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BOC Office

c/o Natural History Museum at Tring,
Akeman Street, Tring, Herts. HP23 6AP, UK
E-mail: info@boc-online.org
Tel. +44 (0)208 8764728 / 07919174898

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CLUB ANNOUNCEMENTS

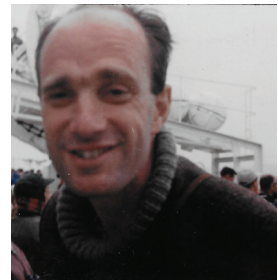
FORTHCOMING MEETINGS

The Club's next meeting will be on Monday 18 October, at 6pm, via the online medium of Zoom, and will feature a presentation by Alexander Lees (Manchester Metropolitan University) on the topic *Does bird feeding help or hinder avian conservation?* Further details of forthcoming meetings in 2021 will be announced online via the Club's website: <https://boc-online.org/meetings/upcomingmeeting>, or follow the Club's Twitter (@online_BOC) and Facebook accounts (<https://www.facebook.com/onlineBOC>). Be sure to keep an eye on them!

OBITUARY

William Richmond Postle Bourne, MA, MB, B CH, MBOU (1930–2021)

Bill Bourne died peacefully at Keith, in Scotland, on 31 May 2021, aged 91. Bill wrote so much: papers in this *Bulletin* are noted below, and are illustrative of the breadth and depth of his ornithological interests and knowledge. Much has been written about him over his working life as a medic, in travel, in research and writing. Bill featured as the 12th in the series 'Personalities' in the April 1978 issue of *British Birds*. The authors' perception of Bill, a legend of energy, knowledge and eccentricity were shown to stand the test of time. He joined the BOC in 1956. When I first met him in 1969 at the Autumn Scientific meeting of the British Ornithologists' Union he encouraged me to do so too, and he proved to be a great friend as I forged my early contacts in the world of exploration, museums, research and societies.



W. R. P. Bourne (© Sheila Bourne)

Bill's energy and resourcefulness are well illustrated in his 1951 solo expedition to the Cape Verdes, as a result of which he contributed to the Bannermans' *History of the birds of the Cape Verde Islands*. His early enthusiasm for birds and their nests was imparted by three maiden aunts. At age seven his father introduced him to egg collecting, which he pursued for ten years, then saw the error, destroyed his collection, and joined the British Trust for Ornithology. He spent most of the war in Bermuda enjoying tropicbirds and terns, and learning about boats and seabirds. From this time his particular interest was the Tubinares. David Bannerman recounts how at the hottest time of year, with little money and no transport of any kind, Bill relied entirely on his wits in his solo Cape Verde endeavour. It says much for his stamina and enthusiasm that he walked across all of São Tiago, over the roughest country, while his journeys between the islands were performed in local schooners. With an interest more in ecology than in specimen collecting just one was taken, an example of a Purple Heron *Ardea purpurea*, from a colony he discovered on São Tiago. He was struck by the paleness of their plumage and the specimen he secured was sent to Paris. After some years, a new race was named by the Abbé René de Naurois in Bill's honour, *A. p. bournei*.

Bill read medicine and zoology at Cambridge, and completed his training at St Bartholomew's Hospital, London. Service in the RAF took him to Malta, Jordan and the Middle East at the time of the Suez crisis, then Cyprus, where he was co-founder and first recorder of the Cyprus Ornithological Society. His passionate interest in islands and seabirds came to the fore when, in 1961, he proposed to found the Seabird Group, which eventually formed in 1965, a timely formation ahead of the *Torrey Canyon* disaster in March 1967. He became its first secretary, whilst in the role of adviser to the Royal Naval Bird Watching Society (RNBWS) he codified the collection of avian data from ships at sea (*Sea Swallow* 13: 9–16), including ocean weather ships in the eastern Atlantic at a time when reports were pouring in. During this period, when I first met Bill, he worked at Watford General Hospital as a geriatrician. Each year he would diligently analyse the RNBWS seabird reports and write them up for *Sea Swallow*, teasing out the distribution of various petrels and shearwaters. In the 1980s he was at sea himself, as a ship's surgeon and medic with the Royal Fleet Auxiliary ships (RFA) that serve to support the fleet at sea. In 1983 RFA *Olwen* took him to high latitudes in the South Atlantic after the Falklands War. A letter from the Vice Chief of the Naval Staff forwarded Bill's



report of watches in ten-minute blocks covering voyages to the Falklands and South Georgia via Ascension Island, where landing was not possible, but he made useful observations offshore. In the Falklands HMS *Bristol* gave Bill the chance to visit New Island and see one of the main seabird colonies. He also visited the British Antarctic Survey base on Bird Island. The RFA also took him beyond the Southern Ocean on one of three voyages to the Arabian Sea. RFA *Tidespring* saw him off Fujairah, from where he wrote complaining of being 'called back from leave three weeks early because they are six doctors under strength'. He noted the temperature regularly over 100°F, and said to be 145° in the boiler room; 'everyone including me has prickly heat, and if I do not look out as much as possible the trip will be wasted – there were Persian Shearwaters [*Puffinus persicus*] this morning, 10th August 1988'.

Many research papers on the taxonomy of petrels emanated from Bill and were published in journals on both sides of the Atlantic. In Europe, one of the islands to attract Bill was Madeira, and its enigmatic *Pterodroma* petrels. Frank Zino recalls their voluminous correspondence and Bill and his wife Sheila's visit in October 1993, including to the breeding site at Pico do Areeiro. He was a great help to those tracking down the *freira*, as it was known to the locals, or *Pterodroma madeira*. Bill came up with the suggestion that it be known as Zino's Petrel to honour the Zino family, who put so much effort into conserving the bird.

So, with that glimpse of a life filled to the brim with action, activity and results, I will sign off in the same way his perfectly typed letters came to me: 'Yours aye, Bill'.

Stephen Chapman

Publications in *Bull. Brit. Orn. Cl.*

- Bourne, W. R. P. 1964. On the occurrence and nomenclature of certain petrels in North America. *Bull. Brit. Orn. Cl.* 84: 114–116.
- Bourne, W. R. P. 1965. The missing petrels. *Bull. Brit. Orn. Cl.* 85: 97–105.
- Bourne, W. R. P. 1968. Notes on the diving-petrels. *Bull. Brit. Orn. Cl.* 88: 77–85.
- Bourne, W. R. P. 1983. The Soft-plumaged Petrel, the Gon-gon and the Freira, *Pterodroma mollis*, *P. feae* and *P. madeira*. *Bull. Brit. Orn. Cl.* 103: 52–58.
- Bourne, W. R. P. 1983. A Gon-gon *Pterodroma (mollis) feae* in Israel. *Bull. Brit. Orn. Cl.* 103: 110.
- Bourne, W. R. P. 1986. Recent work on the origin and suppression of bird species in the Cape Verde Islands, Atlantic Ocean especially the shearwaters, the herons, the kites and the sparrows. *Bull. Brit. Orn. Cl.* 106: 163–170.
- Bourne, W. R. P. 1995. The origin and affinities of Berthelot's Pipit *Anthus bertheloti*. *Bull. Brit. Orn. Cl.* 115: 22–24.
- Bourne, W. R. P. & Casement, M. B. 1996. The migrations of the Arctic Tern. *Bull. Brit. Orn. Cl.* 116: 117–123.
- Bourne, W. R. P. 1999. Bulwer's Petrel *Bulweria bulwerii* on St Helena. *Bull. Brit. Orn. Cl.* 119: 91–93.
- Bourne, W. R. P. 1999. The past status of the herons in Britain. *Bull. Brit. Orn. Cl.* 119: 192–196.
- Bourne, W. R. P. 2001. The status of the genus *Lugensa* Mathews and the birds collected by Carmichael on Tristan da Cunha in 1816–1817. *Bull. Brit. Orn. Cl.* 121: 215–216.
- Bourne, W. R. P. 2002. The nomenclature and past history in Britain of the Bean and Pink-footed Geese. *Bull. Brit. Orn. Cl.* 122: 11–14.

Correction to holotype details for *Chordeiles pusillus novaesi* Dickerman, 1988

Paul Sweet and Thomas Trombone at the American Museum of Natural History, New York (AMNH), have recently drawn to our attention that holotype specimen details given in the description of *Chordeiles pusillus novaesi* by Dickerman (1988, *Bull. Brit. Orn. Cl.* 108: 124) are incorrect. Instead of what is written there, the correct holotype details should read: *Holotype*. Adult female, AMNH 241906, Flores, state of Maranhão, Brazil, collected 1 October 1926 by Emil Kaempfer; original number 3775.

Friends of the BOC

The BOC has from 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).



Which large species of seed finch occurred on Trinidad?

by Dale Dyer

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<http://zoobank.org/urn:lsid:zoobank.org:pub:BDCC2F29-72E8-4A4A-AE9F-D4BDB2710D63>

SUMMARY.—A population of large seed finches, probably extirpated, occurred on Trinidad. Studies of specimens by Phelps & Phelps and by Meyer de Schauensee identified this population as the taxon now known as *Sporophila maximiliani parkesi*, but subsequent literature has often referred to these birds as *S. c. crassirostris* without fresh evidence or analysis. My review of specimens reaffirms their identity as *S. m. parkesi*, and refutes the hypothesis that this taxon should be considered a synonym of *S. m. maximiliani*.

Two species of seed finch (*Sporophila*, formerly *Oryzoborus*) have been documented on the island of Trinidad (Trinidad & Tobago, South America). The populations of both species have been depleted or extirpated due to persecution by cagebird enthusiasts (French 2012). The smaller, dark-billed species is Chestnut-bellied Seed Finch *Sporophila angolensis* Linnaeus, 1776. A larger species with a proportionately heavier bill, pale in the male, is documented on Trinidad by three specimens at the American Museum of Natural History, New York (AMNH) and three at the Natural History Museum, Tring (NHMUK), all initially identified as Large-billed Seed Finch *S. crassirostris* J. F. Gmelin, 1789, without trinomial. The species identity of this larger form, however, has been controversial, with some authorities concluding that it is Great-billed Seed Finch *S. maximiliani* Cabanis, 1851, which is globally Endangered (BirdLife International 2019). *S. crassirostris* and *S. maximiliani* are morphologically very similar, with large, extremely deep bills. Adult males are black with a white patch at the base of the primaries. Females are brown, paler below, with a blackish bill.

History

Ubaid *et al.* (2018) presented the rather complex nomenclatural history of *Sporophila maximiliani*, postulating its type locality to be the Jucu River, Espírito Santo, south-east Brazil. The type locality for *S. crassirostris* has been designated as Cayenne (= French Guiana) (Berlepsch & Hartert 1902). P. L. Sclater (1862) was first to report a larger species of seed finch on Trinidad, listing a male and a female '*Oryzoborus crassirostris*' from Trinidad in his collection. These were the only specimens he recorded as *O. crassirostris*, but he also possessed a pair of '*Oryzoborus maximiliani*' from 'Brazil'. Sharpe (1888) listed Sclater's Trinidad specimens, by then in the British Museum, as *O. crassirostris* along with specimens from Venezuela, Colombia and Guyana, and restricted *O. maximiliani* to 'southern Brazil'. Léotaud's *Oiseaux de l'île de la Trinidad* (1866) provided measurements and descriptions of '*Spermophila crassirostris* - Gml'. Subsequently, Chapman (1894) collected a single '*Oryzoborus crassirostris*' on Trinidad, now at AMNH.

For Hellmayr (1938) species identity of the Trinidad larger form was uncontroversial, as he placed all large pale-billed forms of *Oryzoborus* in species *crassirostris*. Hellmayr defined allopatric ranges for all of these subspecies, restricting *O. c. maximiliani* to 'southern and interior Brazil', and attributing all specimens from Trinidad, Venezuela, the Guianas, northern Brazil, eastern Colombia and north-east Peru to *O. c. crassirostris*. He wrote,

however, that 'I have not been able to correlate certain variations in dimensions and in size of bill with geographic areas' and '(males) from Trinidad and the Orinoco Valley are larger, the tail in particular longer, and have much bulkier, heavier bills, some being fully as large billed as *O. c. maximiliani*'.

Phelps & Phelps (1950) focused on this problem in more detail, and concluded that two taxa occurred in close proximity in northern South America. They described a new subspecies *O. c. magnirostris* from the Orinoco Delta (including the type locality, Misión San Francisco de Guayo, Territorio Delta Amacuro), the lower Caura River, Caicara on the Orinoco River, and Trinidad. The type specimen is part of the Phelps Collection, although it is on deposit at the AMNH along with other Phelps types—and it is not 'inaccessible' as claimed by Ubaid *et al.* (2018). Six other specimens at the AMNH for which Phelps & Phelps (1950) gave sex and locality (though not registration numbers), including the three Trinidad specimens, are paratypes. Their labels have a pencil annotation '*magnirostris*', without initials. Phelps & Phelps (1950) diagnosed *O. c. magnirostris* as differing 'from *O. c. crassirostris* in having a much larger bill and longer wing and tail'. They concluded that the three specimens from Trinidad at NHMUK also are *magnirostris* based on wing and culmen measurements provided by J. B. Macdonald, then curator. They remarked that 'the known ranges of the new form and *O. c. crassirostris* approach each other closely', and speculated that non-breeding flocks may 'approach or even temporarily invade the territory occupied by the neighboring form'. The name *magnirostris* has since been replaced by *parkesi* (Olson 1981) because *magnirostris* is preoccupied.

Paynter & Storer (1970) recognised '*O. crassirostris magnirostris*' and included Trinidad within its distribution ('rare'). However, Herklots (1961) did not follow Phelps & Phelps (1950), instead identifying the taxon on Trinidad as *O. c. crassirostris* without discussion. He had no familiarity with the species in life, and given that he wrote that the male's bill colour is black, it is doubtful that he had even seen specimens.

Meyer de Schauensee (1970a) asserted that nominate *crassirostris* and *parkesi* ('*magnirostris*' therein) 'actually occur together in Venezuela (El Llagual...) and in Guyana (Annai)'. His list of specimens examined included three *crassirostris* and three '*magnirostris*' from 'El Llagual', all attributed to AMNH—they are not there, but he was probably referring to a series from El Yagual at the Carnegie Museum, Pittsburgh. He listed four *crassirostris* from Annai at AMNH, and in a postscript ('Since writing this paper...') referred to two male '*magnirostris*' from Annai, and a male '*magnirostris*' from 'French Guiana, the type locality of *O. crassirostris*', the latter three specimens at the Museum National d'Histoire Naturelle, Paris. The 'additional' specimens mentioned in the postscript, seen in Paris and also NHMUK, were not included in his list of material examined. Meyer de Schauensee (1970a) determined that nominate *crassirostris* was smaller, with a smaller bill, and a proportionately shorter tail than all other forms then included in *crassirostris* (e.g., by Paynter & Storer 1970), and therefore treated it as a monotypic species, with the remaining subspecies united under the oldest name *maximiliani*. This split between *S. crassirostris* and *S. maximiliani*, based on sympatry, has been recognised by subsequent authors (e.g., Ridgely & Tudor 1989, Dickinson & Christidis 2014, del Hoyo & Collar 2016). Note that many authors, e.g., Dickinson & Christidis (2014) and del Hoyo & Collar (2016), have followed the suggestion of Ridgely & Tudor 1989 to place the western South American subspecies *occidentalis* within *crassirostris* rather than *maximiliani*.

Meyer de Schauensee (1970a) listed just one Trinidad specimen, a male at AMNH, which he identified as '*magnirostris*'. He did not note whether he confirmed the identity of the Trinidad specimens at NHMUK. Included in his paper is a map of localities for

specimen records of relevant taxa, though '*grandirostris*' is substituted for *magnirostris* in error. It is '*grandirostris*' to which Trinidad records are attributed on this map.

Specimen review by Phelps & Phelps (1950) and Meyer de Schauensee (1970a) would appear to have established that the Trinidad population belonged to *S. maximiliani parkesi*, not *S. crassirostris*. Despite this, taxonomic placement of the former Trinidad population in the literature since 1970 has been checkered, with many authors reverting to *S. crassirostris* without giving reason or expressing dissent (see Table 1).

Meyer de Schauensee (1970b) treated *crassirostris* and *maximiliani* as separate species in his *A guide to birds of South America*, but listed both as occurring on Trinidad. Inexplicably, Meyer de Schauensee & Phelps (1978) included Trinidad in the range for *O. crassirostris* alone, not *O. maximiliani*.

In their list of specimens examined, Ubaid *et al.* (2018) listed only one of the *parkesi* paratypes at AMNH as *S. m. parkesi*, and the others, including the three AMNH Trinidad specimens, under *S. crassirostris*. They did not map either species on Trinidad. The mensural data and morphological analysis by Ubaid *et al.* (2018) is restricted to comparison of *S. m. parkesi* with *S. m. maximiliani*, although it is unclear how specimens were assigned to *S. m. parkesi* prior to the analysis. Their conclusions therefore appear unsupported. Ubaid *et al.* (2018) discussed the distribution of nominate *maximiliani* in detail, but the other forms not at all.

Methods and Materials

Fifty specimens at AMNH of likely *Sporophila c. crassirostris*, *S. m. maximiliani* and *S. m. parkesi*, including the Phelps holotype, and the six El Yagual specimens from the Carnegie Museum (CM; see appendix), were measured and compared with the goal of discerning diagnostic characters for *S. c. crassirostris* and *S. m. parkesi*, and determining to which species Trinidad specimens belong. Measurements were taken with dial callipers, except tail length, which was taken with a ruler. Culmen was measured from the base, at the skull, to the tip. Wing, tail and tarsus were rounded to the nearest 1 mm, and bill measurements are accurate to 0.1 mm. Incomplete tails were not measured, and depths were not taken of open bills. Of these 56 specimens, 33 are black (adult) males. The remaining 23 specimens are brown. Nine of the brown individuals were labelled female, 12 as male (some denoted 'juv' or 'imm'). Due to uncertainty of methods of ageing and sexing, the brown birds were compared as groups.

