025 (Dave John Limpangog)

Figure 10. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *philippinensis*, Anonang-Lobi Mountains, Leyte, 10 August 2024 (Ron Lemente Taraya; Macaulay Library ML622725859)

Figure 11. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *philippinensis*, Mahagnao Volcano Natural Park, Leyte, 10 February 2026 (Rose Ann Reynado; Macaulay Library ML650632763)

Figure 12. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *philippinensis*, Mahagnao Volcano Natural Park, Leyte, 10 February 2026; probably the same bird as in Fig. 11, with apparent lesion on right foot (Rose Ann Reynado; still from video on Macaulay Library ML650632982)

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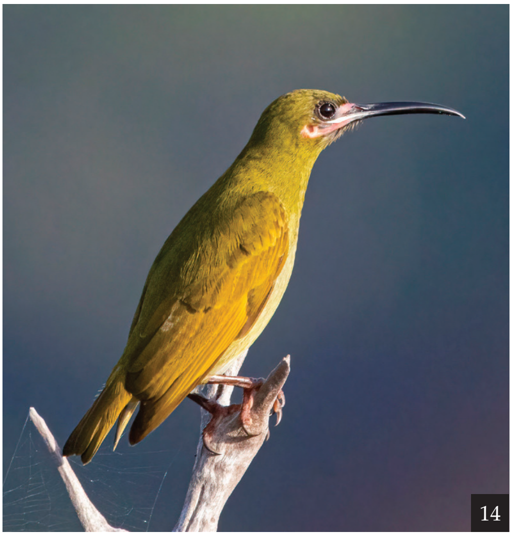
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Figure 13. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *philippinensis*, Mahagnao Volcano Natural Park, Leyte, 2 February 2026 (Vinz Pascua; Macaulay Library ML650427711)

Figure 14. Naked-faced Spiderhunter *Arachnothera* [*clarae*] *philippinensis*, Samar, December 2025 (Ron Lemente Taraya)

Figure 15. Naked-faced Spiderhunter *Arachnothera c. clarae*, Carmen, Davao City, Mindanao, 24 August 2021 (Allan Barredo; Macaulay Library ML364003601)

Figure 16. Naked-faced Spiderhunter *Arachnothera clarae malindangensis* (= *A. c. clarae*), Pasonanca Natural Park, Zamboanga City, Mindanao, 20 April 2024 (Kevin Pearce; Macaulay Library ML617702933)

Figure 17. Naked-faced Spiderhunter *Arachnothera clarae malindangensis* (= *A. c. clarae*), WSMU Experimental Forest, Zamboanga City, Mindanao, 4 May 2024 (Robert O. Hutchinson; Macaulay Library ML618709797)

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Figure 18. Naked-faced Spiderhunter *Arachnothera c. clarae*, Mt. Talomo, Davao City, Mindanao, 25 February 2023 (Robert O. Hutchinson; Macaulay Library ML571033051)

Figure 19. Naked-faced Spiderhunter *Arachnothera c. malindangensis* (= *A. c. clarae*), Pasonanca Natural Park, Zamboanga City, Mindanao, 19 May 2022 (Kevin Pearce; Macaulay Library ML451051711)

Figure 20. Naked-faced Spiderhunter *Arachnothera c. clarae*, Brgy. Carmen, Davao City, Mindanao, 24 August 2021 (Allan Barredo; Macaulay Library ML364003671)

Figure 21. Top to bottom: ventral view of two AMNH *Arachnothera clarae malindangensis* (709979, 801914) and two *A. c. clarae* (783711, 783710) (Nigel J. Collar)

Figure 22. Top to bottom: dorsal view of same material as in Fig. 21 (Nigel J. Collar)

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olive green wash' (Rand & Rabor 1957). However, the sampled material (Figs. 21–22) failed to support these distinctions, and indeed the label of DMNH 783710 (*A. c. clarae* based on geographical origin) bears the following pencilled note by Kenneth C. Parkes (1922–2007), an authority on Philippine birds and co-author of Dickinson *et al*. (1991): 'I cannot separate these [also DMNH 783711] from "malindangensis." KCP.'

Discussion

We recommend splitting the *A.* [*clarae*] complex into three species: (1) a monotypic 'Plush-lored Spiderhunter' *A. luzonensis*, type locality 'Dumagat, Pakil, Laguna, Luzon, Philippines' (Alcasid & Gonzales 1968: 129), endemic to Luzon; (2) a monotypic 'Bare-banded Spiderhunter' *A. philippinensis*, type locality 'Samar' (Steere 1890: 21), with records from Samar, Leyte and Biliran; and (3) a monotypic 'Dark-lored Spiderhunter' *A. clarae*, type locality Davao (Blasius 1890), with records from elsewhere on Mindanao and from Basilan, treating the undiagnosable *A. c. malindangensis* as a junior synonym of *A. clarae* (see Appendix). We discard the vernacular epithet 'naked-faced' with some regret, given its accuracy and the attention it draws to the most unusual loss of feathering on the sub-moustachial area and ear-coverts of all three taxa, but propose alternative names based on other diagnostic characters.

Alcasid & Gonzales (1968) offered a puzzlingly inaccurate and incomplete diagnosis of *A. luzonensis*; neither of their two diagnostic characters is apparent in the specimens examined for this study (Figs. 1–3). However, we identify the striking bluish-grey plush lores (not black as stated by Cheke & Mann 2001, 2025), mottled underparts and barred median coverts of *A. luzonensis* as diagnostic visual signals, found in no other spiderhunter. Combined with its much shorter commissure line, chestnut wing fringes and shorter bill—perhaps caused by ecological release in the absence of the smaller *A. flammifera* (mean bill length of three males from Samar in NHMUK = 32.0 mm), which is sympatric with *A. philippinensis* and *A. clarae*—these features represent a morphological divergence that is patently incompatible with the retention of subspecies rank.

There are far fewer photographs of *A. philippinensis* than the other two species, but we find that they all consistently show a plain whitish commissure line (Figs. 9–14), whereas every one of the several hundred images of *A. clarae* (*nunc sensu stricto*) on ML, when the commissure line is visible, reveals a contrasting bicoloured pattern: mostly orange with a white 'base'. This distinction between the taxa is very striking, and alongside the remarkable bare frontal band of *A. philippinensis* the two taxa offer no compelling semblance of conspecificity.

This proposed new arrangement leaves the Philippines with no fewer than five endemic (and indeed monotypic) spiderhunter species, an advance (as we believe it to be) which, being partly based on 'bare part' attributes, has only been possible thanks to the accessibility of colour photographs online. Clearly the surprising scarcity of *A. luzonensis* specimens has hindered taxonomic assessments of its rank. We know of only nine: two adult males in AMNH; two adult males in DMNH; one unsexed and anomalously blackish specimen in DMNH, which we intentionally left unsampled; one (sex unknown) in the University of Kansas Natural History Museum, Lawrence, which has been sampled for phylogenetic work (Moyle *et al*. 2011; J. W. Myles *in litt*. 2026, see below); and one adult male (the holotype, measured for this analysis) and two juvenile females in PNM. We were unable to locate any other specimens in an online search (VertNet.org) and uncovered nothing through an appeal on eBEAC, the electronic bulletin for European avian curators. Cheke & Mann (2025) asserted that 'Female [*A. luzonensis*] has [a] longer bill' but this was

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evidently a misplaced generalisation of data from the other taxa; to our knowledge, the material needed to justify such a statement does not exist.

The scarcity of specimens would seem to imply that the Plush-lored Spiderhunter might be a fairly rare bird, with potentially important implications for its conservation. In two decades of field work across the Philippines, ROH has encountered *A. luzonensis* less frequently than the other two species. However, eBird (2025) now maps at least 40 localities across Luzon, including some urban areas—although this only fuels the puzzlement over how it was so comprehensively missed by explorers and observers before the mid-1960s. Field studies to clarify the status and ecology of all 'naked-faced' spiderhunter populations would of course be of considerable value.

While this paper was in review, our taxonomic proposal (three-way split) appears to have passed its first scientific test. MRH received preliminary phylogenomic analyses from J. W. Myles (*in litt*. 2026), based in part on nuclear DNA sequences derived from ultraconserved elements, which reveal 'fairly deep divergence' and reciprocal monophyly among the three taxa, with *A. philippinensis* sister to *A. clarae*, and *A. luzonensis* sister to the *A. philippinensis* + *A. clarae* clade. These data provide independent corroboration and support for our morphology-based taxonomic revision. We look forward to seeing the full results of the molecular work and encourage additional sampling and analyses.