Results and Discussion

Measurements.—My mensural data (Tables 2–3) are closely similar to those of Phelps & Phelps (1950), an expected result since the sets of specimens are broadly overlapping. They are also similar to Meyer de Schauensee (1970a), although his tail measurements are smaller (and therefore his tail / wing indices different). The tail / wing proportions found here in *parkesi* are not as different from *crassirostris* as reported by Meyer de Schauensee (1970a). Culmen measurements in Ubaid *et al.* (2018) are much smaller, and perhaps represent exposed culmen rather than culmen from skull, but other measurements are closely similar.

The measurements of black males (Table 2) support Phelps & Phelps' (1950) assertion that there is a population in northern South America that is larger and larger billed than *S. c. crassirostris*, and these are from within the range of *crassirostris*, in some localities co-occurring with it (e.g., El Yagual, Venezuela). These birds, *S. m. parkesi*, are similar mensurally to *S. m. maximiliani* except in being shorter tailed. Two *S. c. crassirostris* ('Bogota' and 'near Granada') are much larger than the rest, and are responsible for the close



Figures 1–2. Lateral and dorsal views of (top to bottom) males of *Sporophila c. crassirostris*, Guyana (AMNH 514238); *S. maximiliani parkesi*, Trinidad (AMNH 59130); *S. maximiliani parkesi*, Misión San Francisco de Guayo, Territorio Delta Amacuro, Venezuela (Phelps Collection 48301, holotype); *S. m. maximiliani* Goiás, Brazil (AMNH 514255) (Dale Dyer)



TABLE 1

Identification of the large species of seed finch on Trinidad by authors since Meyer de Schauensee (1970a).

Publication	Identification of large seed finch occurring on Trinidad	Comments
Meyer de Schauensee (1970b)	<i>Oryzoborus crassirostris</i> <i>Oryzoborus maximiliani</i>	
Meyer de Schauensee & Phelps (1978)	<i>Oryzoborus crassirostris</i>	
ffrench (1985)	<i>Oryzoborus maximiliani</i>	
ffrench (1976, 1991, 2012)	<i>Oryzoborus c. crassirostris</i>	
Ridgely & Tudor (1989)	<i>Oryzoborus crassirostris</i>	Text, but not on map.
Rodner <i>et al.</i> (2000)	<i>Oryzoborus maximiliani magnirostris</i>	Trinidad column shaded for both species, but text places only subspecies <i>Oryzoborus maximiliani magnirostris</i> , not <i>Oryzoborus c. crassirostris</i> , on Trinidad.
Dickinson (2003)	<i>Oryzoborus maximiliani magnirostris</i>	
Restall <i>et al.</i> (2007)	<i>Oryzoborus maximiliani</i>	Map
Kenefick <i>et al.</i> (2007)	<i>Oryzoborus crassirostris</i>	
Ridgely & Tudor (2009)	<i>Oryzoborus crassirostris</i>	Map, but not text.
Jaramillo (2011)	<i>Sporophila c. crassirostris</i>	
Dickinson & Christidis (2014)	<i>Sporophila c. crassirostris</i>	
del Hoyo & Collar (2016)	<i>Sporophila c. crassirostris</i>	
Ubaid <i>et al.</i> (2018)	<i>Sporophila crassirostris</i>	List of specimens, but not mapped.
BirdLife International (2019)	<i>Sporophila crassirostris</i>	
Gill <i>et al.</i> (2020)	<i>Sporophila maximiliani</i>	<i>S. m. parkesi</i> not recognised as a valid subspecies, following Ubaid <i>et al.</i> (2018).

approach or slight overlap of measurement ranges between *S. c. crassirostris* and *S. m. parkesi* (as noted by Phelps & Phelps 1950).

Measurements of AMNH males from Trinidad are very similar to *S. m. parkesi* from Venezuela (Table 4) and larger than *S. c. crassirostris*. This is true also for measurements given in Phelps & Phelps (1950) of the NHMUK Trinidad males. Those for the NHMUK female are smaller, but see below. Leotaud's (1866) wing measurement also fits *S. m. parkesi*.

Mean measurements of brown birds (Table 3) are smaller than for black males, but show the same pattern of size difference between *S. m. maximiliani* and *S. c. crassirostris*. I am unable to determine if sex, maturity, or both are responsible for smaller size in brown birds. Mention should be made here of CM 33264, an 'imm male' *crassirostris* from El Yagual, which has the longest wing measured herein. Its tail / wing index and bill measurements are consistent with identification as *S. crassirostris*. Its tag annotation states 'Wing too long for crassirostris but [illegible]'.

Colour.—Adult male *S. c. crassirostris* are black with a noticeable blue-green sheen. The three male *S. m. maximiliani* are browner black with much slighter blue-green reflections. Most *S. m. parkesi* are similar to nominate *maximiliani*, but the type has a blue-green sheen as strong as some *S. c. crassirostris* males. Blackness and sheen may be related to condition of the plumage. The amount of white at the base of the primaries, as well as on the underwing-coverts and axillaries, varies individually.

The bills of male specimens of *S. c. crassirostris* have most of the maxilla and the sides of the mandible grey, with the tomia and underside of the mandible cream or buff. On photos of live birds the bill appears silver-white (e.g., Angehr 2011). Bills of specimens of *S. m. maximiliani* and *parkesi* are cream with a small but variable dark area at the base. Photos of live *S. m. maximiliani* show a very pale pink bill (e.g., Ubaid *et al.* 2018). I do not see the

TABLE 2

Measurements (in mm) of black males, given in the format: range (mean, number (*n*) of specimens) for each variable. Trinidad specimens are included in *S. m. parkesi*.

	<i>S. m. maximiliani</i>	<i>S. m. parkesi</i>	<i>S. c. crassirostris</i>
Wing chord	75 (75, <i>n</i> = 3)	72–76 (73.9, <i>n</i> = 7)	66–74 (69.0, <i>n</i> = 23)
Tail	71–74 (72.3, <i>n</i> = 3)	65–70 (66.7, <i>n</i> = 7)	55–65 (60.7, <i>n</i> = 23)
Tail/wing	0.96	0.90	0.88
Tarsus	17–19 (18.0, <i>n</i> = 3)	18–19 (18.3, <i>n</i> = 7)	15–18 (16.6, <i>n</i> = 21)
Culmen from skull	16.7–17.5 (17.07, <i>n</i> = 3)	16.9–19.3 (18.13, <i>n</i> = 7)	13.9–16.7 (15.4, <i>n</i> = 23)
Nostril to tip	12.0–12.5 (12.17, <i>n</i> = 3)	11.8–14.0 (12.87, <i>n</i> = 7)	9.9–11.3 (10.63, <i>n</i> = 23)
Bill height (depth)	15.2–15.7 (15.47, <i>n</i> = 3)	14.7–15.6 (15.18, <i>n</i> = 4)	12.0–15.0 (13.11, <i>n</i> = 17)
Maxilla width	10.6–10.9 (10.77, <i>n</i> = 3)	10.0–11.5 (10.86, <i>n</i> = 7)	7.7–9.9 (8.92, <i>n</i> = 23)
Mandible width	13.0–13.9 (13.53, <i>n</i> = 3)	13.7–15.9 (14.44, <i>n</i> = 7)	11.5–14.4 (12.24, <i>n</i> = 21)

TABLE 3

Measurements (in mm) of brown birds, given in the format: range (mean, number (*n*) of specimens) for each variable.

	<i>S. m. maximiliani</i>	<i>S. m. parkesi</i>	<i>S. c. crassirostris</i>
Wing chord	68–74 (72.0, <i>n</i> = 4)	67–72 (69.0, <i>n</i> = 4)	65–78 (68.0, <i>n</i> = 15)
Tail	60–72 (65.8, <i>n</i> = 4)	63–67 (65.7, <i>n</i> = 3)	54–70 (59.9, <i>n</i> = 15)
Tail/wing	0.91	0.95	0.88
Tarsus	18–19 (18.7, <i>n</i> = 3)	18 (18.0, <i>n</i> = 4)	16–18 (16.9, <i>n</i> = 15)
Culmen from skull	16.6–17.4 (16.95, <i>n</i> = 4)	17.2–19.5 (18.22, <i>n</i> = 4)	14.3–16.7 (15.33, <i>n</i> = 15)
Nostril to tip	11.4–13.6 (12.35, <i>n</i> = 4)	11.9–13.5 (12.70, <i>n</i> = 4)	9.2–11.6 (10.38, <i>n</i> = 15)
Bill height	15.3–15.6 (15.45, <i>n</i> = 2)	14.7–15.3 (15.08, <i>n</i> = 4)	11.8–14.2 (12.47, <i>n</i> = 9)
Maxilla width	10.0–11.4 (10.86, <i>n</i> = 4)	10.1–11.1 (10.48, <i>n</i> = 4)	8.2–10.0 (8.83, <i>n</i> = 15)
Mandible width	13.7–15.8 (14.58, <i>n</i> = 4)	13.6–15.0 (14.15, <i>n</i> = 4)	11.1–13.2 (12.09, <i>n</i> = 15)

TABLE 4

Comparison of Trinidad specimens with Venezuela *S. m. parkesi* (black males).

	<i>S. m. parkesi</i> (Venezuela)	<i>S. m. parkesi</i> (Trinidad)
Wing chord	73–75 (73.5, <i>n</i> = 4)	72–76 (74.3, <i>n</i> = 3)
Tail	65–70 (67.0, <i>n</i> = 4)	65–68 (66.3, <i>n</i> = 3)
Tail/wing	0.91	0.89
Tarsus	18–19 (18.3, <i>n</i> = 4)	18–19 (18.3, <i>n</i> = 3)
Culmen from skull	17.2–19.3 (18.33, <i>n</i> = 4)	16.9–19.0 (17.87, <i>n</i> = 3)
Nostril to tip	12.4–13.6 (13.08, <i>n</i> = 4)	11.8–14.0 (12.60, <i>n</i> = 3)
Bill height	14.7–15.6 (15.33, <i>n</i> = 3)	14.7 (<i>n</i> = 1)
Maxilla width	10.6–11.5 (11.0, <i>n</i> = 4)	10.0–11.0 (10.67, <i>n</i> = 3)
Mandible width	14.1–15.9 (14.95, <i>n</i> = 4)	13.7–14.8 (14.13, <i>n</i> = 3)

difference in bill texture that Meyer de Schauensee (1970a) reported ('shiny' in *crassirostris* vs. 'bonelike' in *maximiliani*).

The colour of brown birds is very variable, dull brown above, but ranging from deep tawny-rufous to pale greyish buff below. Individuals of *S. m. maximiliani* are darker, redder and more saturated than *S. crassirostris*, but immatures may be darker than adults, and worn birds are palest. Some *S. crassirostris* marked 'male imm' show a few black feathers, and some white on the primaries. Bills of all are dark.

Conclusion

Adult males of *S. m. parkesi* are diagnosable from *S. c. crassirostris* by larger measurements in all characters, especially bill and tail. Specimens of large seed finches from Trinidad are *S. m. parkesi*, not *S. c. crassirostris*. Criteria in Ubaid *et al.* (2018) for distinguishing *S. maximiliani* from *S. crassirostris* were not stated, nor was rationale given for their placement of several *S. m. parkesi* paratypes (including those from Trinidad) in *S. crassirostris* (p. 569), and without of examination of the *S. m. parkesi* holotype. Thus their morphometric comparison of *S. m. maximiliani* and *S. m. parkesi* is flawed, and the conclusion that they ‘consider *S. m. parkesi* (Olson, 1981) (= *Oryzoborus maximiliani magnirostris* Phelps & Phelps, 1950) as a synonym of the nominate taxon’ unsupported.

S. maximiliani is Endangered (BirdLife International 2019). Any effort to restore its population on Trinidad would probably require reintroduction. Although such a project is unlikely, as the threat is not habitat loss but continued trapping (ffrench 1985, White *et al.* 2015), restoration of the historical Trinidad population would depend on introduction of the correct species.

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Address: Dept. of Ornithology, American Museum of Natural History, New York, NY 10024, USA, e-mail: ddyer@amnh.org

Appendix

List of specimens examined (sex as recorded on label): AMNH = American Museum of Natural History; CM = Carnegie Museum.

S. m. maximiliani

Chapada, Mato Grosso, Brazil: AMNH 32614 (black male), AMNH 32615 (black male), AMNH 32616 (brown male); Goiás, Brazil: AMNH 514254 (brown unsexed), AMNH 514255 (black male); Brazil: AMNH 514257 (brown female), AMNH 514258 (brown female).

S. m. parkesi

Misión San Francisco de Guayo, Territorio Delta Amacuro, Venezuela: Phelps Collection 48301 (holotype, black male, on loan at AMNH); Caicara, Venezuela: AMNH 514247 (paratype, black male), 514246 (paratype, black male), 514248 (brown male); Maripa, Venezuela: AMNH 72640 (paratype, black male); El Yagual, Venezuela: CM 33265 (brown female), CM 33266 (brown male); La Bomba, Cuyuni, Venezuela: CM 33964 (brown female); Leelet, Trinidad: AMNH 514249 (paratype, black male), 514250 (paratype, black male); Princetown, Trinidad: AMNH 59130 (paratype, black male).

S. c. crassirostris

Nauta, Peru: AMNH 514252 (brown male); Jeberos, Peru: AMNH 514253 (brown male); Curaray, Ecuador: AMNH 232568 (black male); Villavicencio, Colombia: AMNH 122692 (black male), AMNH 122693 (brown female); Medellín, Colombia: AMNH 387890 (black male); 'Nouvelle Granada', Colombia: AMNH 4593 (black unsexed); 'Bogota': AMNH 514251 (black unsexed); Las Guacas, Río San Felix, Venezuela: AMNH 177791 (black male), AMNH 177792 (black male), AMNH 177793 (black male), AMNH 177794 (black male), AMNH 177795 (black male), AMNH 177796 (black male), AMNH 177797 (black male), AMNH 441389 (black male); Esuque, Venezuela: AMNH 41246 (black male); El Yagual, Venezuela: CM 33264 (brown male), CM 33267 (black male), CM 33268 (brown male); Solano, Río Casiquiare, Venezuela: AMNH 433622 (brown female), AMNH 433623 (brown female); Annai, Guyana: AMNH 41245 (black male), AMNH 514234 (brown male), AMNH 514235 (black male), AMNH 514236 (black male), AMNH 514237 (black male), AMNH 514238 (black male), AMNH 514239 (brown male), AMNH 514240 (black male), AMNH 514241 (brown female); Essequibo River, Guyana: AMNH 41253 (brown female); Paramaribo, Suriname: AMNH 313627 (black male), AMNH 514243 (black male), AMNH 514244 (brown male); Suriname: AMNH 514245 (brown unsexed), AMNH 514242 (brown male); Cucari, Pará, Brazil: AMNH 128859 (black male).

A new fossil raptor (Accipitridae: *Buteogallus*) from Quaternary cave deposits in Cuba and Hispaniola, West Indies

by William Suárez & Storrs L. Olson[†]

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SUMMARY.—A large, extinct species of *Buteogallus* Lesson is described from post-cranial elements in Quaternary cave deposits in western Cuba and south-central Hispaniola. The new taxon was approximately the same size as females of the extinct continental *B. woodwardi*, but more robust. Some fossils, recently documented from Hispaniola as Accipitridae genus and species indeterminate, are probably referable to taxa previously known from Cuba, including the new species described herein. Osteological comparisons of both living and extinct species indicate that the extinct genus *Amplibuteo* Campbell is synonymous with *Buteogallus*.

A partial skeleton of a large accipitrid from a Quaternary deposit at Cueva de Sandoval, western Cuba, was recorded as *Amplibuteo* sp. by Suárez & Arredondo (1997). This report extended the distribution of the genus to the West Indies; it was previously restricted to fossil localities in the continental Americas (Campbell 1979, Emslie & Czaplewski 1999). The material was subsequently identified (Suárez 2004) as *A. (Morphnus* auct.) *woodwardi* (L. Miller, 1911), a palaeospecies well known from the late Pleistocene of Rancho La Brea (RLB), California, south-west USA (Miller 1911, 1925, Howard 1932, Campbell 1979), but also recorded from the middle and late Pleistocene of Florida (Emslie 1995, 1998). Suárez (2004: 122) noted that Cuban material differed from continental *A. woodwardi* and that ‘the middle trochlea of the tarsometatarsus is proportionally slightly smaller. Although the series of tarsometatarsi from RLB ($n=31$) show a high degree of individual variation, especially in proportions and shape of the shaft and trochleae, no specimen agrees with the Cuban one in this small detail’.

More recently, we examined fossil raptors from the late Pleistocene Talara Tar Seeps, north-west Peru (Suárez & Olson 2009b, 2014; see Seymour 2015) at the Royal Ontario Museum, Toronto, Canada, especially specimens of *Amplibuteo hibbardi* Campbell, 1979, to compare the type species of the genus (Campbell 1979: 83). An incomplete fossil tarsometatarsus from the Dominican Republic (Hispaniola), collected by C. Woods and identified as *Titanohierax* sp. by Olson & Hilgartner (1982: 28) was included in these comparisons and found to represent an undescribed species of *Amplibuteo* together with the previously known Cuban material (see Suárez & Olson 2008: Fig. 1C). Moreover, this specimen from Hispaniola, with better preserved trochleae, matches all characters of the single tarsometatarsus previously interpreted as individual variation within *A. woodwardi* (Suárez 2004).

The extinct genus *Amplibuteo* Campbell was described as closely related to living *Buteo* Lacépède and *Geranoaetus* Kaup (Campbell 1979: 83), but Emslie & Czaplewski (1999: 189) considered it more similar to, and a possible synonym of, *Harpyhaliaetus* Lafresnaye. Following comparison of the two large *Amplibuteo* species—from the Pleistocene of South and North America—and the two living *Harpyhaliaetus*—Black Solitary Eagle *H. solitarius* (von Tschudi, 1844) and Crowned Solitary Eagle *H. coronatus* (Vieillot, 1817)—we observed

a strong resemblance between the palaeospecies and the skeletal morphology of *H. solitarius*, and could not find any generic distinction between *Harpyhaliaetus* and *Amplibuteo*. The tarsometatarsi exhibit only characters of specific value, related to (or derived from) differences in raptorial habits between living (see Seminario *et al.* 2011, Phillips 2012) and fossil species, due to specialisation on particular prey. Some of these osteological characters (see Results), frequently present in other accipitrids, perhaps misled Campbell (1979: 83) who thought *Amplibuteo* more closely related to *Buteo* and *Geranoaetus* than to *Harpyhaliaetus*. But contrarily, Campbell (1979: 83) correctly stated that *Amplibuteo* 'is quite distinct from... *Titanohierax*', a large extinct buteonine hawk from the Bahamas, similar to *Geranoaetus* (Olson & Hilgartner 1982: 27).

Black Solitary Eagle (see Amadon 1949) was considered congeneric with Crowned Solitary Eagle in the genus *Harpyhaliaetus* since Sharpe (1874), but has also been placed in *Urubitornis* J. Verreaux, 1856, and other genera (Peters 1931, van Rossem 1948, Friedmann 1950, Wetmore 1965). This species, which is darker overall than *H. coronatus*, has a plumage pattern (in different ontogenic stages) similar to Common Black Hawk *Buteogallus anthracinus* (Deppe, 1830) and Great Black Hawk *B. urubitinga* (J. F. Gmelin, 1788), being larger and more robust, with a heavier tarsus, shorter tail and general morphology indicative of more rapacious habits (Amadon 1949: 54, Brown & Amadon 1968: 559–560). As we previously indicated (Olson 2007: 111, Suárez & Olson 2008: 296, 2009b: 249, Suárez 2020: 27), strong osteological similarities exist between *Amplibuteo* (or *Harpyhaliaetus*) and other living and extinct species of *Buteogallus* Lesson. *Harpyhaliaetus* is nowadays considered a junior synonym of *Buteogallus* based on morphological and mtDNA sequence data (Amaral *et al.* 2006, 2009, Lerner *et al.* 2008; see Chesser *et al.* 2012), and we concur.

Herein we relocate under *Buteogallus* the fossil material identified as *Titanohierax* sp. from Hispaniola (Olson & Hilgartner 1982), and *Amplibuteo woodwardi* from Cuba (Suárez 2004), and describe it as a new species shared by the two largest islands of the Greater Antilles.

Material and Methods

Comparison was made with all modern Accipitridae in the skeletal collection of the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM; fossils at the Dept. of Paleobiology are registered under the acronym USNM PAL), the American Museum of Natural History, New York (AMNH), and University of Michigan Museum of Zoology, Ann Arbor (UMMZ), including *Buteogallus anthracinus*, Cuban Black Hawk *B. gundlachi* (Cabanis, 1855), Rufous Crab Hawk *B. aequinoctialis* (J. F. Gmelin, 1788), Savanna Hawk *B. meridionalis* (Latham, 1790) and *B. urubitinga*. One skeleton of *Buteogallus* ('*Harpyhaliaetus*') *solitarius* from the Los Angeles County Natural History Museum (LACM 110091) and another of *B.* ('*H.*') *coronatus* from Naturalis, Leiden (uncatalogued) were available for comparison and measurements (see Table 1). Fossil material of Accipitridae examined in the extensive collections of the George C. Page Museum, La Brea Discoveries, Los Angeles, include *B. fragilis* (L. Miller, 1911), *B. daggetti* (L. Miller, 1915), '*Amplibuteo*' *woodwardi*, *Spizaetus grinnelli* (L. Miller, 1911), Golden Eagle *Aquila chrysaetos* (Linnaeus, 1758) and Bald Eagle *Haliaeetus leucocephalus* (Linnaeus, 1766). The type material of '*Amplibuteo*' *hibbardi* and *Buteogallus terrestris* (Campbell, 1979) from Peru (Campbell 1979; see Suárez & Olson 2009b) was examined at the Royal Ontario Museum, Toronto (ROM). Fossils of *B. borraasi* (Arredondo, 1970) from Cuba used in this study are the specimens and deposits listed by Suárez & Olson (2008: 289–293) including the holotype left tarsometatarsus (Dpto. de Paleontología Universidad de la Habana, DPUH 1250). From the Museo Nacional de Historia Natural de Cuba (MNHNCu), La Habana, and William Suárez collection (WS), La

TABLE 1

Measurements (mm) of tarsometatarsi of *Buteogallus irpus* sp. nov., compared to those of other extinct and living congeneric species of approximately similar size, in the format: range (mean, sample size).

Character	<i>B. irpus</i> sp. nov.	<i>B. woodwardi</i>	<i>B. hibbaridi</i>	<i>B. borraisi</i>	<i>B. coronatus</i>	<i>B. solitarius</i>
Total length	132.7	125.6–140.2 (131.6, 20)	132.3–136.5 (134.3, 3 ^A)	162.1–165.2 (163.6, 2 ^B)	118.9	126.0
Proximal width	25.5	21.4–25.5 (23.0, 20)	22.2–25.0 (23.7, 3 ^A)	20.5–22.4 (21.4, 8 ^B)	21.9	20.6
Minimum shaft width	11.3–11.8 (11.6) 2	8.9–11.9 (10.1, 28)	10.1–11.7 (10.9, 2 ^A)	9.2–11.3 (11.0, 7 ^B)	10.2	9.9
Shaft width above metatarsal facet	13.0	10.1–12.4 (11.0, 20)	11.9–12.1 (11.0, 2)	10.4–11.4 (10.8, 7)	11.2	10.0
Distal width	26.3+, 27+	23.1–28.8 (26.1, 25)	25.2–29.3 (27.1, 6 ^A)	24.0–26.3 (25.3, 3 ^B)	25.2	23.4
Width of trochlea III	8.1–8.3 (8.2) 2	6.8–8.4 (7.4, 28)	6.9–8.1 (7.4, 8 ^A)	6.4–7.4 (6.9, 5 ^B)	7.0	6.2

^A Campbell (1979: Table 6).

^B Suárez & Olson (2008: Table 4).

Habana, we examined the holotype left tarsometatarsus of *B. royi* Suárez, 2020 (MNHNCu 75.4909), the holotype distal right tarsometatarsus of *Gigantohierax itchei* Suárez, 2020 (MNHNCu 75.4869), and selected material of *G. suarezi* Arredondo & Arredondo, 2002, including a right tarsometatarsus lacking proximal end and part of the medial border (MNHNCu 75.4728), distal half of left tarsometatarsus (MNHNCu 75.4729), distal end of left tarsometatarsus without trochlea IV (MNHNCu 75.4730), paratype fragmentary tarsometatarsus (WS 80120.E) and paratype shaft of right tarsometatarsus (WS 8012). The holotype tarsometatarsus (MCZ 2257) of *Titanohierax gloveralleni* Wetmore, 1937, on loan from the Museum of Comparative Zoology, Harvard Univ., MA, was also examined. Photographs, measurements and descriptions published by Emslie & Czaplewski (1999) and Steadman *et al.* (2019) were used for comparisons with '*Amplibuteo*' *concordatus* Emslie & Czaplewski, 1999, and to evaluate fossil specimens of accipitrids recorded from Hispaniola, respectively. Osteological terminology is modified from Howard (1929) and Baumel & Witmer (1993). Measurements were taken to the nearest 0.1 mm using digital callipers. The annotation (+) indicates fracture or abrasion to the specimen, and that the given measurement will be less than the original value. A vernacular name for the newly described species is proposed, along with its Spanish equivalent.

Results

Systematic paleontology

Order ACCIPITRIFORMES Vieillot

Family ACCIPITRIDAE Vieillot

Genus *Buteogallus* Lesson, 1830, *Traité d'Orn.*, livr. 2, p. 83. Type, by monotypy, *Buteogallus cathartoides* Lesson, 1830 = *Falco aequinoctialis* J. F. Gmelin, 1788.

Synonym. *Amplibuteo* Campbell, 1979: 77; type species by original designation *Amplibuteo hibbaridi* Campbell, new synonymy.

Characters of the tarsometatarsus described by Campbell (1979: 77) as diagnostic of '*Amplibuteo*', but recorded by him as present in *Buteogallus* (= '*Haryphaliaetus*' and

'*Heterospizias Sharpe*', see diagnosis of '*Miraquila*' Campbell 1979: 74), include: '(1) inner calcaneal ridge of hypotarsus projecting posteriad at approximately 60–70° to vertical axis of shaft [= '*Harpyhaliaetus*']; (2) intercotylar area elevated slightly [= '*Heterospizias*' and '*Buteogallus*']; (3) edge of shaft external to outer calcaneal ridge of hypotarsus without ridge [more similar to '*Harpyhaliaetus*', character of specific value, variable in '*Buteogallus*', see Suárez & Olson 2009b: 250]; (4) anterior metatarsal groove moderately deep [= '*Heterospizias*' and '*Buteogallus*']; (5) internal anterior metatarsal ridge only slightly developed [= '*Buteogallus*']; (6) attachment of tibialis anticus not separated from external anterior metatarsal ridge by groove [= '*Harpyhaliaetus*' and '*Heterospizias*']; (7) middle trochlea short, turned significantly externally in anterior view [= '*Harpyhaliaetus*']; (8) internal trochlea rotated posteriad such that posteromedial edge is at same level as posterolateral edge of middle trochlea [= '*Heterospizias*' and '*Buteogallus*']; (9) internal trochlea projecting distad beyond middle trochlea and rotated significantly externally in anterior view [= '*Harpyhaliaetus*']; (10) internal trochlea with distinct angular proximolateral projection [= '*Harpyhaliaetus*' and '*Heterospizias*']. Therefore, the extinct taxa currently placed in '*Amplibuteo*' are treated herein under '*Buteogallus*', as *B. woodwardi* (L. Miller, 1911) new comb., *B. hibbardi* (Campbell, 1979) new comb., and *B. concordatus* (Emslie & Czaplewski, 1999) new comb., which are all members of the Buteogalline radiation among extinct Accipitridae from America (cf. Olson 2007, Suárez & Olson 2008, 2009b). Specimens of the new species also replicate the general skeletal morphology present in the living *B. solitarius* (or vice versa), being part of a small (apparently monophyletic) assemblage of allopatric-allochronic fossil species that includes *B. concordatus* and *B. woodwardi*, from North America, and *B. hibbardi* from South America.

***Buteogallus irpus* sp. nov.**

Wolf Hawk / Gavilán Lobo

(Figs. 1A–E, 2A–B, 3; Table 1)

References:

Titanohierax gloveralleni: Woods 1980: 8 (part).

Titanohierax sp.: Olson & Hilgartner 1982: 28.

Amplibuteo sp.: Suárez & Arredondo 1997: 100.

Amplibuteo woodwardi: Suárez 2004: 121.

Holotype.—Left tarsometatarsus lacking proximal end, USNM PAL 299573 (Figs. 1A–E, 2A; not 'USNM 244573' [*lapsus calami*], as reported by Olson & Hilgartner 1982: 28). Collected by Charles Woods under 60 cm of red earth, at the type locality, on 24 April 1978. This specimen was incorrectly cited as 'a tarsometatarsus lacking its distal end (USNM 244573, from Cueva de las Abejas)' by Steadman *et al.* (2019: 328).

Paratype.—Cueva de Sandoval (Sandoval III low deposit), c.4 km south of Vereda Nueva, Caimito municipality, Artemisa (formerly La Habana) province, Cuba: partial skeleton WS 365, with one cervical (axis) and three thoracic vertebrae, seven fragments of ribs, fragmentary pelvis, proximal fragmentary right humerus, distal fragments of left humerus, segment of shaft of left ulna, left fragmentary femur without distal end, proximal and distal fragmentary ends of right femur, shaft of left tibiotarsus, proximal right fibula, left tarsometatarsus (lacking inner calcaneal ridge, part of the proximal end of the metatarsal facet, wing of trochlea II and posterior surface of trochlea III) (Fig. 2B), left digit I-phalanx 1 and 2, left digit III-phalanx 2 and 3, right digit III-phalanx 4, right digit IV-phalanx 4. Collected by WS on 2 March 1995. Quaternary, probably late Pleistocene, but not directly dated (see Suárez 2000). For illustrations and description see Suárez (2004: 121–123, Figs. 1–2).



Figure 1. Holotype left tarsometatarsus (USNM PAL 299573) of *Buteogallus irpus* sp. nov., in anterior (A), medial (B), distal (C), posterior (D) and lateral (E) views. Scale = 2 cm.

Measurements of holotype.—Total length as preserved: 124.9 mm; proximal width at distal level of tubercle for tibialis anticus: 17.0 mm; width of shaft at midpoint: 13.2 mm; minimum width of shaft: 11.8 mm; minimum width of shaft at proximal end of metatarsal facet: 13.0 mm; depth of lateral side at proximal end of metatarsal facet: 9.8 mm; distance from proximal edge of metatarsal facet to inner inter-trochlear notch: 30.3 mm; distal width: 27+ mm; width of trochlea III: 8.3 mm; depth of trochlea IV: 12.2 mm (Table 1).

Diagnosis.—Resembles *B. woodwardi* and *B. hibbardi* in size and general morphology, but tarsometatarsus more robust, with shaft expanded at distal end, and trochleae relatively shorter in *B. irpus*.

Measurements of paratype.—See Suárez (2004: 123–124, Table 1, Fig. 3), Table 1.

Type locality and age.—Cueva de las Abejas (18°01'N, 71°40'W; c.20 m), near Cabo Rojo, 8 km south-east of Pedernales, 1.5 km north of Highway 44, Pedernales province, Dominican Republic. Quaternary, probably late Pleistocene, but not directly dated (see Olson & Hilgartner 1982: 28, Steadman *et al.* 2019: 321).

Etymology.—From Latin *irpus*, = wolf, in reference to the ecological role played by this large raptor in controlling the regional 'megafauna' on the two largest islands of the Greater Antilles, occupying the ecological niche of a carnivorous mammal (*cf.* Arredondo 1976, Morgan *et al.* 1980).

Status.—Extinct, known only from fossil material.

Description.—The skeleton of *B. irpus* sp. nov. (Figs. 1–2; see Suárez 2004: Figs. 1–2, Suárez & Olson 2008: Fig. 1) is partially represented by fragmentary material, with the tarsometatarsus best preserved and more diagnostic of the known elements (see Olson



Figure 2. Tarsometatarsi of large extinct West Indian and North American Accipitridae in anterior view (A–F). *Buteogallus irpus* sp. nov.: (A) left without proximal end (holotype, USNM PAL 299573), (B) left (paratype, WS 365 [part of the proximal end of the metatarsal facet is lacking due to fracture, so the complete specimen would be wider at this point]). *B. woodwardi* new comb.: (C) left (RLB D1970). *Gigantohierax itchei*: (D) distal third of right without trochlea IV (holotype, MNHNCu 75.4869). *Titanohierax gloveralleni*: (E) right without proximal end and trochlea II (holotype, MCZ 2257). *Buteogallus borrasii*: (F) right (CZACC 400-659). Images D–F are reversed to facilitate comparisons. Scale = 2 cm.

& Hilgartner 1982: 28, Suárez 2004: 121). Both tarsometatarsi under study (holotype and paratype, see above) represent adults, probably of different sexes. These fossils are similar in general morphology to the equivalent elements in the extant *B. solitarius* and the Quaternary extinct *B. woodwardi* and *B. hibbardi*, but *B. irpus* is much larger and robust than material available of the living species (Table 1). All other modern *Buteogallus* examined, including *B. anthracinus*, *B. gundlachii*, *B. aequinoctialis* (see Olson 2006, for discussion of some skeletal elements of this species), *B. meridionalis* and *B. urubitinga*, are much smaller than *B. irpus* sp. nov., and therefore do not require further comparison. *B. irpus* differs from the extinct *B. woodwardi* (Fig. 2C) and *B. hibbardi* (see Campbell 1979: Fig. 28 A(i)–(iii) = holotype ROM 16905) in having tarsometatarsus with stouter shaft (relatively thinner, more gracile in *B. woodwardi* and *B. hibbardi*), distal end flattened and more expanded bilaterally, especially above the trochleae (distal end thinner, less expanded in *B. woodwardi* and *B. hibbardi*), trochlea II short, poorly projected distad (longer, projected more distad in *B. woodwardi* and *B. hibbardi*), trochlea III small, nearly squared, with thin groove and more laterally angled (larger, less squared, with wide groove and less bent laterad in *B. woodwardi* and *B. hibbardi*). Trochleae deep and massive in distal view (trochleae shallower and less massive in *B. woodwardi* and *B. hibbardi*). The new species is larger than *B. concordatus* (see



Figure 3. Hypothetical reconstruction of Wolf Hawk *Buteogallus irpus* (William Suárez)

Suárez 2004: 122) from the late Pliocene (late Blancan) of Florida and Arizona which is the smallest of the former 'Amplibuteo' species (see Emslie & Czaplewski 1999).

Compared with tarsometatarsi of the continental extinct species *B. daggetti* and *B. terrestris* (the latter known from incomplete specimens), both represent more gracile species, with the former (*c.*40% larger than the average size of *B. meridionalis*, see Olson 2007) being the longest and more gracile of the extinct *Buteogallus* compared. The tarsometatarsus of *B. daggetti* differs from the same elements in *B. irpus* in being extremely elongated, gracile and straight, with a deep anterior metatarsal groove, tubercle for tibialis anticus well centred on the mid-line of the shaft and well separated from the anterior external metatarsal ridge by a wide groove (see Olson 2007: Figs. 1C, 2C, Suárez & Olson 2009b: Fig 1D). *B. daggetti* and *B. terrestris* do not exhibit the characteristic expanded distal end, or the reduction of the trochlea III (see Campbell 1979: Figs. E (i)–(ii), Olson 2007: Figs. 1C, 2C), diagnostic of *B. irpus* sp. nov. The extinct *B. fragilis* and *B. royi* are distinct, apart from their much smaller size when compared to *B. irpus* sp. nov., in having more slender or gracile tarsometatarsi, anterior and posterior metatarsal grooves deeper, and the tubercle for tibialis anticus more proximad (see Suárez 2020: Figs. 9–10).