Acknowledgements

We are most grateful to Paul R. Sweet and Tom Trombone (AMNH), Kristof Zyskowski (YPM), Mark Adams and Hein van Grouw (NHMUK) and Nathan H. Rice (ANSP) for supporting our work in their collections; to Stephen Eccles for facilitating NJC's visits to these collections; to Rolly Urriza (PNM) for measuring the holotype of *A. luzonensis*; to Michaela Forthuber for the catalogue numbers (one of them added since Hinkelmann & Heinze 1990) of the syntypes of *A. clarae* in the Staatliches Naturhistorisches Museum Braunschweig (Germany); to John W. Myles and Rauri C. K. Bowie (Museum of Vertebrate Zoology, Berkeley, CA), for sharing their unpublished phylogeny of the *A.* [*clarae*] complex; to Allan Barredo, Jeorge V. Lacson, Luis Limchiu, Dave John Limpangog, Vinz Pascua, Kevin Pearce, Rose Ann Reynado and Ron Lemente Taraya for allowing the use of their photographs of wild birds; and to two referees for most helpful comments and insights.

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Appendix

Synonyms and taxonomic combinations of *A. luzonensis* (Luzon), *A. philippinensis* (Leyte, Samar, Biliran) and *A. clarae* (Mindanao, Basilan). For clarity of reference, for the latter two species, we provide the geographic range given by each author.

Arachnothera luzonensis Alcasid & Gonzales, 1968
Plush-lored Spiderhunter
(Figs. 4–8)

Arachnothera clarae luzonensis Alcasid & Gonzales, 1968: 129; duPont 1971: 385; Goodman & Gonzalez 1990: 28; Dickinson *et al*. 1991: 386; Gonzalez 1995; Kennedy *et al*. 2000: 327; Cheke & Mann 2008: 318; Allen 2020: 352. Holotype: PNM 4133, in Philippine National Museum (PNM), Manila, Luzon: collected by M. Celestino and J. Ramos, 25 May 1966, at 'Dumagat, Pakil, Laguna, Luzon' (Alcasid & Gonzales 1968).

Arachnothera philippinensis (Steere, 1890)
Bare-banded Spiderhunter
(Figs. 9–14)

Philemon philippinensis Steere, 1890 (Samar). Holotype: NHMUK 1896.6.6.482, adult female in the Natural History Museum (NHMUK), Tring: collected by J. B. Steere, 4 April 1888, at 'Catbalogan', Samar' (Warren & Harrison 1971: 433, Dickinson *et al*. 1991: 387).

Arachnothera philippinensis Ogilvie-Grant 1897: 237 (Samar, Leyte); Whitehead 1899: 231 (Samar, Leyte); McGregor & Worcester 1906: 100 (in part: Samar, Leyte, Mindanao); McGregor 1910: 665 (in part: Samar, Leyte, Mindanao).

Arachnothera clarae Mayr 1946: 233 (in part: Mindanao, Leyte, Samar); Mansibang & Senarillos 2022 (Leyte).

Arachnothera clarae philippinensis Rand 1967: 286 (Samar, Leyte); duPont 1971: 385 (Samar, Leyte); Dickinson *et al*. 1991: 387 (Samar, Leyte, Biliran); Kennedy *et al*. 2000: 327 (Samar, Leyte, Biliran); Cheke & Mann 2008: 318 (Samar, Leyte, Biliran); Allen 2020: 352 (Samar, Leyte, Biliran).

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Arachnothera clarae Blasius, 1890
Dark-lored Spiderhunter
(Figs. 15–20)

Arachnothera clarae Blasius, 1890 (Mindanao); Mayr 1946: 233 (in part: Mindanao, Leyte, Samar); Dickinson *et al*. 1989: 4 (Mindanao); Peterson *et al*. 2008 (Mindanao); Alviola *et al*. 2010 (Mindanao); Paguntalan *et al*. 2011 (Mindanao); Relox *et al*. 2011 (Mindanao); Cagod & Nuñeza 2012 (Mindanao); Paz *et al*. 2013 (Mindanao); Amaroso *et al*. 2022 (Mindanao); Pitogo *et al*. 2024 (Mindanao). Syntypes in Staatliches Naturhistorisches Museum Braunschweig, SNMB 63704 (male) and SNMB 16071 (female), ex. Adolph Nehrkorn (1841–1916): collected by Dr Platen and his wife ('und dessen Gemahlin'), 14 July and 18 September 1889, respectively, at Davao, Mindanao, Philippines (Hinkelmann & Heinze 1990; M. Forthuber *in litt*. 2025).

Arachnothera clarae malindangensis Rand & Rabor, 1957 (Mindanao); Ripley & Rabor 1961 (Mindanao): 12; Meyer de Schauensee & duPont 1962: 170 (Mindanao); Rand 1967: 287 (west Mindanao); duPont 1971: 385 (west Mindanao); Dickinson *et al*. 1991: 387 (north and west Mindanao, Basilan?); Kennedy *et al*. 2000: 327 (north and west Mindanao, Basilan?); Cheke & Mann 2008: 318 (north and west Mindanao, Basilan); Allen 2020: 352 (north-east, north and west Mindanao, Basilan). Holotype: FMNH 227696, adult male in the Field Museum of Natural History (FMNH), Chicago: collected by D. S. Rabor, 11 May 1956, at 'Masawan, Mt. Malindang, Zamboanga Peninsula, Mindanao' (Rand & Rabor 1957: 17, Dickinson *et al*. 1991: 387).

Arachnothera clarae clarae Rand 1967: 286 (east Mindanao); duPont 1971: 385 (east Mindanao); Dickinson *et al*. 1991: 387 (Mindanao); Kennedy *et al*. 2000: 327 (central Mindanao); Cheke & Mann 2008: 318 (central Mindanao); Allen 2020: 352 (central and south Mindanao).

ISSN-2513-9894 (Online)

A new and cryptic fantail species from the Babar Islands, Maluku Province, Indonesia

by *James A. Eaton & Alex J. Berryman*

Received 19 December 2025; revised 24 February 2026; published 3 June 2026

http://zoobank.org/urn:lsid:zoobank.org:pub:785C0729-CBF4-41B1-9883-C76D7D5532CB

Summary.—The Babar Islands, in the Banda Sea, Indonesia, have long been known to host several endemic avian taxa, but only recently have some of these been elevated to species rank. Here we investigate the internal taxonomy of Cinnamon-tailed Fantail *Rhipidura fuscorufa* P. L. Sclater, 1883, a monotypic passerine found on the Tanimbar Islands (from which it was described) and, 135 km to the west, on the Babar Islands. We compare differences between these populations using 19 specimens and 18 sound recordings, finding that while morphologically they differ subtly (Babar birds are slightly darker above, less extensively cinnamon below), the two have consistently different songs. Moreover, across 132 playback experiments, we find that both populations always ignore allopatric song but typically respond to sympatric song. On the basis that these lines of evidence likely represent barriers to reproduction, we consider the population on the Babar Islands to be taxonomically distinct from that on the Tanimbar Islands. In the absence of an available name, we describe it as a new species.

Cinnamon-tailed Fantail *Rhipidura fuscorufa* is endemic to Indonesia, where it occurs on the island groups of Tanimbar and Babar (Fig. 1; Coates & Bishop 1997, Eaton *et al*. 2016). It was described as a new species by Sclater (1883) from a series of specimens collected by

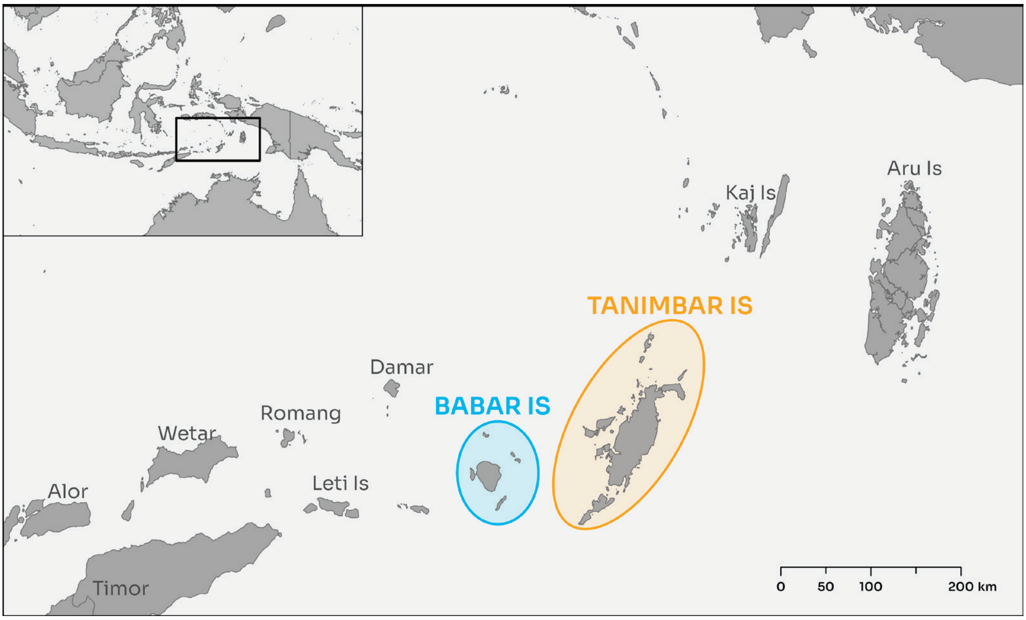

Figure 1. Map of the Banda Sea islands, highlighting the position of the Babar and Tanimbar Islands (the range of Cinnamon-tailed Fantail *Rhipidura fuscorufa*).