B. irpus differs from comparable elements in extinct *B. borraisi* from Cuba, in having: humerus (see Suárez 2004, Figs. 2A–C, Suárez & Olson 2008, Fig. 2A) larger and robust, proximal head less projected, capital groove wider and deeper, and ligamental furrow larger (smaller and gracile, head more projected, capital groove thin and shallow, and ligamental

furrow smaller in *B. borrasii*). Ulna (in *B. irpus* sp. nov. known only by a segment of middle shaft, see Suárez 2004: Fig. 2D) robust, with better-developed inner and outer papillae of secondaries (more gracile, both papillae smaller or less developed in *B. borrasii*). Femur (see Suárez 2004: Fig. 2F–G) also more robust, with attachment of round ligament smaller and deeper (expanded, shallow and vertically oriented in *B. borrasii*), shaft cylindrical in cross section, less compressed anteroposteriorly at ends (more ovoid and compressed in *B. borrasii*), prominent anterior intermuscular line, more distally extended along the mid-line of the shaft (less developed, more laterally located and restricted to the proximal half of shaft in *B. borrasii*, see Suárez & Olson 2008: Fig. 3A), pneumatic foramen large and oval-shaped (consistently smaller and rounded in *B. borrasii*), and large condyles (smaller in *B. borrasii*). Tibiotarsus (in *B. irpus* sp. nov. known only by a proximal segment of shaft, see Suárez 2004: Fig. 2I) robust with fibular crest short and greatly projected (gracile, fibular crest larger but less projected in *B. borrasii*, see Suárez & Olson 2008: Fig. 3E). Tarsometatarsus (Figs. 1–2; see Suárez 2004: Fig. 2J–L, Suárez & Olson 2008: Fig. 1) shorter, wider, with robust shaft well expanded above the trochleae, and shallow anterior and posterior metatarsal grooves (gracile and slender, not expanded above the trochlea with deeper grooves in *B. borrasii*). Trochleae distally placed on shaft, trochlea III short, with marked lateral orientation. Phalanx I-digit 1 (see Suárez 2004: Fig. 2M) shorter, robust and not too curved downward (longer, less robust and more curved in *B. borrasii*). Ungual phalanges less curved than in *B. borrasii* (see Suárez 2004: Fig. 2N–O, Suárez 2020: Fig. 8H).

Compared with the holotype tarsometatarsus of *Titanohierax gloveralleni* (MCZ 2257) from the Bahamas (Fig. 2E), the same element in *B. irpus* is slightly smaller, shorter and robust, and less flattened, as it is less compressed anteroposteriorly at the distal end, the trochleae are shorter (trochlea II unknown in *T. gloveralleni*), especially trochlea IV, in which the lateral rim (distal view) is also less pronounced (longer, more projected distally, with lateral rim pronounced in *T. gloveralleni*), posterior metatarsal groove shallow (much deeper in *T. gloveralleni*) and metatarsal facet not as highly placed, or proximal (see Wetmore 1937: 430, Olson & Hilgartner 1982: 28).

B. irpus is considerably smaller compared to the huge Cuban species *Gigantohierax suarezi*, with the following characters (*cf.* Suárez 2004: 122–123): femur shaft straight, nearly circular in cross-section (curved anteroposteriorly, greatly compressed in *G. suarezi*), anterior intermuscular line centred on shaft (lateral in *G. suarezi*), proximal and distal end not expanded (greatly expanded in *G. suarezi*), poor pneumaticity proximad (great pneumaticity in *G. suarezi*), head thinner and rounder with long neck, attachment of round ligament smaller (head broad or expanded, with short neck and attachment of round ligament large, vertically oriented, in *G. suarezi*), iliac facet wide (thin in *G. suarezi*), distally the rotular groove is shallow (deep in *G. suarezi*), and reduced but deeper popliteal area (large and shallow in *G. suarezi*). The tarsometatarsus is less compressed anteroposteriorly, being more triangular in cross-section (more compressed, flatter or less triangular in *G. suarezi*), and external proximal half of shaft nearly flat (convex in *G. suarezi*). Differs from *G. itchei* (Fig. 2D) also from Cuba, in having femur smaller, not flared or flattened (compressed anteroposteriorly) at proximal end, with less pneumaticity proximad (wider, flaring greatly proximad, with a distinctive concavity formed by the most proximal pneumatic foramen in *G. itchei*). The tarsometatarsus also lacks the diagnostic thinner and deep anterior metatarsal groove on a flattened shaft, with less anteroposterior compression at the distal end, resulting in a narrower distal end compared to *G. itchei* (see Suárez 2020: 26–27). For additional comparisons, descriptions, measurements and illustrations of fragmentary elements of the paratype skeleton WS 365 with other taxa, including *B. fragilis* and extinct West Indies accipitrids such as *B. borrasii*, *Titanohierax gloveralleni* and

Gigantohierax suarezi, see Suárez (2004: 121–124, Figs. 1–3, Table 1) and Suárez & Olson (2008: Fig. 1).

Discussion

The systematic position of several extinct American *Buteogallus* species has been obscured by the presence of eagle-like large sizes, with erroneous placements in the genera *Aquila* Linnaeus, '*Wetmoregyps*' L. Miller, '*Amplibuteo*' and '*Miraquila*' (Miller 1928, Arredondo 1970, Campbell 1979). No complete tarsometatarsi of *B. terrestris* are known from the Talara Tar Seeps, Peru, and this fossil species' relationships with living Buteogallines are more difficult to establish, although a strong resemblance to the skeleton of *B. meridionalis* exists (Suárez & Olson 2009b: 250). We report here that a variation previously considered a diagnostic character of *B. terrestris* by Campbell (1979: 74), i.e. the inner calcaneal ridge of hypotarsus projecting posteriad at 90° to vertical axis of shaft (see Suárez & Olson 2009b: 250) occurs in some tarsometatarsi of *B. meridionalis* (e.g., USNM 319439). So, this character is invalid in the diagnosis of *B. terrestris*.

The presence of *B. irpus* in Cuba and on Hispaniola is probably due to a similar Quaternary fauna present at one time on both islands (see mammals of the Greater Antilles in Silva Taboada *et al.* 2007: Table 4.1). This distribution suggests that some large raptors formerly known only from Cuba may also be found on Hispaniola. Recently, Steadman *et al.* (2019) reported 24 fossil bones (tibiotarsus, tarsometatarsus, hallux, pedal phalanges) as Accipitridae genus and species indeterminate, which they considered close to genus *Geranoaetus*, from Quaternary cave deposits on Hispaniola (= Haiti and the Dominican Republic), and representing, according to these authors, a single taxon. Illustrations, descriptions and measurements therein indicate instead that the material corresponds to two different-sized accipitrids. The largest of the two incomplete tibiotarsi reported (huge size and supratendinal bridge more horizontal, see Steadman *et al.* 2019: Fig. 1B), agrees with, and was tentatively identified as *Gigantohierax* sp. by Suárez (2020: 25). The smaller and more fragmentary tibiotarsus (Vertebrate Paleontology Collection of the Florida Museum of Natural History, Univ. of Florida, Gainesville, UF 241755) is from Cueva de las Abejas, as is true for the holotype of *B. irpus* sp. nov., and also was collected by C. Woods. It is probable that this fragment of tibiotarsus represents the new species described here. This bone, according to published illustrations, possesses a supratendinal bridge more vertically oriented than in *G. suarezi*, but more horizontal than in *B. woodwardi* or *B. hibbaridi*, probably in accordance with the reduction and configuration of the trochleae in the tarsometatarsus of *B. irpus* sp. nov. *Gigantohierax* is the most distinctive and probably oldest genus of Accipitridae in the West Indies, resembling Old World vultures in some characters, and its osteology and relationships will be described elsewhere (Suárez *et al.* unpubl.). In conclusion, Hispaniola and Cuba appear to have shared two large eagle-sized hawks, both endemic to the West Indies, and not related to the extinct Bahamian genus *Titanohierax* Wetmore, which is so far confined to the Lucayan archipelago (Wetmore 1937, Olson & Hilgartner 1982, Suárez 2020).

The abundance of reptiles and mammals derived from the endemic regional 'megafauna' in the West Indies provided a series of prey (see Steadman *et al.* 2019), potentially partitioned by raptors based on their respective sizes (for a comparable pattern in large Tytonidae from the West Indies, see Suárez & Olson 2015). The evolution in the Antillean subregion of probably pre-Quaternary, highly specialised raptorial lineages (see Suárez & Olson 2009a), which became extinct in the Holocene apparently linked to the extinction of the 'megafauna', corresponds with other non-raptorial, ancient bird lineages also identified on these islands (*cf.* Olson 1978, 1985, Olson & Wiley 2016, among others).

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Addresses: William Suárez, P.O. Box 16477, West Palm Beach, FL 33416, USA, e-mail: ws@wsbirdingtours.com. Storrs L. Olson[†], Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA.

The status of Great-winged Petrel *Pterodroma macroptera* in the south-west Atlantic Ocean, with notes on separation from dark-morph Trindade Petrel *P. arminjoniana*

by *Fernanda Caminha Leal Valls, Maurício Tavares, Robert Louis Flood & Leandro Bugoni*

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SUMMARY.—Great-winged Petrel *Pterodroma macroptera* is currently considered uncommon in the south-west Atlantic Ocean. However, via a compilation of all recent records available, we found evidence of a regular, wider distribution from breeding colonies in Tristan da Cunha and Gough towards South America. We review these records, report a new beach stranding in Brazil, which is the northernmost record in the south-west Atlantic, and discuss the problems of at-sea separation of Great-winged Petrel from the darkest-plumaged Trindade Petrel *P. arminjoniana*.

Great-winged Petrel *Pterodroma macroptera* breeds on islands in subantarctic waters, at the Tristan da Cunha group (including Gough), the Crozets, Marion, Prince Edward, the Kerguelen group, and on islands off Western Australia (Shirihai 2007, Flood & Fisher 2015). Typically, it ranges at sea between 35° and 55°S, from the South Atlantic to south-west Australia (BirdLife International 2018, Howell & Zufelt 2019), but is considered uncommon in the south-west Atlantic Ocean (e.g., Flood & Fisher 2015, Howell & Zufelt 2019). However, records since 1959 indicate a wider regular distribution reaching South America (and south of the breeding islands; Table 1). Our compilation includes records from 20°W to South America based on the published literature, one seen in February 2020 beyond the shelf break about halfway between Uruguay and the Falkland Islands (RLF pers. obs.), and from eBird (2021).

In addition, on 24 May 2019 a beached Great-winged Petrel (Fig. 1) was collected on Tramandaí beach (30°02'S, 50°08'W), in northern Rio Grande do Sul state, southern Brazil (Fig. 2). Notable for being the northernmost continental record, it was found during a beach monitoring survey following a storm associated with a cold front. Several other Procellariiformes were also found, including Cory's *Calonectris borealis* and Great Shearwaters *Ardenna gravis*. Dissection and biometrics were undertaken in December 2019. The specimen is an immature female, aged by a well-developed bursa of Fabricius, and sexed by microscopic evaluation of the gonads. The lack of evidence of past or active moult aged it as a juvenile (Bugoni & Furness 2009). Overall, the bird was brownish black, with a greyish chin and blackish bill. Underwings were dark with contrasting pale grey reflective larger coverts and remiges. Legs and toes were blackish.

Biometrics were taken using a flexible tape and vernier callipers (Fig. 1): total body length 408 mm, wing length 305 mm (and fairly slim), tail length 130 mm, culmen length 34.9 mm, height of bill at its base 15.5 mm, width of bill at its base 17.1 mm, tarsus 44.8 mm and middle toe 63.6 mm. Bill length was measured from the tip of the mandibular unguis because the maxillary unguis was missing (a minimum value only for reference, Fig. 1b). Wingspan was estimated at 1,040 mm by doubling the value for the right-hand wing. Body mass after drying and cleaning was 361 g.

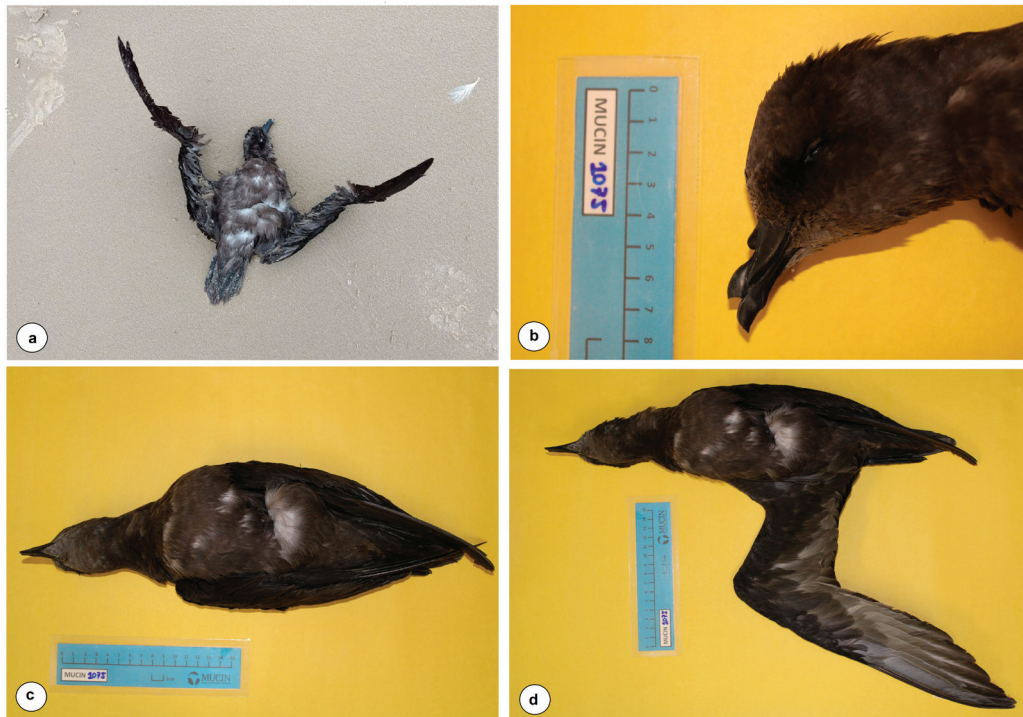


Figure 1. Great-winged Petrel *Pterodroma macroptera* collected in Rio Grande do Sul, Brazil (MUCIN 1075): (a) when found, on 24 May 2019, on Tramandaí beach, (b) head, in lateral view, lacking final portion of the maxillary unguis, (c) ventral view, and (d) ventral view and left underwing, with larger coverts and remiges appearing grey, contrasting with the rest of the brownish-black underwing-coverts (Maurício Tavares)

To confirm the identification, we compared our measurements to those of Great-winged, Trindade *Pterodroma arminjoniana* and Kerguelen Petrels *Lugensa brevirostris* in Flood & Fisher (2015); see Table 2. The data are consistent only with Great-winged Petrel. Compared to Trindade Petrel, Great-winged Petrel body length and wingspan are both 5% longer and wing length 6% longer (Luigi *et al.* 2009); vs. Kerguelen Petrel, Great-winged Petrel body and wing lengths are both 17% longer (Table 2; Maurício *et al.* 2014).

In addition, ectoparasites were collected for qualitative analysis, tissue and organ samples were taken for the Banco Nacional de Amostras de Albatrozes e Petréis (Brazilian Albatross and Petrel Sample Bank), and back and breast feathers for trace element analysis. The gastrointestinal content indicated no debris in the esophagus, pro-ventricle, ventricle, and intestine cavities. Cephalopod beaks were found in the proventricle ($n = 1$) and ventricle ($n = 12$); these were identified as three upper and eight lower beaks, from eight different specimens, of which two were *Histioteuthis* sp. There was no subcutaneous fat, and pectoral musculature was slightly thick, especially the supracoracoideus muscle, which was very slim, consistent with an emaciated specimen. The complete skeleton, primaries, and rectrices are deposited at the Museu de Ciências Naturais, Universidade Federal do Rio Grande do Sul, Imbé, Rio Grande do Sul, registration number MUCIN 1075.