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H. O. Forbes on the Tanimbar Islands (type locality: 'Loetoe, Larat, and Moloe'). Fifteen years later, *R. fuscorufa* specimens were also procured from Babar (the main island in the Babar group and the only one subject to specimen collection) by C. Schadler and J. G. F. Riedel, but in reviewing their material Finsch (1901) concluded the specimens to be (translation our own): 'consistent with specimens from [the Tanimbar Islands]', a sentiment repeated twice by Hartert (1901, 1906), who also had available to him material from Babar collected by H. Kühn (Hartert 1906), and from the Tanimbar Islands collected by Kühn and W. Doherty (Hartert 1901). In the *c*.120 years that have followed, the prevailing taxonomic treatment in global and regional reference works has been to treat *R. fuscorufa* as a monotypic species (e.g. White & Bruce 1986, Dickinson & Christidis 2014, del Hoyo & Collar 2016, Eaton *et al*. 2016, 2021, BirdLife International 2025, AviList Core Team 2025), although it bears mention that Watson *et al*. (1986) made the unusual decision to treat *fuscorufa* as a subspecies of *R. rufiventris sensu lato* (Vieillot, 1818). This, however, finds little morphological support (Büttikofer 1893, Eaton *et al*. 2016, 2021, pers. obs.) and the only genetic dataset covering them (Nyári *et al*. 2009) found *R. fuscorufa* and *R. rufiventris* are not sister species (although only two of the *c*.20 taxa of *R. rufiventris*—*gularis* from New Guinea and *setosa* from New Ireland—were sampled).

The internal taxonomy of *R. fuscorufa* has scarcely been discussed since Finsch (1901) and Hartert (1901, 1906), based on museum specimens alone, considered Babar and Tanimbar populations to be identical. White & Bruce (1986) made no comment on it, and more recent authors who have mentioned the species (e.g. Bishop & Brickle 1998, Trainor & Verbelen 2013, Noske & Robson 2023) discuss only aspects of its ecology. Following JAE's first visits to Babar in 2011 and 2014, and being struck by apparently consistent differences in the song compared to Tanimbar birds, Eaton *et al*. (2016) commented that 'Marked vocal differences on Babar suggest undescribed taxon'. This was repeated in Eaton *et al*. (2021), but the issue has so far not been systematically investigated, which we rectify here.

Methods

Morphology.—All specimens housed at the American Museum of Natural History, New York (AMNH) and the Natural History Museum, Tring (NHMUK), were measured and inspected for plumage differences (full list of specimen numbers given in Appendix 1, Supplementary Material). All measurements were taken by AJB with digital callipers as: (1) wing length from carpal joint to the tip of the longest primary feather, while applying gentle pressure to the primary-coverts; (2) tail length from point of insertion to the tip of the longest tail feather, measured by inserting the ruler under the tail; (3) tarsus from the notch on the back of the intertarsal joint to distal base of the longest toe; and (4) bill length from the tip of the maxilla to the skull. Where appropriate, colours were compared and recorded using the standardised colour nomenclature of Smithe (1976). A total of 19 specimens was examined, comprising 12 from the Tanimbar Islands (five males, four females, three unsexed) and seven from the Babar Islands (two males, five females; all probably collected on the main island of Babar). We compared individual biometric traits using Welch's unpaired *t*-tests.

Vocal analysis.—Both populations of Cinnamon-tailed Fantails have three main vocalisations: (1) a song, most commonly heard at dawn and dusk, comprising a series of whistles organised into individual strophes; (2) a rambling, variable duet of upslurred and downslurred notes, often heard in response to playback; and (3) short, squeaky *yep* notes used as a contact call (Eaton *et al*. 2021; pers. obs.). For this study we concentrate on the first of these, assuming that differences in this vocalisation are most likely to function as a barrier to mate recognition and reproduction. (In our experience, there is no obvious difference in the contact calls of the species.) Across all recordings, as well as the authors' collective

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experience, we found no evidence for more than one song type on each island and believe them to be homologous vocalisations—this was directly tested in our playback experiments (see below). Excluding multiple recordings of the same bird, and recordings too poor in quality to measure, we collated 18 recordings of *R. fuscorufa* song: Tanimbar Islands (*n* = 11) and Babar (*n* = 7) (see Appendix 2, Supplementary Material). Recordings all came from Yamdena (the largest island in the Tanimbar group) and the main island of Babar—the other islands in the Tanimbar and Babar groups are very close to these islands and there is no known taxonomic variation in any species *within* each group; hence, we assume our sample to be representative of these island groups more broadly.

For each recording, we measured four temporal and three frequency parameters as follows: (1) number of notes in a strophe; (2) duration of the strophe; (3) mean time between notes; (4) mean length of notes; (5) minimum frequency of the strophe; (6) max. frequency of the strophe; and (7) the difference between the peak frequency of the first and last note in a strophe. Introductory call-like notes were excluded from all parameters as they are randomly variable in number in both populations. None of the measured parameters was found to be collinear using a Pearson's correlation test (threshold set at 0.7). Sonograms were visualised and measured in Raven Pro Version 1.6 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY) with an optimised window size of 1,048 for all recordings. In each recording, all strophes sung by the same bird were measured to account for individual variation and the mean of each parameter for each individual was calculated (thus giving each individual equal weight in the final sample). Differences were analysed statistically using Welch's unpaired *t*-tests applying a Bonferroni correction where the threshold for statistical significance is set at $p<0.05/n_v$. The magnitude of differences ('effect size') was measured using a Cohen's *d* coefficient. The diagnosability of each parameter was assessed using the Isler criterion (Isler *et al*. 1998), a test originally developed for vocal differences in suboscine passerines but which in recent years has also been used in several reviews of vocalisations in Asian passerines (e.g. Gwee *et al*. 2019, Yue *et al*. 2020, Berryman *et al*. 2025a). It is based on two conditions: (1) that there is no overlap between the ranges of measurements of the two populations being compared; and (2) that the means and standard deviations of the population with the smaller set of measurements (a; Babar) and the population with the larger set of measurements (b; Tanimbars) fulfil the following requirement: $\bar{x}_a + t_a SD_a \le \bar{x}_b - t_b SD_b$

where t_i refers to the t-score at the 97.5th percentile of the *t*-distribution for *n*–1 degrees of freedom (where *n* refers to the sample size of each population). Since this criterion does not allow for overlap between the two sets of measurements, the measurements of one taxon must be consistently greater than the other. The Isler criterion uses the standard deviation of the sample points rather than the taxon mean, and as such is more conservative than a Welch's unpaired *t*-test.

Playback experiments.—To test the significance of vocal divergence between populations explicitly, we conducted playback experiments over multiple years during recreational visits to Yamdena (Tanimbars) and Babar (JAE: 2014, 2016–18, 2022–24; AJB: 2024–25). Each playback experiment was independent and comprised a bird or pair being played a loud recording of either sympatric song (a recording of a bird from the same island) or allopatric song (from another island) for up to two minutes. Responses were recorded as: 'no response' (bird behaved indifferently to recording), 'moderate response' (e.g. bird called back but did not approach) or 'strong response' (e.g. bird approached the speaker and vocalised). In scenarios where birds were already vocalising before the playback experiment commenced, a positive response was noted only if the bird's behaviour obviously changed. Because Cinnamon-tailed Fantails are frequently found in pairs, two birds would often respond

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to a recording; in such instances, this was counted as only a single response. In total, 132 playback experiments were carried out ($n = 77$ Tanimbar Islands, $n = 55$ Babar Islands), with a roughly equal mix of allopatric and sympatric songs played (see Table 2).

Results

Morphology.—Populations of *R. fuscorufa* from the Tanimbar Islands and Babar are very similar in plumage but differ consistently in two minor characters. First, Tanimbar birds have their forehead, crown, nape, mantle and back slightly paler and warmer than those from Babar (Fig. 2), a feature we have also noted in the field and is apparent in photographs (Fig. 3). The upperparts of Tanimbar birds fall somewhere between Olive Brown (28) and Dark Brownish Olive (129), while those from Babar are closest to Vandyke Brown (121) (capitalised colours and codes correspond to Smithe 1976). Second, the cinnamon belly of Tanimbar birds averages slightly more extensive, usually reaching the lower breast; in Babar specimens, it appears to be always confined to the belly (Fig. 2). The two populations do not differ in any mensural character we measured (Table 1).

Vocal analysis.—The songs of the two Cinnamon-tailed Fantail populations differ considerably (Fig. 4). The song of Babar birds is typically a series of single whistles that rise in pitch towards the end, while that of Tanimbar birds typically combines very short with longer whistles rendering it a much more rhythmic cadence, and pitch typically goes up and down. While strophes of Tanimbar and Babar birds are similar in duration (mean 3.3 vs. 2.8 seconds respectively), those of Tanimbar birds contain significantly more notes (mean 10.7 vs. 6.6), which average shorter (mean 0.13 vs. 0.24 second) and have shorter gaps between them (mean 0.20 vs. 0.33 second)

Figure 2. Comparison of specimens of Cinnamon-tailed Fantail *Rhipidura fuscorufa* at the American Museum of Natural History, New York (AMNH): dorsal (top) and ventral (bottom). Birds from Babar (left side from left to right: AMNH 651390, 651388, 651389) and Tanimbars (right side from left to right: AMNH 651399, 651393, 651392). Note darker, less rufous/warm upperparts of Babar birds (Alex J. Berryman)

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Figure 3. Photographs of Cinnamon-tailed Fantail *Rhipidura fuscorufa* from Babar (left) and the Tanimbars (right), both taken in November 2022 (James A. Eaton)

TABLE 1

Measurements of *Rhipidura fuscorufa* from the Babar and Tanimbar Islands. Values in **bold** represent the mean of each character (rounded to nearest mm) with standard deviation; parenthetic values are the range. In no character did the mean between sexes or populations differ statistically. *The combined total for specimens from the Tanimbar Islands includes three unsexed specimens.

Population		Wing	Tail	Bill	Tarsus
Tanimbar Islands	Males (*n* = 5)	**86 ± 1.0** (85–87)	**85 ± 2.9** (82–88)	**19 ± 0.4** (19)	**13 ± 0.4** (13–14)
	Females (*n* = 4)	**84 ± 0.1** (84–85)	**83 ± 0.9** (83–84)	**19 ± 0.4** (19)	**14 ± 0.8** (13–14)
	Combined* (*n* = 12)	**85 ± 1.6** (82–87)	**85 ± 3.9** (81–89)	**19 ± 0.3** (19)	**14 ± 0.5** (13–14)
Babar Islands	Males (*n* = 2)	**84 ± 3.3** (82–87)	**82 ± 4.3** (79–85)	**19 ± 0.6** (19–20)	**14 ± 0.1** (14)
	Females (*n* = 5)	**85 ± 1.4** (84–87)	**85 ± 5.5** (78–93)	**19 ± 0.2** (18–19)	**13 ± 0.5** (13–14)
	Combined (*n* = 7)	**85 ± 1.8** (82–87)	**84 ± 5.1** (78–93)	**19 ± 0.4** (18–20)	**14 ± 0.5** (13–14)

(Table 2). The minimum and max. frequencies of the two populations are similar, but the structure of notes is very different. While the pitch of Tanimbar strophes is fairly level (or fluctuates randomly), songs of Babar birds ascend in pitch (Fig. 4). This results in a small difference in the peak frequency of the first and last notes in Tanimbar birds (mean 85 Hz; range 0–290 Hz), but a large one in Babar birds (mean 593 Hz; range 459–689 Hz). Overall, the impression—to the human ear—is of two very different songs.

In statistical comparison, the two populations are significantly different in four of the seven vocal parameters measured, and three of these prove 'Isler' diagnosable: (i) mean time between notes, (ii) mean length of notes, and (iii) delta peak frequency between the first and last notes (Table 2). These same three parameters also had very high effect scores of

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TABLE 2

Mean and standard deviation (in **bold**), and range (in parentheses) of each vocal parameter of Tanimbar and Babar populations of Cinnamon-tailed Fantail *Rhipidura fuscorufa*. The p-values represent the statistical probability of differences in the mean between the two populations using Welch's unpaired t-tests, where * denotes that the significance threshold is met with a Bonferroni correction. The magnitude of differences (effect size) was measured using Cohen's d coefficient. The diagnosability of parameters was analysed using the Isler criterion (Isler *et al*. 1998), where YES = diagnosable.

Population	Number of notes in a strophe	Length strophe (s)	Mean time between notes (s)	Mean length of notes (s)	Minimum frequency of strophes (Hz)	Max. frequency of strophes (Hz)	Delta peak freq. first and last note (Hz)
Tanimbars ($n = 11$)	**10.7 ± 2.7** (8–18)	**3.3 ± 0.7** (2.3–5.1)	**0.20 ± 0.02** (0.17–0.24)	**0.13 ± 0.02** (0.11–0.17)	**1,620 ± 104** (1,333–1,699)	**2,207 ± 306** (1,957–2,924)	**85 ± 87** (0–290)
Babar ($n = 7$)	**6.6 ± 1.2** (5–9)	**2.8 ± 0.6** (2.1–3.9)	**0.33 ± 0.03** (0.30–0.39)	**0.24 ± 0.04** (0.19–0.29)	**1,579 ± 53** (1,510–1,652)	**2,364 ± 63** (2,270–2,466)	**593 ± 73** (459–689)
Statistics	$p < 0.001$* $d = 1.8$ Isler: NO	$p = 0.128$ $d = 0.8$ Isler: NO	$p < 0.001$* $d = 5.4$ Isler: YES	$p < 0.001$* $d = 3.8$ Isler: YES	$p = 0.287$ $d = 0.5$ Isler: NO	$p = 0.127$ $d = 0.6$ Isler: NO	$p < 0.001$* $d = 6.2$ Isler: YES

TABLE 3

Results of playback experiments on Cinnamon-tailed Fantails *Rhipidura fuscorufa* being played sympatric or allopatric song (see Methods). Values in **bold** represent response scores, calculated as the proportion of birds subjected to experiments that responded to playback of each song type. Total sample sizes in parentheses. SR = strong response, MR = moderate response, NR = no response. Shading denotes the results of allopatric playback experiments.

		Song played	
		Tanimbar	**Babar**
Population tested	**Tanimbar**	**0.82** ($n = 38$) 18 SR, 13 MR, 7 NR	**0.00** ($n = 39$) 39 NR
	Babar	**0.00** ($n = 25$) 25 NR	**0.85** ($n = 30$) 12 SR, 14 MR, 4 NR

5.4, 3.8 and 6.2 respectively (Table 2). For context, Cohen (1988) described effect sizes greater than 0.8 as large, whilst Tobias *et al*. (2010) used higher thresholds of 2–5 as 'Medium' and 5–10 as 'Major'. The two populations are clearly separated in PCA space (Fig. 5); a PCA variance summary table for bioacoustic data is provided in Appendix 3.

In addition to the sample available to analyse, on visits over many years to the Tanimbar Islands (JAE: 2011, 2014, 2016–18, 2022–24, AJB: 2024–25) and Babar Islands (JAE: 2011, 2014, 2016–18, 2022–24, AJB 2025), we have heard dozens of birds singing strophes consistent with those described here, with neither population showing much variation.

Playback experiments.—Populations of *R. fuscorufa* on the Babar and Tanimbar Islands can perfectly discriminate sympatric from allopatric song; in all instances there was no response when birds from the Babar ($n = 25$) and Tanimbar Islands ($n = 39$) were played allopatric song. Conversely, birds usually (>80% of occasions) responded to playback of sympatric song (Table 3).