Separation of Great-winged Petrel from dark-morph Trindade Petrel

Great-winged Petrel and dark-morph Trindade Petrel with largely dark underwings are tricky to identify (Flood & Fisher 2015), especially in the South Atlantic where they are sympatric. The latter breeds on Ilha da Trindade (20°30'S, 29°19'W; Leal *et*

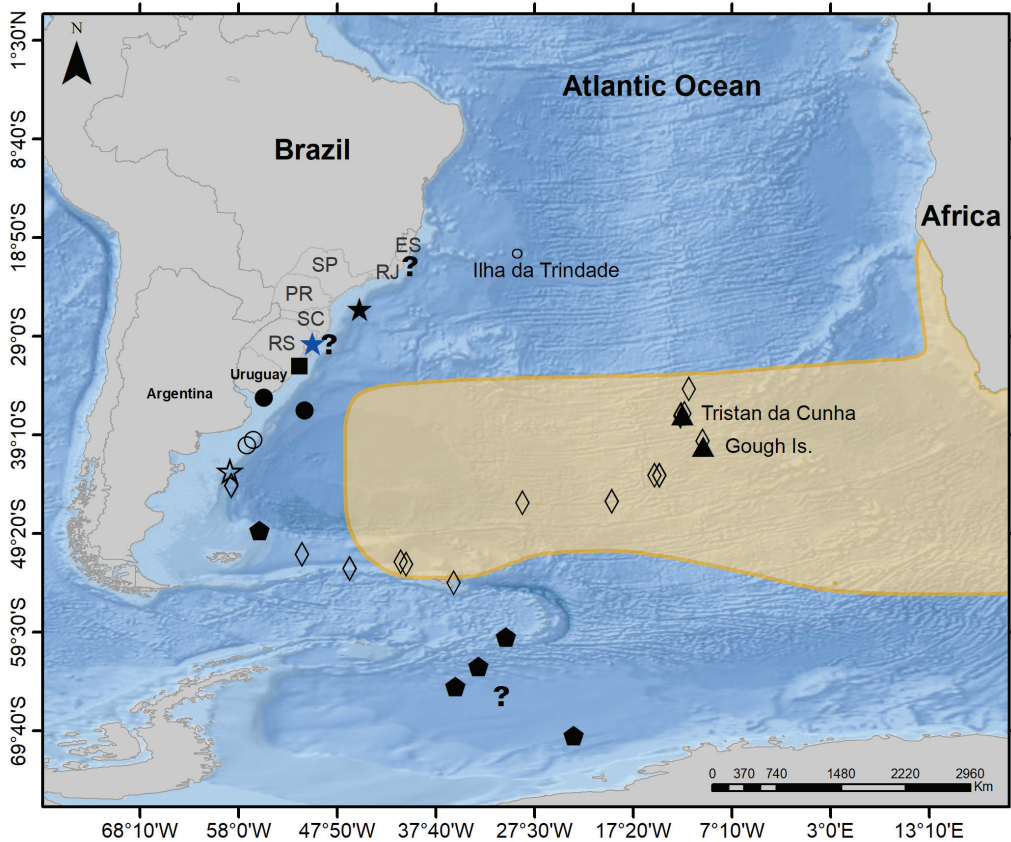


Figure 2. Great-winged Petrel *Pterodroma macroptera* distribution (shown in dull yellow) based on BirdLife International (2018). New record on the Brazilian coast reported herein (blue star); the only previous documented record in Rio Grande do Sul (RS) state, in southern Brazil (filled square); two records in Uruguay (filled circles); three records in Argentine waters (unfilled circles); the most recent record in the south-west Atlantic, in February 2020 (unfilled star); and records in the Falklands, South Georgia, and Southern Ocean waters are all shown (pentagons). Documented records in the central and south-west Atlantic from eBird (2021) (unfilled diamonds) and questionable records from Harris & Hansen (1974) and Mazar Barnett & Pearman (2001) are indicated by ?. Breeding colonies in the Atlantic at Tristan da Cunha and Gough are indicated (filled triangles). The case study individual identified as Trindade Petrel *Pterodroma arminjoniana* photographed in 2019 in Brazilian waters (filled star) is depicted in Fig. 3. Brazilian states: Espírito Santo (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR) and Santa Catarina (SC).

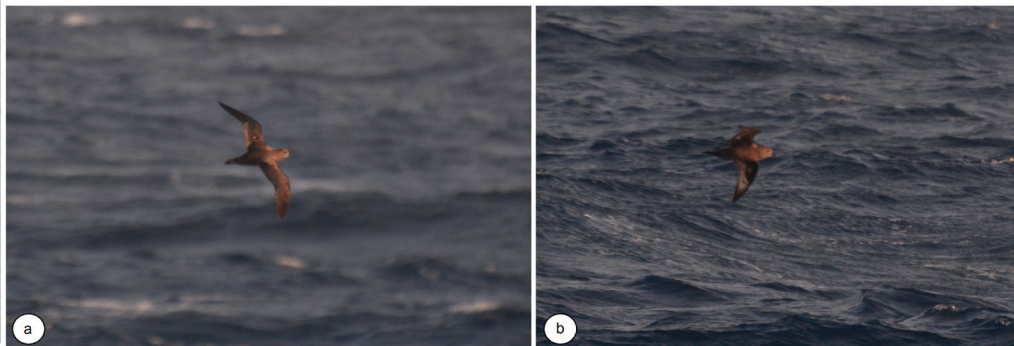


Figure 3. Trindade Petrel *Pterodroma arminjoniana* off the Brazilian continental shelf, August 2019: (a) all-dark upperparts and (b) underside showing the underwing pattern with whitish at the bases of the primaries and greater primary-coverts (Fernanda C. L. Valls)



Figure 4. Dark-morph Trindade Petrels *Pterodroma arminjoniana*, Ilha da Trindade, South Atlantic: (a) small squarish head of an intermediate to dark morph; (b) all-dark upperparts; (c) dark underwings showing a trace of the pale bases to the primaries and greater primary-coverts; (d) a more typically patterned individual, with a broad whitish panel on the underwing, but the greater coverts are dark distally, forming a narrow crescent on the tips of the greater primary-coverts; and (e) dark underparts and the blackish legs, feet and toes (Leandro Bugoni)

TABLE 1

Records of Great-winged Petrels *Pterodroma macroptera* in the south-west Atlantic Ocean (west of 20°W). No. of observations or 'X' is used to indicate presence. * = questionable records; ** = supported by photographs.

Date	Location	Coordinates	No. of birds (X = present)	Source
Dec 1959	south of South Georgia	60°S, 30°W	3	Mazar Barnett & Pearman (2001)
Apr 1960	Argentine continental shelf	40°S, 57°W	1	Mazar Barnett & Pearman (2001)
Jan 1970	Argentine continental shelf	39°21'S, 56°20'W	3	Mazar Barnett & Pearman (2001)
Sep 1973*	Brazilian continental shelf	20°S, 39°W–24°S, 42°W	3	Harris & Hansen (1974)
Sep 1973*	Brazilian continental shelf	29°07'S, 47°44'W	3	Harris & Hansen (1974)
Apr 1977	South Georgia waters	-	1	Mazar Barnett & Pearman (2001)
Feb 1980	South Georgia waters	-	1	Mazar Barnett & Pearman (2001)
Aug 1982	Falkland Islands	49°S, 55°W	3	Mazar Barnett & Pearman (2001)
Aug 1982	Falkland Islands	49°S, 55°W	6	Mazar Barnett & Pearman (2001)
Mar 1985	South Georgia waters	-	1	Mazar Barnett & Pearman (2001)
Feb 1990	Cape Pembroke, Falkland Islands	-	1	Mazar Barnett & Pearman (2001)
Feb 1992	Argentine continental shelf	39°02'S, 57°03'W	1	Mazar Barnett & Pearman (2001)
Jan 1994	Southern Ocean	64°09'S, 30°10'W– 65°12'S, 25°41'W	25	Mazar Barnett & Pearman (2001)
Feb 1994*	Southern Ocean	67°59'S, 26°24'W– 67°52'S, 26°57'W	2	Mazar Barnett & Pearman (2001)
Feb 1994	eastern Weddell Sea	69°05'S, 21°24'W	64	Montalti <i>et al.</i> (1999)
Feb 1994	Southern Ocean	66°08'S, 33°09'W	1	Mazar Barnett & Pearman (2001)
Dec 1995	north of South Georgia	-	1	Mazar Barnett & Pearman (2001)
May 2003	Uruguayan coast	34°50'S, 55°56'W	1	Jiménez <i>et al.</i> (2012)
Mar 2004	Rio Grande do Sul, Brazil	33°09'S, 52°39'W	1	Bugoni (2006)
Mar 2007	Uruguayan waters	36°04'S, 51°00'W	1	Jiménez <i>et al.</i> (2012)
Apr 2012	north of Shag Rocks, South Georgia	-	1	Flood <i>et al.</i> (2012)
Apr 2012	South Georgia and north-east of Falkland Islands	-	10	Flood <i>et al.</i> (2012)
Apr 2012**	South Georgia and South Sandwich Islands	52°28'S, 40°46'W	X	eBird (2021)
Apr 2012**	South Georgia and South Sandwich Islands	52°16'S, 41°18'W	X	eBird (2021)
Apr 2012	South Georgia/Falkland Islands	-	2	Flood <i>et al.</i> (2012)
Apr 2012	north of Falkland Islands	-	3	Flood <i>et al.</i> (2012)
Apr 2012	South America continental shelf	-	3	Flood <i>et al.</i> (2012)
Jun 2016**	South Georgia and South Sandwich Islands	54°26'S, 35°51'W	1	eBird (2021)
Mar 2018**	South Georgia and South Sandwich Islands	52°57'S, 46°35'W	1	eBird (2021)
Apr 2018**	South Atlantic	46°11'S, 28°46'W	1	eBird (2021)
Feb 2019**	Argentine continental shelf	44°24'S, 58°44'W	3	eBird (2021)
May 2019	Rio Grande do Sul, Brazil	30°02'S, 50°08'W	1	This study
Feb 2020	beyond the shelf break (Uruguay to Falkland Islands)	43°35'S, 57°42'W	1	RLF pers. obs.

TABLE 2

Measurements (mm) of Great-winged Petrel *Pterodroma macroptera* specimen (MUCIN 1075) found on Tramandai beach, Rio Grande do Sul, Brazil, compared to other specimens previously reported in the literature and other potential confusion species such as Trindade Petrel *Pterodroma arminjoniana* (Luigi et al. 2009, Leal et al. 2019) and Kerguelen Petrel *Lagenosa brevirostris* (Schramm 1983, Mauricio et al. 2014) with their respective samples sizes (n). * = indicates mean values from live individuals.

Species	Body length	n	Wing length	n	Tail length	n	Height of bill at its base	n	Width of bill at its base	n	Tarsus length	n	Culmen length	n	Wingspan	n	Source
<i>P. macroptera</i> (MUCIN 1075)	408		305		130		15.5		17.1		44.8		34.9		1,040		This study
<i>P. macroptera</i> (MINHN 6235)	400		323		125		15.0		15.3		43.5		36.7		1,060		Jiménez et al. (2012)
<i>P. macroptera</i> (CAFURG 360)																	Bugoni (2006)
<i>P. macroptera</i> *			307 ± 6.8	52							44.4 ± 1.09	53	36.3 ± 0.98	54			Schramm (1983)
<i>P. arminjoniana</i> *	388.9 ± 15.9	69	286.7 ± 8.8	496	114.8 ± 4.7	480					37.7 ± 1.5	443	29.6 ± 1.3	445	987.1 ± 26.0	69	Luigi et al. (2009)
<i>P. arminjoniana</i> males*			298 ± 89.4	10	118 ± 35.4	10	13.2 ± 4.0	10			38.7 ± 11.6	10	30.7 ± 9.2	10			Leal et al. (2019)
<i>P. arminjoniana</i> females*			291 ± 87.3	10	112 ± 33.2	10	14.6 ± 14.6	10			40.3 ± 12.1	10	30.3 ± 9.1	10			Leal et al. (2019)
<i>L. brevirostris</i> (CAFURG 450)	350		260		138						37.6		27				Maurício et al. (2014)
<i>L. brevirostris</i> *			257 ± 6.4	121							39.5 ± 1.24	121	26.7 ± 1.47	118			Schramm (1983)

al. 2019), c.1,200 km east of the coast of the Brazilian state of Espírito Santo, and its at-sea range is reasonably well known (Leal et al. 2017, Ramos et al. 2017). During its year-round breeding, Trindade Petrel reaches the Subtropical Convergence zone and even subtropical waters off southern Brazil, Uruguay, and Argentina (Leal et al. 2017). Our compilation of Great-winged Petrel records (Table 1) demonstrates that its at-sea range overlaps quite extensively with that of Trindade Petrel. Thus, correct at-sea identification is essential to determine the distributional limits of Great-winged Petrel.

On 31 August 2019, at 07.00 h, during a seabird census onboard the research vessel MV *Searoute*, a long-winged ‘all-dark’ *Pterodroma* was observed and photographed (Fig. 3) nearly 200 km off the state of Santa Catarina, southern Brazil (26°42’S, 45°17’W), and c.600 km beyond the most northerly Great-winged record in southern Brazil, but well south of the northernmost claim, off Espírito Santo, mentioned by Harris & Hansen (1974) (Fig. 2). As dark-morph Trindade Petrel is known to occur in the area (Leal et al. 2017, Ramos et al. 2017), the August 2019 *Pterodroma* makes an interesting identification case study.

The side of the vessel used to census seabirds was chosen to avoid backlit effects on birds that can make identification difficult (Tasker et al. 1984). Ocean depth was 2,250 m, the wind north-northwest 14 knots, or 4 on the Beaufort scale. The survey formed part of the Projeto de Caracterização Ambiental da Baía de Santos coordinated by Petrobras.

At first glance, the bird resembled a Sooty Shearwater *Ardenna grisea*, having long wings and an ‘all-dark’ body. Sooty Shearwater, Great-winged Petrel and dark-morph Trindade Petrel can be confused with one another (Flood & Fisher 2015). However, the bird’s buoyant flight style and wings bent at the carpal joint recalled a *Pterodroma* rather than a shearwater. Photographs revealed a fairly heavy and short bill, unlike the relatively long- and



slim-billed shearwater. Dark-morph Soft-plumaged Petrel *Pterodroma mollis* and 'all-dark' Kerguelen Petrel potentially occur in the area, but were easily eliminated by structural and plumage characteristics (e.g., Maurício *et al.* 2014, Flood & Fisher 2015). The only other 'all-dark' *Pterodroma* petrel considered plausible is dark-morph Trindade Petrel (Fig. 4).

Dark-morph Trindade and Great-winged Petrels are similar-sized medium-large *Pterodroma* (Flood & Fisher 2015) with long, fairly slim wings, and 'all-dark' upperparts and underparts. The challenge of separating Great-winged from the darkest Trindade Petrels with restricted white in the underwing (e.g., Fig. 4) is not widely appreciated and may have led to misidentifications. For example, it is reasonable to query the three Great-winged Petrels on a single day in September off Espírito Santo and Rio de Janeiro (Harris & Hansen 1974), at the same latitude as Ilha da Trindade and well within the distribution of Trindade Petrel (Leal *et al.* 2017, Ramos *et al.* 2017).

Separation requires careful study of the underwing pattern and structure. The basic colour of 'all-dark' Trindade Petrel is dark greyish brown to blackish brown, typically with a complex 'dark-and-whitish' underwing pattern. In some cases only the bases of the primaries and greater primary-coverts are whitish, indistinctly paler (Fig. 4), or not pale. The darkest birds are brownish black, even including the legs and toes (Luigi *et al.* 2009; Fig. 4e). Trindade Petrel is the 'rangier' of the two, with a small squarish head, steep sloping forehead, long caudal projection, and medium-length tail normally held closed so that it tapers to a point (Fig. 4; Flood & Fisher 2015). Great-winged Petrel is basically brownish black, but the underwing has reflective larger coverts and remiges that may contrast pale grey (Howell & Zufelt 2019). It is less 'rangy' than Trindade, with a larger head, longish caudal projection and mid-length wedge-shaped tail that is normally held partly open. Trindade Petrels without the typical underwing pattern, thus like Great-winged Petrel, must be identified using structure alone.

Photographs of the August 2019 *Pterodroma* (Fig. 3) show a blackish-brown bird with whitish bases to the underside of the primaries and greater primary-coverts. It is vital to establish if the whitish markings result from reflected light as in the Great-winged Petrel photographs in Howell & Zufelt (2019: 140). In our photographs, the whitish is well defined in clear contrast with a dark crescent on the distal 'third' of the greater primary-coverts. This is a plumage characteristic and not an artefact of reflected light. General colour is unreliable as the photographs were taken in the early morning. The main structural characteristic evident is a long caudal projection and a tail that tapers to a point. Although the photographs are not sharp, the pattern of the underwing and the structure of the rear end are sufficient to prove that the bird was a Trindade Petrel.

Conclusions

Our compilation of records indicates that Great-winged Petrel regularly occurs in offshore south-west Atlantic waters, north as far as the Subtropical Convergence Zone in southern Brazil. These are not shown as areas of regular occurrence in field guides (e.g., Flood & Fisher 2015, Howell & Zufelt 2019). Our case study illustrates the challenge of separating Great-winged and the darkest Trindade Petrels. Continued at-sea studies and systematic beach surveys for stranded individuals will help to confirm the status of these species in the south-west Atlantic. Beach surveys are regular (e.g., Valls *et al.* 2015, Tavares *et al.* 2020), but systematic censuses of pelagic seabirds are scarce (Mott & Clarke 2018). We recommend greater effort in systematic at-sea surveys in the south-west Atlantic with a special focus on these species.

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Addresses: Fernanda C. L. Valls & Leandro Bugoni, Laboratório de Aves Aquáticas e Tartarugas Marinhas, Instituto de Ciências Biológicas & Instituto de Oceanografia, Universidade Federal do Rio Grande—FURG, Campus Carreiros, Av. Itália km 8, 96203-900, Rio Grande, RS, Brazil, e-mail: fernandaclvalls@gmail.com. Maurício Tavares, Centro de Estudos Costeiros, Limnológicos e Marinhos, Campus Litoral Norte, Universidade Federal do Rio Grande do Sul—CECLIMAR/CLN/UFRGS, Av. Tramandai 976, Centro, 95625-000, Imbé, RS, Brazil, and Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Prédio 43435, 91540-000, Porto Alegre, RS, Brazil. Robert Louis Flood, FitzPatrick Institute of African Ornithology, University of Cape Town, Town, Rondebosch 7701, South Africa.



What's in a name? Nomenclature for colour aberrations in birds reviewed

by *Hein van Grouw*

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SUMMARY.—A review is presented of the seven commonest types of colour aberrations in birds together with suggestions for a standardised universal nomenclature to identify and distinguish these aberrations. These aberrations are: Leucism (congenital absence of melanin-producing cells), Progressive Greying (progressive loss of melanin-producing cells), Albino (total absence of melanin due to lack of the key enzyme), Brown (incompletely coloured melanin), Ino (even less completely coloured melanin), Dilution (altered deposition of melanin) and Melanism (altered distribution of melanin). It is proposed that these terms should be based not only on the resulting plumage but also should distinguish the underlying processes resulting in the aberrant pigmentation. By reviewing previously used terms for colour aberrations, and cross-referencing these with my proposed terminology, errors in earlier names are pointed out, and resulting in a more comprehensive nomenclature for colour aberrations found in wild birds.