ISSN-2513-9894
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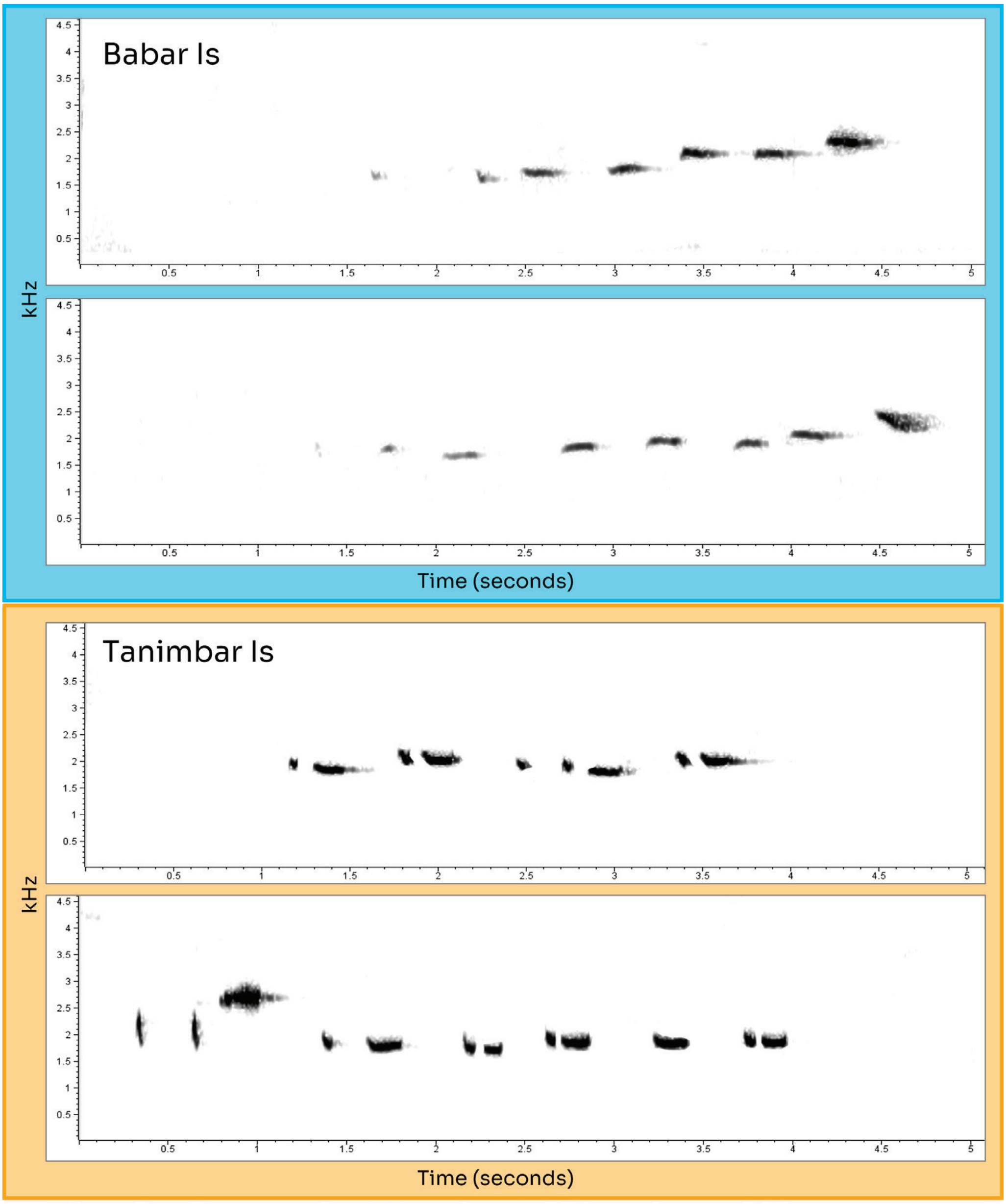

Figure 4. Example spectrograms of Cinnamon-tailed Fantail *Rhipidura fuscorufa* song. From top to bottom: Babar XC 161447 (Frank Lambert), XC 939421 (Philippe Verbelen); Tanimbars XC 161629 (Frank Lambert), ML 613983295 (Andrew J. Spencer). Sonograms were visualised in Raven Pro Version 1.6 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY) with an optimised window size of 1,048 for all recordings.

Discussion

Despite currently being treated as monotypic, our data find discrete differences between Tanimbar and Babar populations of *R. fuscorufa*. Morphologically the two populations differ subtly in upperpart coloration, and vocally they are highly divergent, with strong evidence from playback experiments that differences in song are strong enough to provide a pre-

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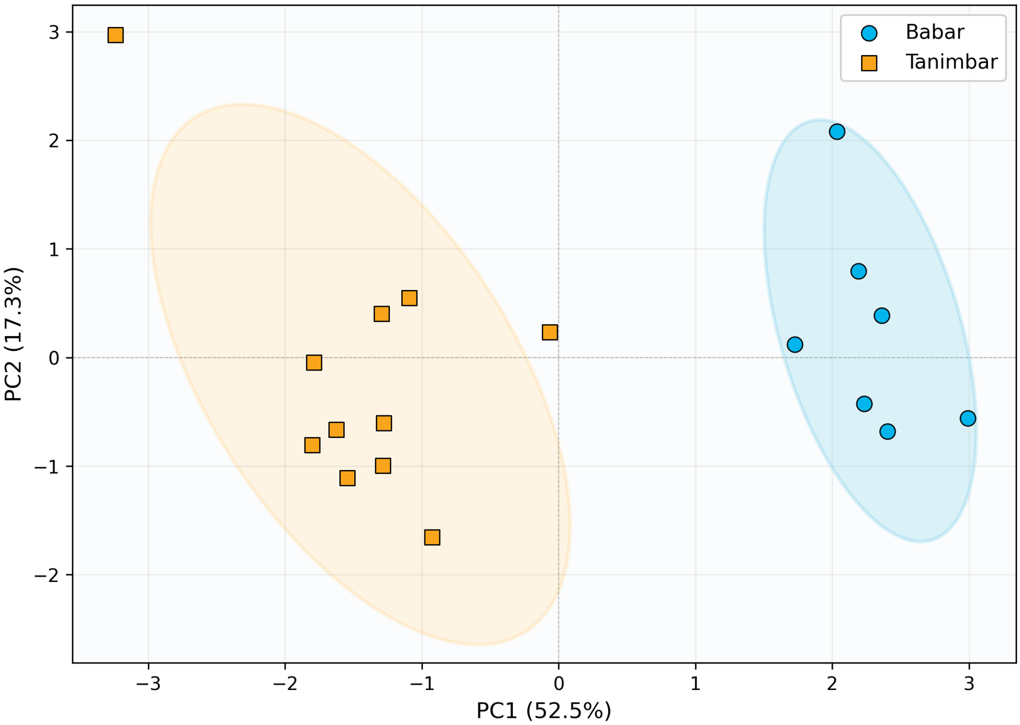

Figure 5. Principal component analysis (PCA) biplot for all vocal parameters (see Methods) showing differences in populations of Cinnamon-tailed Fantail *Rhipidura fuscorufa* on the Tanimbar Islands and Babar. Explained variance for each axis is given in parentheses.

mating reproductive barrier. On this basis we consider that populations of *R. fuscorufa* on Babar merit taxonomic separation from those on the Tanimbars. We are unaware of an available name for the Babar population, and describe it here as:

Rhipidura laguceria sp. nov.

Holotype.—American Museum of Natural History, New York (AMNH 651390), male collected by C. Schadler, at Tepa, Babber [Babar] (07°52′06.3″S, 129°35′43.7″E), Indonesia, on 10 April 1898 (Fig. 2).

Paratypes.—AMNH 651388, female collected by H. Kühn on 7 September 1905 at Tepa, Babber [Babar]; AMNH 651389, female collected by H. Kühn on 21 August 1905 at Tepa, Babber [Babar] (Fig. 2).

Diagnosis.—Differs from Tanimbar *R. fuscorufa* in its consistently darker forehead, crown, nape, mantle and back that are often discernible in the field (pers. obs.); it also has, on average, less extensive buffish on the underparts, being largely confined to the belly (not extending to the lower breast). The most pronounced difference, however, is in the two species' song: *R. fuscorufa* delivers strophes of 8–18 staccato whistles which randomly change in pitch, while *R. laguceria* emits a series of 6–8 notes that steadily ascend in pitch (Fig. 4). Birds on each island are unresponsive to allopatric song.

Northern Fantail *Rhipidura* [*rufiventris*] *hoedti* (of Romang, Damar, Leti, Moa and Sermata) and *R.* [*r.*] *assimilis* (Kai Islands)—sometimes recognised specifically as Banda Sea Fantail and Kai Fantail respectively (Eaton *et al*. 2016, 2021, del Hoyo & Collar 2016)—has an obvious white-streaked grey breast-band, greyer head and upperparts (with a much

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broader supercilium in *assimilis*), plain wings lacking extensive cinnamon, much less richly coloured belly (appearing almost whitish in *hoedti* and pale buff in *assimilis*) and white (not cinnamon) outertail feathers. They also have very different vocalisations (Eaton *et al*. 2021).

***Description of holotype*.**—Forehead, crown, nape, ear-coverts, mantle and back Dark Brownish Olive (129); feathers above front of eye narrowly tipped white to form an inconspicuous white eyebrow (more noticeable on right side than left side). Throat unmarked white; breast feathers also white with very narrow variably brownish tips and margins, giving faintly scalloped appearance. Blends to cinnamon on rest of underparts (in shade closest to Yellow Ochre 123C, but marginally paler) including flanks and vent. Primaries Dark Brownish Olive (129), slightly paler on undersurface. Secondaries same colour but outer margin Cinnamon (123A) becoming incrementally broader towards inner secondaries (ss7–9), which have almost their entire outer margin also Cinnamon; inner margin of these feathers very narrowly fringed Pale Pinkish Buff (121D). Primary-coverts and alula Dark Brownish Olive (129); greater coverts same but outer margin broadly fringed Cinnamon. Lesser and median coverts Dark Brownish Olive, some feathers with narrow Cinnamon tips. Underwing-coverts Cinnamon. Rump and uppertail-coverts Dark Brownish Olive, latter with Clay Color (123B) tips. Tail: rr1–2 are Fuscous (21); r3 pair with some Cinnamon (123A) at the tip; rr4–6 entirely Cinnamon. Bare parts all dark post-mortem (original colours unknown).

***Measurements of holotype*.**—Wing 86.6 mm, tail 85.1 mm, bill (to skull) 18.6 mm, bill width (at nostril) 6.0 mm, bill depth (at nostril) 4.3 mm, tarsus 13.8 mm.

***Variation in the type series*.**—Variation within specimens inspected (including those not designated as paratypes) minimal. AMNH 651388 differs from the holotype only in having cinnamon parts of wing fractionally paler (but still closest to Cinnamon 123A) and prominent white eyebrow on both sides. Scalloping on lower breast slightly less prominent. Iris, feet and bill documented as black on label. AMNH 651389 like AMNH 651390 but white eyebrow less prominent on both sides of head and does not extend behind the midpoint of the eye. Slightly broader Pale Pinkish Buff (121D) inner margins of secondaries.

***Measurements of paratypes*.**—AMNH 651388 (female) wing 87.4 mm, tail 93.0 mm, bill (to skull) 18.4 mm, bill width (at nostril) 6.2 mm, bill depth (at nostril) 4.7 mm, tarsus 13.4 mm; AMNH 651389 (female) wing 84.9 mm, tail 87.6 mm, bill (to skull) 18.8 mm, bill width (at nostril) 6.6 mm, bill depth (at nostril) 4.2 mm, tarsus 13.5 mm.

***Geographic distribution*.**—Endemic to Babar, Indonesia, and perhaps occurs too on the island's five small satellites, although these have not been explored ornithologically.

***Etymology*.**—Because the pleasing song of this taxon is its most distinctive attribute, we name the species for its vocalisations (*lagu ceria* = Indonesian for 'cheerful song'). We employ the name as a noun in apposition.

***Vernacular names*.**—While the English names 'Tanimbar Fantail' and 'Babar Fantail' are ostensibly appropriate for *R. fuscorufa s. s.* and *R. laguceria* respectively, the Tanimbar islands host two other sympatric fantail species—Supertramp Fantail *R. semicollaris* and Long-tailed Fantail *R. opistherythra*—the second of which is also endemic to the islands. Accordingly, we prefer the English names 'Trembling Fantail' for *R. fuscorufa* and 'Cheerful Fantail' for *R. laguceria*, given that their distinctive vocalisations have led us to propose separating them taxonomically.

***Taxonomic rank*.**—In describing *R. laguceria* as a species we follow a modern interpretation of the Biological Species Concept whereby we attempt to infer reproductive incompatibility (*sensu* Helbig *et al*. 2002) by combining morphological and bioacoustic data. If considering its minor morphological divergence alone, *R. laguceria* would probably most

ISSN-2513-9894
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appropriately be accorded subspecific rank. However, in our view the substantial and consistent vocal differences of the two populations render them better treated as species.

Using bioacoustic data alone—or as the dominant data type—to infer species limits in oscines remains exceptional, largely because oscine song is generally thought to be learned, not inherited, and differences between populations might therefore be phylogenetically less informative (Marler & Slabbekoorn 2004, Touchton *et al*. 2014). Nevertheless, oscines regularly discriminate behaviourally against allopatric song (e.g. Soha & Marler 2000, Berryman *et al*. 2025a) and vocal divergence has been used increasingly to advocate for species rank in oscines, even when morphological differences are absent or minor (Freeman & Montgomery 2017); for example, in Eastern *Phylloscopus orientalis* and Western Bonelli's Warblers *P. bonelli* (Helb *et al*. 1982), Karamoja *Apalis karamojae* and Maasai Apalises *A. stronachi* (Boesman & Collar 2023), Little *Bradypterus baboecala* and Highland Rush Warblers *B. centralis* (Dowsett-Lemaire 2022), Javan *Myiomela diana* and Sumatran Robins *M. sumatrana* (Ng *et al*. 2020), Seram *Hypsipetes affinis* and Ambon Golden Bulbuls *H. flavicaudus* (Berryman *et al*. 2025a) and Banda *Myzomela boiei*, Tanimbar *M. annabellae* and Babar Myzomelas *M. babarensis* (Berryman *et al*. 2025b). The vocalisations of *R. laguceria* and *R. fuscorufa* differ to a degree comparable to these examples.

In addition to the statistical comparison of measured bioacoustic parameters, we explicitly tested the ability of Babar and Tanimbar populations to identify sympatric song. Across 132 playback experiments, we determined that Babar birds are easily able to discriminate sympatric from allopatric song, suggesting that these differences are biologically relevant and indicative of reproductive incompatibility (Alström & Ranft 2003, Remsen 2005, Brambilla *et al*. 2008). In this regard, we agree with Freeman *et al*. (2017) that 'taxon pairs that are currently ranked as subspecies but that largely ignore song from allopatric populations merit recognition as distinct biological species'.

No genetic data are currently available to support or refute our suggestion of species rank. The only published phylogeny to include *R. fuscorufa s. l.*—published by Nyári *et al*. (2009)—only sampled from the population on the Tanimbar Islands. Future genetic enquiry is naturally desirable; however, its absence does not, in our view, provide a barrier to species rank given the significance of the vocal differences outlined above.

From a yardstick perspective, other fantail taxa have recently been split as species with similar justification to that we offer above. Both Eaton *et al*. (2016, 2021) and del Hoyo & Collar (2016) independently used similar lines of evidence to divide 'Northern Fantail' *R. rufiventris* into multiple species, whilst Rheindt *et al*. (2020) described Peleng Fantail *R. habibiei* as a species separate from the morphologically very similar Sulawesi *R. teysmanni* and Taliabu Fantails *R. sulaensis* in part because of its distinctive vocalisations. Vocalisations were also the main line of evidence that led del Hoyo & Collar (2016) to split the visually almost identical Mindanao *R. superciliaris* and Visayan Blue Fantails *R. samarensis* (see also Boesman 2016), and were also cited as a key reason for separating Streaked Fantail *R. verreauxi* into three and Brown Fantail *R. drownei* into two (del Hoyo & Collar 2016, AviList Core Team 2025).

Conservation status.—*R. fuscorufa sensu lato* is currently listed as Least Concern on the IUCN Red List (BirdLife International 2025). Following its division, *Rhipidura fuscorufa s. s.* and *R. laguceria* naturally have much smaller ranges which meet the initial thresholds for listing as threatened under Criteria B1 and B2 of the IUCN Red List (IUCN 2012); however, both species are highly tolerant of habitat degradation (the only plausible threat), and are commonly found in edge habitats, clearings and glades, as well as scrub with taller mango trees (Trainor & Verbelen 2013; pers. obs.). Indeed, both fantails seem to favour heavily modified habitats and shun closed-canopy forests. Accordingly, neither species meets any

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of the subcriteria for listing as B1 or B2, and should therefore continue to be listed as Least Concern.

Avian endemism on Babar.—Babar and its five satellites have always been isolated from other Banda Sea islands by virtue of the deep seas surrounding them. Given this isolation, it is perhaps unsurprising that the island has an endemic component to its avifauna, although only recently, with the advent of molecular and bioacoustic approaches, has this been fully recognised. Babar was first explored ornithologically in the 1860s—though more substantially collected in the 1880s and 1890s—but this work ended abruptly in 1905 when Kühn's local workers left due to 'hostile behaviour of some of the natives' (Hartert 1906, Trainor & Verbelen 2013). These early efforts resulted in seven bird taxa being described as endemic to Babar, all at subspecies rank: Little Bronze-cuckoo *Chrysococcyx lucidus salvadorii*, Southern Boobook *Ninox boobook cinnamomina*, Supertramp Fantail *Rhipidura semicollaris reichenowi*, Timor Stubtail *Urosphena subulate advena*, Pied Bushchat *Saxicola caprata cognatus*, Snowy-browed Flycatcher *Ficedula hyperythra audacis* and Golden Whistler *Pachycephala pectoralis sharpei* (per Eaton *et al*. 2021).

More than 100 years passed before ornithologists revisited Babar, when P. Verbelen and C. Trainor explored the island—and several others in the Banda Sea—in 2009 and 2011 respectively, with the aim of improving knowledge on the island's birds, including their vocalisations and taxonomy (results published in Trainor & Verbelen 2013). In October 2011, a Birdtour Asia group visited the island for a day, since when at least 16 birdwatching tours have visited Babar and occasionally sound-recorded the island's birds.