'There has been some confusion in the past in the recording and description of variant plumages ... and this paper represents an attempt to clarify some parts of it.' (Harrison 1963a)

Colour aberrations in birds have been my main research for more than 30 years, during which I have learnt that identifying and naming these aberrations still present problems for ornithologists. An important reason for this is probably that the appearance of similar heritable aberrations (mutations) may differ radically between species, and sexes and ages of the same species, all depending on the normal pigmentation. This, plus the fact that the individual might be too far away or moving too quickly to see well, often makes it difficult to distinguish the different aberrations from each other. The main reason for the difficulties, however, may be the unfamiliarity with the different forms in combination with the numerous terms used seemingly randomly for these colour aberrations.

When attempting to identify an aberration, it is important to know exactly how the original plumage colour of the relevant species should look! With that in mind, observe in what way the colour (pigmentation) is changed. However, having done that, what do we call it?

Knowledge of melanin pigmentation development and genetics has been gained mostly via studies of domesticated species such as mice and chickens. Genetic studies in mammals, especially mice, are probably the most thorough (Lamoreux *et al.* 2010, Eizirik & Trindade 2021). From an early stage, it became obvious that different mammal species had a similar series of heritable coat colour variants (Searle 1968). This marked the launch of scientific comparative genetics in mammals, and one result was that similar mutations were allocated the same name in all species. The similarity was based on the relevant gene action on the pigmentation process, and not necessarily on the appearance of the final coat colour, as this can differ between species. Establishing some uniformity in the nomenclature of mutations in birds, however, has so far been greatly neglected.

TABLE 1
Names used for colour aberrations in birds by earlier authors.

van Grouw (2021)	Frauenfeld (1853)	von Pelzel (1865)	Pavesi in Picchi (1903)	Rensch (1925)	Harrison (1963a,b)	Davis (2007)
<i>Defects in the development of melanin cells (White Spotting)</i>						
Leucism	Allochromatism	Partial Albinism	Allochromatism	Partial albino and Leucism	Leucism and non-melanin	Partial Amelanism
Progressive greying	Geratochromatism	Partial Albinism	Geratochromatism	Partial albino	Leucism	Partial Amelanism
<i>Defects in melanin synthesis (Albinism)</i>						
Albino	Leucochromatism	Complete Albinism	Leucochromatism	Albino	Albino	Total Amelanism
Brown	Chlorochromatism	Incomplete Albinism	Isabelism	Chlorochromatism and Schizochromism	Dilution and Non-eumelanic schizochromism (fawn) and Erythrism	Aeumelanism
Ino	Chlorochromatism	Incomplete Albinism	Flavism		Non-melanin	Not recognised
<i>Defects in the melanin deposit into the feathers (Dilution)</i>						
Dilution (pastel)	Chlorochromatism	Incomplete Albinism	Chlorochromatism, Isabelism and Flavism	Chlorochromatism and Schizochromism	Dilution and Non-phaeomelanic schizochromism (grey)	Hypomelanism and Aphaemelanism
Dilution (isabel)				Schizochromism		
<i>Defects in the type of melanin produced (Melanism)</i>						
Melanism	Allochromatism	Melanism and Erythrism	Melanism and Erythrism	Eumelanism and Phaeomelanism	Melanism and Erythrism	Hypermelanism



Figure 1. Ino in European Greenfinch *Carduelis chloris*, bred and held in captivity; the reduction of both melanins results in the underlying carotenoids being more clearly visible. Rather than an increase of carotenoid pigment, the predominantly yellow plumage is the result of decreased melanin, making a term like Flavism an incorrect name for this aberration (© Pieter van den Hooven)

In fact, a standardised nomenclature for melanin mutations will cover almost all colour mutations in birds. For example, names for supposed carotenoid mutations, like Xanthochromism, Flavism and Erythrism, are often applied to birds that are afflicted by a melanin mutation. Any reduction of melanin results in the underlying carotenoids becoming clearer (Fig. 1). So, instead of an increase of carotenoid pigment, a predominantly yellow (or red) plumage is often the result of decreased melanin. Therefore, mutations should not be named for the final plumage colour, as different mutations can cause a similar effect, and vice versa, but to reflect the relevant aberration in the pigmentation process, as this is the same each time.

I have been working for many years (van Grouw 2006, 2010, 2013) to achieve a comprehensive nomenclature for colour aberrations in wild birds, as have others during the last almost 175 years (Table 1).



I use traditional terminology, mostly from the earlier period in genetic science, but try to define and clarify original meanings. I will highlight areas of disagreement with earlier terminology based on the resulting appearance by considering the underlying reasons for the aberrations. Different mutations with a similar phenotypic result were often lumped under a single name. Finally, some earlier terms, like 'Leucism', have become disassociated from their original meaning (white feathers), leading to confusion, with names randomly used to identify aberrant-coloured birds. The name, however, should not be based on the resulting plumage alone, as the underlying processes vary. It is important to bear in mind, however, that almost all aberrations can be identified only by their appearance (phenotype), as breeding tests and / or feather analyses are often impossible with wild birds. By considering the underlying processes, a more comprehensive nomenclature for colour aberrations in wild birds will be presented.

Where unreferenced statements concerning colour aberrations in birds (inheritance, pigmentation) are made herein, they are based on personal findings during unpublished research into this subject over the last 30 years, involving both practical breeding experiments with captive birds and examination of >4,000 aberrant-coloured specimens in museum collections.

Melanin mutations

Melanins are the most common pigments in birds and can be distinguished in two forms: eumelanin and pheomelanin. Depending on concentration and distribution within the feather, eumelanin is responsible for black, grey and / or dark brown colours, whereas pheomelanin is responsible for warm reddish brown to pale buff. Together, both melanins can produce a wide range of greyish-brown colours. Besides melanins, two other common pigments in birds are carotenoids and psittacins (the latter only in parrots). These pigments are collectively responsible for most yellow (and green), orange and red plumage. Birds cannot synthesise carotenoids themselves; these must be acquired via the diet. Parrots, however, can synthesise psittacine, so any yellow, orange and red/pink in these species is not diet related.

Due to two very popular bird species in captivity, mutations in carotenoids (Canary *Serinus canaria*) and psittacins (Budgerigar *Melopsittacus undulatus*) have been well studied. Known inheritable abnormalities in these pigments are: (1) total absence; (2) decreased concentration (Fig. 2); (3) change in type (colour)—normally from red to orange or yellow, but not vice versa; and (4) change in distribution, or Carotenism as it is sometimes termed, and often goes together with an increase in concentration (Fig. 3). In parrots



Figure 2. Blue in Great Tit *Parus major*, Fijnaart, the Netherlands, January 2016; due to the strong reduction of yellow carotenoid, the usually yellow and greenish tracts are whitish and bluish grey, respectively (© Alois van Mingerot)

it often occurs also in combination with an altered melanin distribution.

In Canaries all four forms are known (Perez-Beato 2008) although (3), the change in type (from yellow to orange / red), is due to past hybridisation with Red Siskin *Spinus cucullatus* (Lopes *et al.* 2016). Also among parrots (not only Budgerigar) all four forms occur (Martin 2002). The change in type (colour), however, is very rare and recorded in only a few species, whereas the others are more widespread throughout the different species. A total absence of psittacin in parrots is commonly known as Blue; a decreased concentration as Par-blue among breeders, and the change in distribution of psittacin, together with an increased concentration and an altered melanin pattern, is termed Opaline (Martin 2002). For carotenoids, categories 1–3 can also be diet-related. In parrots, categories 3–4 can also occur due to poor physical health. Compared to melanin mutations, carotenoid / psittacin mutations are rare. In this paper I therefore focus on melanin mutations.

Melanin is produced by specialised skin cells known as melanin cells or melanocytes, which develop from melanoblasts formed in the ‘neural crest’—the embryonic spinal cord. Normally, melanoblasts migrate at an early embryonic stage to the mesodermal layers of the skin. Finally incorporated in the skin and feather follicles, melanoblasts develop into melanin cells to provide the feather cells with melanin. The chemical process to produce melanin in the melanin cells is termed melanin synthesis and the final melanin pigment is deposited, via dendritic processes, into the growing feather cells (Crawford 1990). Heritable changes (mutations) in this process may produce aberrant-coloured plumage. In general, different melanin mutations can be divided into four major categories (Lamoreux *et al.* 2010): (1) defects in the development of melanin cells (White Spotting); (2) defects in melanin synthesis (Albinism); (3) defects in the melanin deposit into the feathers (Dilution); and (4) defects in the type of melanin produced (Melanism).

Lastly, the loss of pigment resulting in aberrant plumage can also be caused by external factors. The commonest is dietary imbalance, which normally shows as a mixture of normal pigmentation disrupted by its absence in individual feathers (van Grouw 2018). Other causes resulting in a lack of pigment in parts of the plumage are former injuries / traumas with melanin cell damage as an effect. These aberrations are not included in my proposed nomenclature (Table 2).

Defects in the development of melanin cells (White Spotting)

Two distinct groups of mutations fall into this category; those in which melanin cells are absent in the skin from the outset, and mutations in which the melanin cells progressively disappear, or become less productive. The first I term **Leucism**, from the Greek *leukos* (= white), and the second **Progressive Greying** (see below). In Leucism the lack of melanin is



Figure 3. Increase of carotenoid pigments in European Goldfinch *Carduelis carduelis*, bred and held in captivity; the increased concentration is often coupled with a changed distribution in the carotenoids (© Pieter van den Hooven)

TABLE 2
Proposed nomenclature for the most common colour aberrations in birds.

Colour aberration	Effect on melanins	Effect on plumage and skin colour
<i>Defects in the development of melanin cells (White Spotting)</i>		
Leucism	Total absence of both melanin pigments in either parts or all of the plumage and skin due to a neural crest disorder resulting in the congenital absence of melanin cells from some or all of the skin areas.	All-white plumage all over or all-white feathers mixed with normal-coloured ones. Pink bill and feet or normal-coloured bill and feet depending on where in the skin the cells are missing. Always melanised eyes. In partial Leucism white feathers are often in patches and bilaterally symmetrical divided over the plumage.
Progressive greying	Total absence of both melanin pigments in either parts or all of the plumage (and skin) due to progressive loss of melanin cells in some or all of the skin areas with age.	All-white plumage all over or all-white feathers mixed with normal-coloured ones. Pink bill and feet or normal-coloured bill and feet. Always normal-coloured eyes. In an early stage white feathers are often randomly spread in the plumage.
<i>Defects in melanin synthesis (Albinism)</i>		
Albino	Total absence lack of both melanins in feathers, eyes and skin due to the heritable absence of the enzyme tyrosinase in the pigment cells.	All-white plumage all over, red eyes and pink feet and bill.
Brown	Eumelanin changed in colour (qualitative reduction) due to incomplete melanin synthesis. Pheomelanin unaffected.	Original black is brown, original reddish/yellowish brown unaffected. Plumages bleaches rapidly further in the (sun)light. Eyes normal and feet and bill slightly lighter than normal.
Ino	Reduction of melanin and remaining melanin changed in colour (qualitative reduction) due to incomplete synthesis of both melanins.	Original black is very pale brown/cream to dark brown, original reddish/yellowish brown hardly visible to slightly paler. Eyes, feet and bill pinkish to hardly noticeably different.
<i>Defects in the melanin deposit into the feathers</i>		
Dilution	Normal-coloured melanin is deposited in an abnormal clumped fashion in the feather cells (both melanins or eumelanin alone).	Original black is bluish- or silvery-grey. Original reddish/yellowish brown is buff/cream or unaffected. Eyes normal and in most forms of Dilution feet and bill are normal-coloured too.
<i>Defects in the type of melanin produced</i>		
Melanism	Aberrant production and distribution into the feather cells of normal melanin (not necessarily an increase of pigment).	Increase of black and/or reddish brown, or an altered pattern (the latter not necessarily darker). Eyes, feet and bill normal.
<i>Melanin aberrations do not affect carotenoid pigments which, if present in the relevant species, remains present.</i>		

a result of the congenital and heritable absence of melanin cells from some or all of the skin where they would normally provide the growing feather with colour (carotenoid pigments, if present in the relevant species, remain). The extent of white can vary, from just a few feathers (partially leucistic, Fig. 4A) to all-white plumage (100% leucistic, Fig. 4B); the skin also lacks melanin for individuals in the latter category.

Partially leucistic birds may have a normal-coloured bill and feet, depending on where the colourless patches occur, but all such birds have melanin-pigmented eyes. The embryonic origin of melanin pigments at the back of the eyeball is different from the rest of the body; eye pigments are formed mainly from the outer layer of the optic cup (Lamoreux *et al.* 2010) and, as leucism affects only the migration of melanocytes originating from the neural crest, it has no influence on eye pigmentation with an optic cup origin. So, in Leucism iris colour may be affected, the rest of the eye is normally melanised and therefore the pupils are black.



Figure 4. Leucism in Common Moorhen *Gallinula chloropus*. (A) Durham, England, January 2010, partial Leucism is, unlike Progressive Greying, very often patchy and bilaterally symmetrical (© Glen Roberts); (B) Moordrecht, the Netherlands, May 2017, full or 100% Leucism causes the absence of all melanin all over the body except the eyes. Like all melanin mutations, Leucism does not affect the carotenoids (in this species only in the feet and bill), which are still present (© Rob Belterman)

The white pattern in partially leucistic birds is often patchy and bilaterally symmetrical due to the way the melanoblasts migrated to the rest of the body in the early embryonic stage, leaving certain areas without melanin cells. The pattern can be caused by a delay in the migration of melanoblasts from the neural crest to the skin. Due to this, some melanoblasts reach certain parts of the body where the skin is too far developed to incorporate them, resulting in these parts lacking colour. Another possibility is that, from the outset, insufficient melanoblasts develop in the neural crest, and therefore not all parts of the body are provided with melanin cells. Whatever the cause, in the commonest forms of Leucism in birds the parts of the body furthest away from the neural crest are left without melanin cells, resulting in the face, the wingtips, the feet and the belly being affected (Fig. 4A). The white pattern in Leucism is static, i.e., it occurs already in juvenile plumage and the amount and pattern of white feathers does not change with age. A good example of a heritable form of Leucism established in a wild bird population was found in Common Ravens *Corvus corax* on the Faeroes (van Grouw 2014).

Leucism can be defined as a neural-crest disorder resulting in lack of melanin in all or parts of the plumage and skin. Another name used for Leucism is Piebaldism. As in certain animal species 'piebald' is the name of a specific white-spotting gene, I prefer Leucism, a term introduced by Rensch (1925) for all-white birds as a result of 100% Leucism (see also Figs. 4B, 28). Although Rensch defined it accurately; 'an abnormal absence of melanin pigment resulting in white feathers but with normal coloured eyes', the definition has taken a twist since 1925 into 'an abnormal reduced concentration of melanin resulting in 'washed-out' colours' (Hess 2011), resulting in the term Leucism nowadays being often incorrectly used for aberrations in the category Dilution. Also, Harrison (1985), at least, added to the confusion: 'Partial loss of pigment, affecting all the colours present and reducing them in intensity, is rare. It is called 'dilution' by bird breeders and 'leucism' in scientific writing, although the latter term is also used at times for various form of schizochroic loss of single pigments which makes the plumage appear paler'.

Although Leucism is very common in domestic and captive birds, it is rather rare in the wild. Far more common causes for lack of pigmentation in feathers are aberrations causing a progressive disappearance of melanin cells, which in mammals is often called 'Progressive Greying'. Whereas the result of Leucism is present at birth, Progressive Greying is a



Figure 5. At an early stage, the white feathers caused by Progressive Greying are often randomly spread over the plumage: (A) House Sparrow *Passer domesticus*, Garlieston, Scotland, April 2010 (© Gavin Chambers); (B) Common Blackbird *Turdus merula*, Overijssel, the Netherlands May 2018 (© Harvey van Diek)



Figure 6. Progressive Greying in Common Coot *Fulica atra*, De Meern, the Netherlands 27 June 2009; in some forms of this mutation almost the entire plumage loses its melanin (© Erwin van Laar)

condition that becomes visible after the bird reaches a certain age. This is, however, generally not related to 'being old' (geriatric greying); it can start at any time after the normally pigmented juvenile plumage is fully developed. From the onset of the condition, the bird gains an increasing number of white feathers with each moult (see Appendix 1). In the early stages, these are usually randomly spread over the bird (Fig. 5), and in certain cases (almost) the entire plumage can become white (Fig. 6).

Eurasian Jackdaws *Corvus monedula*, however, seem to be an exception, with the loss of pigment apparently related to old age (Fig. 7). In this case, the number of white feathers increases rather slowly compared to Progressive Greying in other species. In addition, the presence of some pigment in many of the affected feathers suggests a decreased activity of the melanin cells, rather than their disappearance altogether (geriatric greying in humans is likewise the result of decreased melanin cell activity). Further research is required to establish if older Jackdaws can indeed lose pigment due to their age.

The causes of many forms of Progressive Greying are still unknown. There are certainly straightforward heritable forms (van Grouw & Hume 2015) and a nice example is also found in the domestic Canary *Serinus canaria* (see Appendix 2). Pigment disorders such as vitiligo (pigment disease in humans) may also be responsible for some of the heritable forms of progressive loss of melanin cells, but for most forms in birds a straightforward genetic base appears to be lacking (van Grouw 2018).



Figure 7. Progressive Greying in the same Eurasian Jackdaw *Corvus monedula*, Sliedrecht, the Netherlands (A), June 2014, and (B) April 2016 (two annual moults later). The number of white feathers increased rather slowly compared to Progressive Greying in other species and, in addition, the presence of some pigment in many of the affected feathers suggests that Progressive Greying in this species may be geriatric (© Johan Bink)

Progressive Greying is a term used mainly in mammalian genetics for mutations that develop white hairs due to the progressive loss of melanin cells. Due to the progressive loss of melanin cells birds can develop feathers without melanin, making it sensible to use the same term for these aberrations in birds. Others have suggested Progressive Depigmentation, which is also appropriate.