Although Babar had historically not been considered to host any endemic *species*, this has begun to change. Having been first collected in 1883—and described a year later (Meyer 1884)—genetic analysis uncovered unexpectedly deep divergence between Babar's endemic whistler taxon (*sharpei*) and others in the 'Golden Whistler' complex (Jønsson *et al*. 2014), leading Eaton *et al*. (2016) to propose it as an endemic species, Babar Whistler *Pachycephala sharpei*, a position now accepted by AviList Core Team (2025). Berryman *et al*. (2025b) very recently described Babar Myzomela *Myzomela babarensis* as a species new to science based on very distinctive vocalisations compared to Tanimbar Myzomela *M.* [*boiei*] *annabellae*, within which it was previously subsumed. Hence, if both the myzomela and the present species are accepted as valid species, *R. laguceria* becomes the third bird species endemic to Babar, and the second of which to have been totally overlooked by the earliest explorers. A more comprehensive study of Southern Boobook taxa than that undertaken by Gwee *et al*. (2017) may feasibly also lead to the elevation of Babar's endemic form, *cinnamomina*, to species rank based on its noticeably different appearance and unique secondary vocalisation (JAE pers. obs.).

Acknowledgements

We thank all those who made available their sound-recordings for analysis. AJB thanks P. Sweet and S. R. Bello at AMNH, and A. Bond and M. Adams at NHMUK, for facilitating visits to the specimens in their care. Peter Boesman and a second, anonymous referee provided helpful comments which improved the manuscript.

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Supplementary Material

Accompanying data for analysis. The spreadsheet contains three tabs: Appendix 1, a full list of museum specimens measured and inspected for plumage differences; Appendix 2, a full list of sound recordings used for the bioacoustic analysis; and Appendix 3, a PCA variance summary table for the bioacoustic data.

ISSN-2513-9894
(Online)

Mansfield Parkyns, the Shoebill *Balaeniceps rex* and its type specimen

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Received 29 January 2026; revised 3 March 2026; published 3 June 2026

http://zoobank.org/urn:lsid:zoobank.org:pub:D1DB03C7-44B5-48DD-8C29-030F5E85086D

Summary.—Mansfield Parkyns (1823–94) returned to Britain in 1849 from an extended trip to Abyssinia, the Sudan and Egypt, during which time he had acquired two specimens of Shoebill *Balaeniceps rex* Gould, 1850, from *c.*10°N on the White Nile in Sudan. Along with much of his remaining bird collection, one of these was donated by his daughters to the Nottingham Natural History Museum at Wollaton Hall in 1926, whereas the other was presented to the then British Museum (Natural History), now Natural History Museum (NHMUK), in the same year. More recently, there has been uncertainty as to whether Gould used one specimen or both for his description and, if only one, which. Drawing extensively on unpublished archival information, this paper concludes that the NHMUK specimen should be treated as the holotype.

Following his return to Britain after an extended visit to what was then Abyssinia and to the Sudan from 1843 to 1849, the traveller Mansfield Parkyns (1823–94) placed at least some of his surviving bird collection in the hands of John Gould, who quickly seized on one striking new species to describe. This was the Shoebill *Balaeniceps rex*, whose scientific name means King Whalehead, and which was formerly often known as the Whale-headed Stork (Newton 1893–96, Collar 1994). It was briefly, but formally (see Bruce & McAllan 1990), named by Gould (1850: 1315) as '… a new form in birds obtained from the interior of Africa, by Masfield [*sic*] Parkyns, Esq., *Balaeniceps rex* is a stock with a perfectly anomalous beak of immense power, somewhat resembling that of Cancroma [= Boat-billed Heron *Cochlearius cochlearius*], while in stature it nearly equals the Maraboa [= Marabou Stork *Leptoptilos crumenifer*] and Adjutant [= Greater Adjutant *Leptoptilos dubius*].'

Soon afterwards, Gould (1852) provided a more comprehensive account of the species, including detailed generic and specific characteristics (sex not mentioned), a set of measurements (although whether from just one individual or an average is not clarified), and some insightful comments on its probable relationships. Mansfield Parkyns had in fact obtained at least two specimens, as first indicated in print by Jardine (1852: 11), who noted that 'both sexes were procured' when mentioning Gould had sent him '… the specimen considered to be a male' for examination. Jardine (1852) also provided a set of measurements that, where comparable, relatively closely approximated those given by Gould (1852).

Much or almost all (see below) of the bird collection that Parkyns still possessed when he died was deposited during the 1920s in the Nottingham Natural History Museum (NOTNH) at Wollaton Hall, currently part of Nottingham City Museums & Galleries (NCMG). In August 1994, NOTNH opened a major temporary exhibition entitled *The Long Walk—Birds and tales of Africa*, celebrating the life and travels of Mansfield Parkyns. Just prior to this, in June 1994, two NOTNH staff, Chris Paul and Graham Walley, contacted the Natural History Museum (NHMUK) Bird Group to enquire about the type status of Parkyns' two specimens of *Balaeniceps rex*, one now at Wollaton Hall and the other at NHMUK, Tring, the latter being the only Parkyns bird specimen that NHMUK possesses.

ISSN-2513-9894 (Online)

Subsequently, the NOTNH specimen was brought to NHMUK, and staff from both institutions measured them together. However, they proved to be sufficiently similar in size to preclude any strongly supported deduction as to whether one, or both, were the types. Following subsequent outside enquiries concerning their type status received by NHMUK Bird Group staff, the research described here was undertaken in an attempt to reach a definitive understanding of the issue.

Mansfield Parkyns, the second son of a wealthy landowner, grew up in Ruddington, Nottinghamshire. He matriculated at Trinity College, Cambridge, in autumn 1840, but was sent down for inappropriate behaviour before he could take a degree (Whitehead 1940, Baigent 2004). Having 'A strong craving for a more adventurous mode of life …' (S. 1895: 319), he then set off while still a teenager on his remarkable travels, initially through Europe, arriving in Constantinople in autumn 1842, then on to Egypt, eventually leaving via Suez for Abyssinia (now Ethiopia and Eritrea) towards the end of March 1843 (Whitehead 1940). A stay of well over two years in Abyssinia followed, during which he integrated himself remarkably well with ordinary people, and on which he subsequently published a two-volume account (Parkyns 1853). Towards the end of 1845, Parkyns crossed into the Sudan, where he again travelled widely, residing there until early 1848, when he returned to Egypt for at least a year before arriving back in Britain in 1849 (Whitehead 1940, Cumming 1987). In the words of Sir Francis Galton (1908: 93), whom Parkyns showed round Khartoum and joined on a trip on the White Nile in 1846, 'Of the many travellers whom I have known I should place Mansfield Parkyns (1823–1894) as perhaps the most gifted with natural advantages for that career.'

Cumming (1987: 6) recorded that Parkyns had developed an early interest in natural history and that at the age of 19 he was '… an informed ornithologist, a competent taxidermist …'. However, Parkyns himself made clear in a letter of March 1851 to Sir William Jardine (NHMUK Library 89 o G; Sauer 2001: 508) that 'I left England when only 18 years of age, being altogether unacquainted with ornithology or in fact with any branch of Natural History. Being anxious to do my best to make my tour of pleasure combine as much of the useful as possible, I took some lessons in skinning on the road & collected some birds & a few animals.' His 'some birds' seemingly ultimately amounted to roughly 2,000 specimens, which were sent to England in three batches: the first, of Abyssinian material, comprised about 1,200 specimens, of which at least 200 were pilfered in transit; the second, which included birds and specimens of other taxa, sat in Aden for four years, during which one case was lost and the other destroyed by rats; the third, including approximately 600 birds from Nubia and the White Nile, arrived safely (Whitehead 1940, Cumming 1987).

Following its description, knowledge of the remarkable Shoebill provoked great interest among ornithologists, who discussed it in a flurry of correspondence from mid-December 1850 onwards (e.g., see Sauer 2001). This included a letter of 2 January 1851 from Gould to Prince Charles Lucien Bonaparte, containing the statements that 'I have just described the most extraordinary bird that has yet come under my notice … I have given it the generic name of Balaeniceps and have called it B. rex; I have a beautiful skin quite perfect at my house; it was killed on the upper part of the white nile [*sic*] and brought to this country by an intrepid English traveller, a private gentleman of the name of Parkyns …' (Sauer 2001: 482). This letter is interesting both for its early date, so soon after description, but also for its suggestion that Gould may have used only one specimen.