Although the causes for different forms of Progressive Greying are not always clear, juvenile plumage is always normally pigmented, and the loss of melanin can start at any point after juvenile plumage is fully grown. Without knowing the bird's history or breeding tests, it is often impossible to determine the true nature of the form of Progressive Greying in a wild bird, but Progressive Greying as a group of aberrations is certainly the commonest cause of white feathers in wild birds (van Grouw 2012, 2013, 2018).

Defects in melanin synthesis (Albinism)

The enzyme tyrosinase, naturally present in melanin cells, catalyses melanin synthesis, but due to inheritable causes (mutations) it can become absent or less active, with no or incomplete melanin synthesis as a result (Lamoreux *et al.* 2010). Although the usually black melanin granules can range from pale cream / beige-coloured to dark brown when synthesis is incomplete, in medical science any mutation affecting normal melanin synthesis is defined as 'albinism'. There is, however, just one true **Albino**, all other mutations can be categorised as forms of albinism but they are not Albino.

The term 'albino' was first used by the Portuguese in the early 18th century for albino people among the blacks in Africa. In birds, Albino, from the Portuguese *albo* and Latin *albus*, meaning white, can be defined as a total lack of melanin in feathers, eyes and skin due to the hereditary absence of the enzyme tyrosinase in the pigment cells. The result is an all-white bird or, depending on the species, one coloured by carotenoids / psittacin alone (Fig. 8). The red or pinkish hue that can be seen in the eyes and skin is caused by blood vessels, visible through the colourless tissue (Fig. 9). Due to the absence of tyrosinase in an Albino, melanin cannot be produced, thus the concept of a 'partial albino' is false.

Albino birds are rarely seen in the wild, although the mutation is not uncommon and occurs quite frequently in most populations. The reason for the apparent scarcity is that the absence of melanin in the eyes makes them highly sensitive to light, with a poor depth of



Figure 8. Albino European Goldfinch *Carduelis carduelis*, bred and held in captivity; Albino, and all other melanin mutations, does not affect carotenoid pigments (© Pieter van den Hooven)

Figure 9. Albino in Eurasian Magpie *Pica pica*, bred in the wild but lived in captivity for 17 years; the red or pinkish hue in the eyes and skin is caused by blood vessels, visible through the colourless tissue (Hein van Grouw)

Figure 10. Albino in Common Blackbird *Turdus merula*, Agelo, the Netherlands, April 2018; most Albino birds will, due to their poor eyesight rather than their white plumage, die in accidents shortly after fledging (© Wim Wijering)

Figure 11. Brown in Eurasian Jackdaw *Corvus monedula*, Noordwijk, the Netherlands, June 2015. The term Schizochroism was introduced for aberrations in which melanin and carotenoid was 'separated'. Harrison (1963b) confusingly used the term also for mutations in which, in his opinion, eumelanin and pheomelanin were separated. He used the mutation Brown in corvids, which he called 'fawn', as an example of this, being of the incorrect opinion that the plumage in *Corvus* contains both eumelanin and pheomelanin. A corvid, however, without eumelanin will be white, not brown, as they lack underlying pheomelanin. Brown is the result of incompletely synthesised eumelanin and not the absence of this pigment. Unfortunately, Schizochroism is still used by some authors to identify random aberrations (© Alois van Mingerot)

vision. It is mainly their poor eyesight, rather than their white plumage, that makes albinos vulnerable, and most die soon after fledging (Fig. 10).

Another common mutation affecting melanin synthesis is called *TYRP1^b*, after the enzyme 'tyrosinase-related protein 1' which is involved in normal melanin synthesis (Lamoreux *et al.* 2010). This mutation was formerly called 'brown' (hence the *b* in the name) and is responsible for less active tyrosinase (Kobayashi *et al.* 1998). Other names for this mutation in medical science are Rufous Albinism and Brown Albinism (Manga *et al.* 1997). For our purpose **Brown** perfectly reflects its effect on the pigment: incomplete melanin synthesis causes the eumelanin to remain dark brown instead of becoming black (Fig. 11).

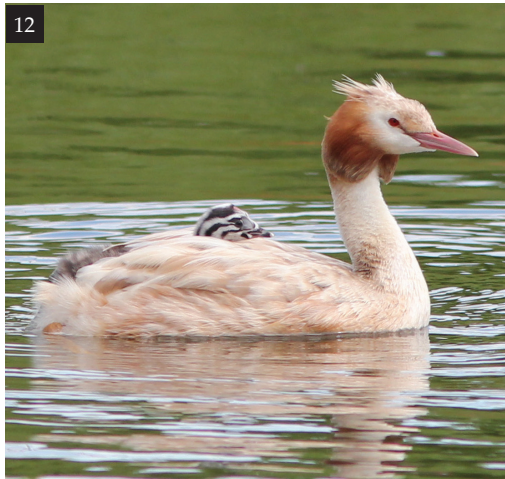


Figure 12. Brown in Great Crested Grebe *Podiceps cristatus*, Drachten, the Netherlands, July 2018. The mutation Brown affects eumelanin alone, not pheomelanin, so the originally black (eumelanin) crest and fringes to the ruff are now brown, but the reddish-brown (pheomelanin) flanks and in the ruff is unchanged. Contrary to popular belief, aberrant individuals often survive well and many also find a partner and breed (© Auke Terluin)

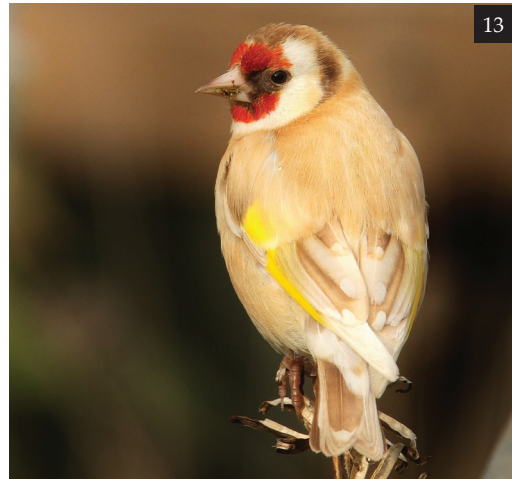


Figure 13. Brown in European Goldfinch *Carduelis carduelis*, UK, January 2014; the bleaching effect of sunlight on aberrant brown eumelanin is already clearly visible (e.g., the tertials and primary tips). Melanin mutations do not affect the carotenoid pigments so the red and yellow are unchanged (© Graeme Conduit / British Trust for Ornithology)

Pheomelanin, where it is present in the relevant species, is unaffected (Fig. 12). Just after hatching, birds with the mutation Brown have plum-coloured eyes, but these are virtually indistinguishable from normal-coloured eyes by adulthood. Likewise, in Brown, the bill and feet are only slightly paler than in normal-coloured individuals.

Brown is the commonest but also probably the most misidentified heritable aberration in birds (van Grouw 2012, 2013). It is caused by a single recessive and sex-linked genetic mutation, which is identical in all bird species (but is not sex-linked in mammals), and therefore in the wild mainly females with this mutation are encountered. In records, Brown is known by many different names: albino, fawn, isabella, leucistic, schizochroistic, erythristic, cinnamon and pale morph are only the most common, but the same terms are also often used for mutations in the category Dilution. A possible reason for the difficulty in identifying this mutation in wild birds is that incompletely oxidised eumelanin caused by the mutation Brown is very light sensitive and bleaches rapidly in sunlight (Figs. 13–14). Within a couple of months, fresh, but aberrant, Brown plumage can become nearly white, making correct identification challenging.

Many other mutations affecting melanin synthesis are caused by variations of the gene *SLC45A2*, which codes for the protein 'solute carrier family 45 member 2' in the melanin cells, and acts as a regulator in melanin synthesis. Although the precise function of *SLC45A2* is unknown, it probably transports molecules necessary for normal melanin synthesis (Domyan *et al.* 2014). Several different mutations (alleles) of the *SLC45A2* gene, which is located on the sex-chromosome in birds, are recorded in many different species. These mutations have different effects on the final melanin pigmentation; in some hardly any melanin is produced resulting in near-white plumage, whilst in others it is only slightly paler than normal. What all appear to have in common is that at least some of the melanin present is incompletely oxidised and therefore (much) paler than normal. Also, in all pale forms, the colour of the eyes and skin is to some degree also affected.



Figure 14. Brown in Eurasian Jackdaw *Corvus monedula*, Noordwijk, the Netherlands, (A) July 2012. This second-calendar-year bird shows, in three feather generations, the bleaching effect of sunlight on aberrant colour due to the mutation Brown. The much worn and bleached, nearly white primaries and secondaries are still juvenile, whereas the body plumage is subadult, less old and therefore less bleached, and the dark brown flight feathers and wing-coverts are new, adult feathers not yet affected by the light and therefore their colour is afflicted by the mutation alone (© Piet Broekhof); (B) May 2014, the same bird almost two years later, now fully adult and just before the next annual moult. As all feathers are roughly the same age, the plumage is equally bleached further by the light (© Bart van Beijeren).



Figure 15. Ino in Common Raven *Corvus corax*, Vancouver Island, Canada, 2008; due to the mutation this young bird's fresh plumage is cream-white but in a few months' time will be bleached further and almost white, and the bird will be hardly distinguishable by its plumage from Albino or 100% Leucistic (© Mike Yip)

Figure 16. Ino in Common Blackbird *Turdus merula*, Maarsbergen, the Netherlands, June 2007; as Ino mutations also affect eumelanin in the skin (bill and feet), the bill clearly shows the yellow carotenoid pigment naturally present in females, but normally obscured by the overlying dark eumelanin (© Erwin van Laar)

The near-white form is often termed Sex-linked Imperfect Albinism (Figs. 15–16), due to its inheritance and because the plumage is nearly white. In medical science it is known as Oculocutaneous Albinism type 4 (Gunnarsson *et al.* 2007). For the darker (less pale) forms, many names are used, frequently based on those used in aviculture for that particular mutation in a certain species. One of these names, unfortunately used also in science, is



Figure 17. Dark form of Ino in Carrion Crow *Corvus corone*. (A) Bred in the wild but held in captivity, September 2006, this crow had just finished its first incomplete moult and the colour of the fresh plumage resembles that of the mutation Brown, but the pinkish skin (bill and feet) show it is not Brown (Hein van Grouw). (B) Durham, England, June 2013, same mutation as (A), but different individual. Like the Eurasian Jackdaw *Corvus monedula* in Fig 14A, this second-calendar-year crow shows, across three feather generations, the strong bleaching effect of sunlight on aberrant colour due to an Ino mutation. The much worn and heavily bleached, nearly white primaries and secondaries are still juvenile; the body plumage subadult, less old and therefore less bleached; and the brown inner primaries are new, adult feathers, not yet affected by the light and therefore still afflicted by the mutation alone. The pinkish bill and feet distinguish it from the mutation Brown (© Billy Cannybud)

Figure 18. Ino in Great Crested Grebe *Podiceps cristatus*, Haaksbergen, the Netherlands, August 2017; the eyes are reddish due to the reduction of melanin, but the eyesight of an Ino bird, even in the palest forms, is much better than that of an Albino. Any adult wild bird with 'white' plumage and reddish eyes is probably Ino, not Albino (© Wim Wijering)

Diluted (Domyan *et al.* 2014), which incorrectly suggests a mutation in the category Dilution (defects in the melanin deposited in the feathers). As plumage colours caused by *SLC45A2* mutations bleach rapidly in sunlight, these birds often appear even paler than that caused by the mutation itself (Fig. 17).

I term all mutations of the *SLC45A2* gene **Ino**, a name also used in European aviculture for the pale form (Sex-linked Imperfect Albinism) in many captive finches. Although Ino mutations (from the Greek or Latin *Ine* = 'belonging to' or 'like') can be categorised as a form of albinism, they are not Albino, and many are far from white. For the palest form, which is rather easy to recognise, the name Ino is sufficiently accurate. Darker forms can be termed **Dark Ino** as, without breeding tests, the actual mutation involved is impossible to establish.

In Ino the eyes are reddish due to the reduction of melanin, but the eyesight of an Ino, even in the palest forms, is much better than that of an Albino. Any adult wild bird with 'white' plumage and reddish eyes is probably an Ino, not an Albino (Fig. 18). As the



Figure 19. Ino or similar mutations in Eurasian Magpie *Pica pica*; the remaining colour in these individuals has a brownish hue, rather than a greyish tone, and the skin lacks visible melanin, pointing to mutations affecting the melanin synthesis (Albinism), probably Ino. (A) Noordwijk, the Netherlands 6 August 2017 (© Annelies Marijnjs); (B) Hisingen, Boh, Sweden, June 2020 (© Jon Håkansson); (C) Hisingen, Boh, Sweden, December 2020 (© Lennart Hjalmarsson). Contrary to popular belief most colour aberrant birds do survive well. The same individual is depicted in (B) and, six months later in partially adult plumage, (C).

inheritance of all Ino forms is recessive and sex-linked, mainly females will be found in the wild.

There are other mutations on other genes known to affect melanin synthesis and these often resemble Ino mutations in appearance (Fig. 19). As mentioned earlier, mutations in wild birds can be identified almost only by their appearance (phenotype) whilst their genotype is unknown. However, as these can be broadly categorised as ‘melanin synthesis-affecting mutations’, recording such birds as Ino is not wholly incorrect.

Defects in the melanin deposit into feathers (Dilution)

Many different genes and mutations are known in the category **Dilution** (from the Latin *dilutior* meaning ‘paler’ or ‘weaker’). One thing they have in common is that the aberrant colour is caused by an abnormal transport of the melanin pigment granules from



Figure 20. Dilution in male House Sparrow *Passer domesticus*, Maarn, the Netherlands, December 2010; in this mutation both melanins are strongly affected (© Erwin van Laar)

Figure 21. Dilution in female House Sparrow *Passer domesticus*, bred and held in captivity. Sparrows possess both forms of melanin, and this form of Dilution affects only eumelanin (© Pieter van den Hooven)

the melanin cell into the feather cells. Instead of being uniformly deposited, the pigment granules clump together, resulting in blue-greyish tones where the original colour was black. So, the melanin pigment itself is normal-coloured but, due to the way it is distributed into the feather cells, we perceive it differently. This can be compared with a black-and-white photo in a newspaper; a high concentration of black ink dots close together are perceived as black, whilst fewer black dots in the same-sized area appear grey.

Although there are many different Dilution mutations, and each one dilutes colour in a slightly different way, such mutations are rare compared to those in the category Albinism. Dilution can be separated into two main forms. The commonest is a dilution of both eumelanin and phaeomelanin (Fig. 20). Black feathers turn greyish, and reddish or yellow-brown tracts become buff or cream-brown. The degree of dilution within a single mutation can vary individually, but most mutations cause a visible melanin reduction of *c.*50%. All birds with this form of dilution look like a pale, washed-out version of their normal counterparts, and can be termed **Pastel** (from the Latin *Pastellus*, a pale, delicate colour). The second form is a dilution of eumelanin alone, with phaeomelanin unaffected (Fig. 21). Black feathers turn grey, but reddish or yellow-brown ones remain unchanged. This form of Dilution can be called **Isabel** (from the Latin *isabellinus*; greyish yellow). In species with only eumelanin in their plumage it is impossible to distinguish a dilution mutation as being Isabel or Pastel (Figs. 22–23). In species with both melanins, e.g. sparrows, the phaeomelanin often seems to be even brighter in colour due to the reduction of the overlying eumelanin.

Dilution mutations affecting only the phaeomelanin are rare, and aberrant plumage with apparently diluted phaeomelanin alone is often caused by mutations in the Albinism category. As aberrant-coloured wild birds can be identified only by their phenotype, it must be taken for granted that misidentifications occur.

Defects in the type of melanin produced (Melanism)

Melanism, from the Greek *melanos* (= dark-coloured), is usually defined as an increased amount of dark pigmentation (melanin). A melanin cell is able to produce both melanins, but not simultaneously. It can, however, rapidly switch from producing one to the other.



Figure 22. Dilution in Eurasian Jackdaw *Corvus monedula*, Terschelling, the Netherlands, March 2014; because corvids possess only one form of melanin (eumelanin), it is impossible to determine if this form of Dilution would affect both melanins if present (© Bert Bruggeman)

Figure 23. Dilution in Common Moorhen *Gallinula chloropus*, Pichlingersee, Austria, April 2017; as the plumage of this species contains eumelanin alone, it is impossible to know if this form of Dilution would affect both melanins if present (© Hans-Peter Sahrhage)

Switching from eumelanin to phaeomelanin, and the reverse, is genetically determined. Via a mutation the melanin cell can be instructed to produce only one of the two pigments producing completely eumelanised or phaeomelanised plumage (van Grouw 2017). Timing of melanin production can also be affected and can change original plumage markings and patterns (van Grouw 2017). Melanism therefore does not necessarily imply an increase of dark pigment, but may be the result of a changed distribution in the same quantity of melanin. Consequently, a better definition of Melanism would be, a condition characterised by abnormal deposits of melanin in skin and feathers. ‘Abnormal deposit’ covers both changed distribution *and* an increased amount.

To summarise, the appearance of melanistic birds is mostly darker than normal, but not always. Melanism can affect birds’ plumage in three ways: (1) all of the plumage is darker and appears blackish (eumelanin), dark brown (both melanins) or reddish brown (phaeomelanin); (2) normally dark markings are bolder and noticeably ‘overrun’ their typical boundaries (the rest of the plumage is often somewhat darker as well (Figs. 24–25); and (3) the normal pattern and pigment distribution is changed, but the plumage is not necessarily darker (it can even be brighter).