Gould also discussed his description of *Balaeniceps* in a note of 11 January 1851 to Sir William Jardine, who responded from Cheltenham on 17(?) January, asking questions about it and showing great eagerness to see it: 'As you say the remarkable bird is not for sale I presume it belongs to some private person – How can it be seen in London – I fear I can not

ISSN-2513-9894 (Online)

depend on getting up before end of next month' (Sauer 2001: 489). By 29 January, Jardine pressed Gould further by asking 'If you … can let me have one of Balaeniceps send it down to Cheltenham [*sic*]' (Sauer 2001: 495); this indicates that by now he knew that Parkyns had collected more than one specimen. Gould responded on 31 January that: 'As you are so desirous of seeing Balaeniceps and I wish you to see it myself I have put it in a Box and sent it off by Mail Train tonight without saying a word to anyone'; he further noted that: 'Mansfield Parkyns, Esq. to whom it belongs tells me its food consists of fish and lizards. The specimens male and female were killed on the upperpart of the White Nile.' (NHMUK Library 89 o G; Sauer 2001: 496).

By 7(?) February, Jardine was asking Gould: 'Could you give me Parkins [Mansfield Parkyns] address – I wish to write to him about how he got Balaeniceps –' (Sauer 2001: 500), and by 10 February he had written to him. As he was away at the time, Parkyns did not respond to Jardine until 24 or 25 March, but the information provided when he did was important: 'I am sorry that as regards the King Stork, I can give you but little information – You must be aware that it is no easy matter to collect birds in the country & climate in which I have travelled. The excessive heat & having been occupied in other matters prevented me from doing as much as I should have wished – The bird was neither of my own shooting nor skinning – as I was in the habit of taking one line of country myself & sending persons (natives) in various directions I could not always obtain the exact information I required from them on their return after some months absence. The bird was shot on the White Nile at somewhere about the 10th degree of latitude N – I was not aware of its being an uncommon bird nor did the natives make any remark on it – I have never seen the bird elsewhere nor know ought of its habits' (NHMUK Library 89 o G; Sauer 2001: 508).

This somewhat vague response places the collection location of *Balaeniceps* firmly in the Sudan, well south of Khartoum. Exactly how and where Parkyns acquired his two specimens has been the subject of much subsequent speculation (e.g., von Heuglin 1873, Newton 1893–96, Whitehead 1940), but this is not central to the issue of the two specimens' type status. More importantly here, Gould's letter of 31 January to Jardine raises the question as to how it was possible for him and/or Parkyns to be confident of the sexing of the two specimens of this sexually monomorphic species, given that Parkyns was clearly not present when the skins were prepared. In a detailed study of one nest in Zambia, Buxton *et al*. (1978: 206) noted that 'The presumed female … was somewhat smaller than the mate; had a shorter, more pinkish bill with fewer dark markings and less pronounced median ridge;' and that these inferred differences were consistent with those of a captive pair observed by Fischer (1970). However, more recently Muir & King (2013: 187), based on observations in captivity, unequivocally stated that 'Visual sexing is difficult, and it is strongly recommended that unsexed or juvenile birds undergo DNA sexing.'

In his March 1851 letter to Jardine, Parkyns had further noted 'I have a collection of about 400 or more birds setting up [i.e. being mounted] by Leadbeater …' (NHMUK Library 89 o G; Sauer 2001: 508); Leadbeater was a London natural history agent (Sharpe 1906). These specimens Parkyns then placed in cases that adorned Woodborough Hall, the house he then acquired in Nottinghamshire, and which was his main residence for the remainder of his life. In 1854, he married Emma Louise Bethell, with whom he first had one son, who died young, and then eight daughters, all of whom survived. After his death in 1894, Woodborough Hall was sold and his personal effects, presumably including all the surviving bird specimens still in his possession, were divided equally among his daughters (Cumming 1987).

In October 1926, the Revd. W. E. Buckland, husband of Mrs Ada Buckland, a daughter of Mansfield Parkyns, wrote to Prof. Carr, then the curator at Wollaton Hall, that: 'We

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have here in my Garage 10 large cases of stuffed birds, upwards of 100 specimens which Mr. Mansfield Parkyns, the Abyssinian Traveller, brought to England in 1850. They were beautifully set up by Mr. Leadbeater and were until recently in the Hall at Woodborough. … The collection is the property of my wife and her sisters, who are daughters of Mr. Parkyns. … the specimens ... were ejected from the Hall at Woodborough into a damp barn, where Mrs Buckland saw them and whence, by gift of Mrs Dowson they were brought here' (NCMG Archives 687). This offer was accepted and NOTNH subsequently recorded the acquisition as NH Acq. Ref. 1926.01a. In his letter of 13 November 1926, W. E. Buckland had also noted that 'There is another set of cases at my daughter's house near Gravesend' (NCMG Archives 687), and four cases from this source were also soon acquired and recorded as NH Acq. Ref. 1926.01b. NCMG currently appears to have approaching 200 of Parkyns' bird specimens. As to what happened to the rest of the original '400 or more birds', subsequent acquisition by NOTNH of a small number of Parkyns specimens reveals that all were clearly not acquired in 1926; moreover, W. E. Buckland commented in a letter of 12 March 1927 that 'We are sorry to hear that the specimens [presumably the donated ones] have suffered greatly from damp and moth' (NCMG Archives 687), so some may even have been lost from those that were presented.

Nevertheless, both *Balaeniceps rex* specimens were clearly present in the initial planned donation, although one did not in fact go to NOTNH as, in his 13 November 1926 letter, W. E. Buckland also noted that 'I am now writing to Mr. N. B. Kinnear, British Museum (Natural History) [BM(NH)], Cromwell Road S.W.7. asking him to make arrangements to take out from the case, pack and remove one specimen of Balaeniceps rex' (NCMG Archives 687). Norman Kinnear was then on the BM(NH) bird staff, and there remains in NHMUK Archives a file of his notes relating to his clear interest in Mansfield Parkyns and *Balaeniceps rex* (NHMUK Library & Archives MSS KIN). A further letter of 23 November 1926 from W. E. Buckland to Prof. Carr reveals: 'Yesterday Mr. Kinnear sent down the Taxidermist who removed one specimen of the Balaeniceps rex as arranged, the type bird for the Natural History Museum. The case opened quite easily and has been fastened up again. So you can remove the cases at your convenience, but please let me have notice' (NCMG Archives 687). The specimen taken by BM(NH) was that noted as V4282A from Case B in a specimen list subsequently drawn up in 1927 by a T. Wells of the BM(NH), who had been requested by NOTNH to check the identities of their Parkyns specimens (NHMUK Library & Archives DF/ZOO/200/88); the specimen retained by the NOTNH was V4282B from the same case.

As confirmation of the type status of the BM(NH) specimen, the minutes of a meeting of 22 January 1927 of the Standing Committee of the BM(NH) record that the Trustees '… directed that their best thanks be returned to the daughters of the late Mr. Mansfield Parkyns for their donation of the type specimen of the Whale-headed Stork (*Balaeniceps rex*)' (p. 8). An effusive letter of thanks to Mrs A. Buckland was duly written on 1 February 1927 by S. F. Harmer, then Director of the BM(NH), stating:

> 'I have very much pleasure in complying with the instructions of the Trustees of the British Museum to send their thanks to the donors of the type-specimen of the Whale-headed Stork (Balaeniceps rex). … The specimen has been entered as the gift of the daughters of the late Mr. Mansfield Parkyns. … Scientific work in Ornithology, as in other branches of Zoology, is greatly facilitated by having type-specimens in the National Museum, where they can be referred to by specialists. … We are very much indebted to you and to Mr. Buckland for the interest you have taken in making arrangements for the transference of this specimen to the British Museum, …' (NHMUK Library & Archives DF/ADM/1001/75).

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The specimen in question was registered in BM(NH) in November 1926 as 1926.11.19.1, a male from the Sudan, the type of the species, presented by the late Mansfield Parkyns' daughters (Mrs A. Buckland, Mrs Cardew, Mrs Harriott, Mrs Caldwell, Mrs Arnold Saunders and Mrs Barratyne). Overall, from the above there is little doubt that the *Balaeniceps rex* specimen gifted to the BM(NH) was understood in 1926 by all interested parties to be the individual that Gould (1850, 1852) used to describe the species. Subsequently, it was referred to unequivocally as the holotype in the BM(NH) non-passerine bird types catalogue (Warren 1966). Unless evidence to the contrary is forthcoming, specimen NHMUK 1926.11.19.1 should therefore be treated as the holotype of *Balaeniceps rex* based on Art. 72.4.1.1 (ICZN 1999), which states that 'any evidence, published or unpublished, be taken into account to determine what specimens constitute the type series'. The specimen now residing in Wollaton Hall clearly retains great scientific interest but seemingly has no formal name-bearing status. As a matter of wider interest, use of molecular techniques to check that the NHMUK specimen is indeed a male and the other possibly a female, although NCMG has no record as to its sex, would seem highly worthwhile.

Acknowledgments

We are very grateful for assistance from Hein van Grouw, Chris Paul, Graham Walley, Sheila Wright and the late Michael Cooper and Don Sharp. Mark Adams, Nigel Collar, and our two referees, Bob Dowsett and Lincoln Fishpool, made helpful comments on the manuscript.

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ISSN-2513-9894 (Online)