Earlier nomenclature

Many names for the different colour aberrations have been proposed during the last 175 years. These names, however, were seemingly randomly used by others to identify aberrations in published records, creating much confusion.

Until the second half of the 20th century insufficient knowledge of feather pigmentation and possible aberrations resulted in the latter being mistakenly identified and named as species. With recent DNA work many of these ‘new species’ have been unmasked (e.g. Collinson *et al.* 2017, Kirschel *et al.* 2018, Schweizer *et al.* 2020, see also van Grouw 2010,

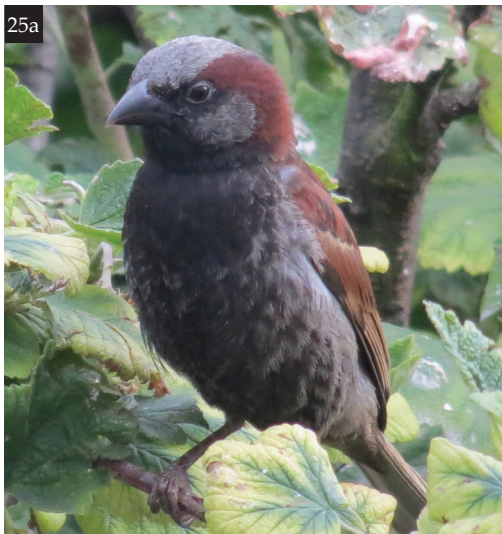


Figure 24. Melanism in Great Tit *Parus major*, Rotterdam, the Netherlands, November 2008; the black patterns are bolder and 'overrun' their typical boundaries, whilst the rest of the plumage is also somewhat darker (© Harvey van Diek)

Figure 25. Melanism in House Sparrow *Passer domesticus*, Surrey, England, (A) June 2014, in old and worn breeding plumage, and (B) October 2014, in fresh plumage with grey fringes which will wear off during winter, as usual, so in summer plumage the deep black on the underparts shows best. The black bib overruns its usual border, and the rest of the plumage is not obviously darker (© Paul Davies)

2017 for more examples). Hachisuka (1926), in his description of the melanistic Common Pheasant *Phasianus colchicus*, which he correctly recognised as an aberration (mutation), highlighted the problem and noted that such cases would always prove misleading unless a definitive nomenclature was developed. He proposed that all mutations should be distinguished by the term 'mutation', abbreviated as 'mut', within the scientific name. The melanistic Common Pheasant was therefore named by Hachisuka (1926) *Phasianus colchicus*

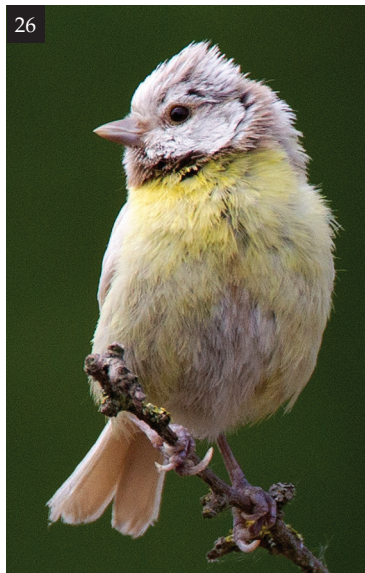


Fig 26. Brown in Blue Tit *Cyanistes caeruleus*, Wageningen, the Netherlands, May 2020. Even if Hachisuka's (1926) recommendation for scientifically naming mutations had been accepted, there still would be the problem of which names to use for the different mutations; here *C. caeruleus* mut. *brunneus*, or *C. c.* mut. *erythraeus*, or something else? (© Harvey van Diek)

Figure 27. Progressive Greying in Common Coot *Fulica atra*, Leuten, the Netherlands, April 2018; the progressive loss of pigment, resulting in increasing numbers of white feathers, was first recognised by Frauenfeld (1853) but until recently largely ignored by ornithologists (© Erwin van Laar)

mut. *tenebrosus* (*tenebrosus* = dark), claiming that this was the first time that a mutant form had been correctly described. Although Hachisuka favoured naming mutations in scientific names, the nomenclature of mutations has never been regulated by the *International code of zoological nomenclature* (ICZN 1999, and previous incarnations). However, even were the *Code* to accept this recommendation, the naming of the causative aberration would nevertheless have presented problems (see Fig. 26).

The earliest published attempt I could find to seriously categorise the different colour aberrations was by Frauenfeld (1853), who divided them into several groups, of which the most important were 'true Albino' (Leucochromatism from the Greek *leukos* for 'white', and chromatism from the Greek *khroma* for 'colour'), 'bleached colours' (Chlorochromatism from the Greek *khloros* for 'green' or 'yellow'), 'colour variety' (Allochromatism from the Greek *allokotos* for 'unusual'; Melanism and Leucism were included here) and 'discolouring with age' (Geraiochromatism from the Greek *geras* or *girateia* for 'old age'). Interestingly, the latter category shows that Frauenfeld had noticed Progressive Greying aberrations; a phenomenon that was to remain undocumented for another century (Fig. 27). Subsequently, Frauenfeld (1873) revised his list of categories to include 'blackish colours' (Melanochromatism) and 'reddish colours' (Erythrochromatism), probably based on von Pelzeln (1865), who divided colour aberrations into two groups, Albinism and Melanism, based on a decrease or increase of pigment in the plumage. Within Albinism von Pelzeln (1865) distinguished 'complete Albinism' (all-white plumage with red eyes), 'incomplete Albinism' (overall plumage paler than normal but original patterns still visible) and 'partial Albinism' (parts of the plumage are white but the rest is normal). He made similar divisions within Melanism: 'complete Melanism' (all-black plumage), 'incomplete Melanism' (overall darker plumage but original patterns still visible) and 'partial Melanism' (only some parts of

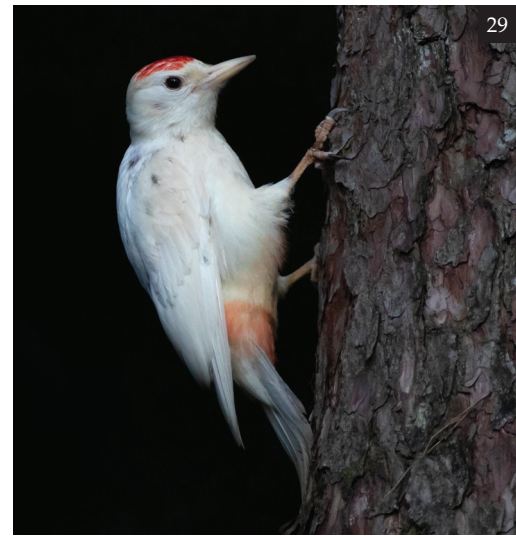


Figure 28. Leucism in Common Blackbird *Turdus merula*, Didam, the Netherlands, July 2014. Rensch (1925) introduced the term Leucism for birds with white feathers but coloured eyes. In science this term is still used for mutations causing the absence of melanin-producing cells (resulting in white feathers but coloured eyes), but birdwatchers incorrectly use the term for aberrations with pale plumage (© Harvey van Diek)

Figure 29. Near-total absence of melanin in Great Spotted Woodpecker *Dendrocopos major*, Ermelo, the Netherlands, July 2019. The term Schizochroism was introduced by Haecker (1908) for aberrations in which one pigment is absent but the other is unaffected. However, different mutations can result in the absence of melanin, like Albino, Leucism, and unknown mutations as in this woodpecker. Therefore, Schizochroism is an unsuitable term as it does not distinguish between these totally different mutations (© Jaap Denee)

the plumage are black, whilst the rest is normal-coloured). Von Pelzeln (1865) distinguished a fourth category within Melanism, Erythrism (overall reddish-brown plumage).

P. Pavesi (*in* Picchi 1903), like von Pelzeln (1865), divided aberrations into two groups based on pigmentation decreases and increases, and used the terms ‘Hypochromatism’ (from the Greek *hupó* for ‘under’) and ‘Hyperchromatism’ (from the Greek *hupér* for ‘over’).

Rensch (1925), who proposed a set of terms to clear ‘the rather chaotic confusion in terminology for colour aberrations’ (‘geradezu chaotische Verwirrung in der Terminologie dieser Abweichungen’), also divided, following von Pelzeln and Pavesi, the different aberrations into two main categories based on the amount of pigment, and used the same terms—Hypochromatism and Hyperchromatism. In the first category, the decrease of pigment, he included (1) Albinism; comprised of albino (with red eyes), partial albino, and leucism (Fig. 28), (2) Schizochromatism and (3) Chlorochromatism. The second category, Hyperchromatism, for the increase of pigment included (1) Melanism, divided into eumelanism and phaeomelanism and (2) Lipochromatism. The term Schizochromatism (from the Greek *schizo* = ‘split’, ‘separation’ or ‘division’) was introduced by Haecker (1908) for aberrations in which one pigment was absent while the other was unaffected. Haecker gave as an example two specimens of Black Woodpecker *Dryocopus martius*. One was fully white but still had red on the head, whilst the other was normally black-coloured but with white on the head where usually it is red. In the first bird the melanin was absent but carotenoid was still present (Fig. 29), and in the second bird these were reversed.

C. J. O. Harrison (1963a,b), a former curator at the Natural History Museum, London, distinguished two forms of Schizochromatism, which he called Schizochroism. Both Black Woodpeckers mentioned by Haecker (1908) are an example of the first of Harrison’s categories, which he termed melano-carotenoid schizochroism, the white bird being

non-melanin and the black bird with a white head patch lacking carotenoid. As melanin aberrations do not affect the carotenoid pigment, at least three different aberrations could have caused the appearance of the red-headed white woodpecker: Albino, Leucism and Ino. Although producing a similar appearance, the nature of these aberrations is totally different and they should not be grouped under the same name. Harrison's (1963b) second category was 'melanic schizochroism' in which the two types of melanin are separated into non-eumelanin and non-phaeomelanin forms, which he termed Fawn and Grey variants, respectively. These 'Fawn variants', however, are not the result of separated melanins as will be demonstrated later in this paper.

Some aberrations, like true Albino (with red eyes) were identified correctly by earlier authors and all of them used the same term. Most of the suggested names, however, as already demonstrated above, also covered different aberrations with similar effects but of a totally different nature (see Table 1). Another example is Erythrism which, since von Pelzeln introduced it, was used by others for any aberration causing a colour more reddish or reddish brown than normal. The mutation Brown, certain forms of Dilution, Ino and Melanism, and an increase of red carotenoid, however, can all cause more reddish-looking plumage. Harrison (1963b) also had an opinion on erythrism, confusing matters further. According to him 'erythristic plumage is one in which the normal eumelanin, and possibly phaeomelanin also, is replaced by a third chestnut-red melanin'. There is, however, no third melanin and, as shown below, Harrison was confused by the brown form of eumelanin, mistaking it for phaeomelanin. Based on the mutation Brown (see below) in Carrion Crows *Corvus corone* (which he called 'Fawn'; the 'non-eumelanin' form of Schizochroism), Harrison (1963b) incorrectly opined that the plumage of crows *Corvus* contains both eumelanin and phaeomelanin. A corvid, however, lacking eumelanin will be white, and not brown, as they have no underlying phaeomelanin. The mutation Brown prevents eumelanin from being fully synthesised and so the plumage does not become black but remains brown (Fig. 11).

Two years later, Harrison (1965) was still convinced of the existence of an 'unnamed chestnut-red melanin' writing, 'Irrespective of its biochemical relation with other melanins the chestnut-red melanin exists as a visible and well-defined entity and it seems preferable to have some term by which to refer to it. In the apparent absence of other names, I would suggest that it should be referred to as "Erythromelanin", since it is the pigment usually present in the colour variants which we know as "erythristic" forms.' Based on the crow example and others given by Harrison (1963b, 1965; from specimens at NHMUK) he indeed confused the brown form of eumelanin for phaeomelanin, and wrongly assumed that phaeomelanin was the 'erythromelanin'.

Recently Davis (2007) published an overview of the many pigment abnormalities in birds and proposed a nomenclature in an attempt to finally establish uniformity. An important prerequisite was that terminology should reflect what happens to the pigments rather than the resulting plumage appearance. Davis therefore introduced what he believed to be a new terminology, to avoid confusion between historical and current interpretations, by incorporating a prefix. 'Amelanism' (prefix *a-* meaning 'not' or 'without') as a preposition for the absence of melanin, 'hypomelanism' for decreased pigment concentration, and 'hypermelanism' for increases. However, this was not new at all: as mentioned above, P. Pavesi (*in* Picchi 1903) had already used 'Hypochromatism' and 'Hyperchromatism' to divide aberrations with decreased or increased pigmentation, respectively, as had Rensch (1925).

Conclusions

The mutation Brown is probably the commonest heritable colour aberration in birds, but its importance, or even existence, has been overlooked. Depending on the author,

Brown has been included in Chlorochromatism, Schizochroism (Fawn) or Erythrism (terms also often used for mutations in the category Dilution, see Table 1). Davis (2007) referred to Brown as ‘Aeumelanism’ and stated, correctly, that it is inherited as a sex-linked, recessive trait. He defined it as ‘the abnormal absence of eumelanin from the plumage, skin, eyes, or all three areas’. In this mutation the number of eumelanin pigment granules is unchanged, but the pigment’s colour is altered due to incomplete synthesis. Because eumelanin is present, Aeumelanism is also an inappropriate term for this mutation. Davis (2007) further introduced the term Amelanism, partial (1) or total (2), which he defined as: the absence of all melanin from (1) parts of the plumage, skin, eyes, or all three areas [Leucism and Progressive Greying] and (2) from all plumage, eyes and skin [Albino]. The absence of all melanin results in white feathers (carotenoid pigments, if present in the relevant species, remain present) but, although the final appearance is broadly similar—white plumage—the nature and genetic background are different. To explore the different causes and occurrences of plumage irregularities correctly it is vital to distinguish aberrations by their causes, not their appearance (see Fig. 28).

A simple scheme to identify and name the commonest colour aberrations in birds is a must. Which names are used is less important provided they are universal, easy to use and cover the aberration appropriately. Many names proposed by earlier workers (e.g., Chlorochromatism, Schizochroism, Erythrism, Amelanism) lump multiple aberrations together, each with a separate cause and genetic background. Furthermore, names like Aeumelanism and Schizochroism are inappropriate for the aberration they refer to (Brown), as they incorrectly suggest an absence of eumelanin. As stated, it is vital to distinguish



Figure 30. Mutation affecting melanin synthesis in Barn Swallow *Hirundo rustica*, Steensel, the Netherlands, June 2013; as eumelanin is not developed (synthesised) these parts of the plumage are white, but phaeomelanin is normally developed. This may or may not be a mutation genetically related to Brown, but without breeding tests this will remain unknown. Like this mutation, many others can affect coloration, but all are far rarer in wild birds than those described herein, and therefore not covered by the presented nomenclature (© Theo van de Mortel)

aberrations by their causes, not their appearance, which may give erroneous indications as to the real occurrence of certain aberrations. Although the names I use perhaps do not *explain* the cause, they effectively distinguish the differing genetic backgrounds. My list is not exhaustive, but it covers the mutations most likely to be encountered by birdwatchers (Table 2). Other mutations affecting bird coloration are far rarer in wild birds (Fig. 30) and therefore not covered herein.

The rather simple names I use for common melanin mutations, based mainly on traditional names used in earlier genetic work appear to function well, but may be refined further. The aim here is to aid progress towards an international, usable nomenclature for colour abnormalities in wild birds that distinguishes, as far as possible, the nature and causes of each abnormality. Only then can we document the occurrence and frequency of different colour irregularities effectively. However, where an identification is uncertain, it is preferable for observers not to attempt to name the aberration in a publication, but just carefully describe and, if possible, photograph the bird, thereby placing the information on record, but preventing any misinterpretation as the result of an incorrect name.

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- Address:* Bird Group, Dept. of Life Sciences, Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK, e-mail: h.van-grouw@nhm.ac.uk

Appendix 1: Progressive Greying in progress

Frauenfeld (1853) had already noticed that normally coloured birds can lose the pigment in their plumage later in life, a phenomenon unappreciated by many later workers, and the majority of birdwatchers appear unaware of it, despite further evidence becoming available from ringers. In the late 1950s, Band (1956) reported that a ‘normal’ adult male Common Blackbird trapped in Lancashire on 24 November 1950 was retrapped on 4 December 1955 with ‘considerable patches of white over most of its plumage’. In response to Band’s observation, several other ringers also reported cases of ‘albinism related to age’ (Foott 1956, Spencer 1956, Wigzell 1956). Spencer (1956) noticed that birds became whiter over successive years and called it ‘progressive albinism’, and Rankin (1954) also reported an increase in white feathers over time.

A good example of Progressive Greying in progress was identified in a male Common Chaffinch *Fringilla coelebs* that returned to the same territory in four successive years. Sceptics may argue that one cannot be sure that it was the same bird, as it was not ringed, but the chance that four different individuals with white feathers appeared at the same spot each year is almost beyond imagination. The following information was provided by Jann Hansen, who observed the bird and took the photos. The individual was first seen in late March 2018 near Gothenburg, Sweden (Fig. 31A), when it was very shy and disappeared after a few days. In late March 2019, presumably the same bird returned (Fig. 31B). The number of white feathers had increased considerably. It was less shy and, after several disputes with rival males, established a territory but failed to attract a mate. In early April 2020 the bird returned to its territory (Fig. 31C). The number of white feathers had increased a little more. That year it found a mate, and they built a nest but whether they bred successfully is unknown. In late March 2021 the ‘white’ male returned again (Fig. 31D) and once more established a territory, but no nest had been found at the time of writing.



Figure 31. Progressive Greying in Common Chaffinch *Fringilla coelebs* in four successive years, Jonsered, Sweden (A) 25 March 2018, (B) 11 April 2019, (C) 16 April 2020, and (D) 31 March 2021; after 2020 the number of white feathers hardly increased (© Jann Hansen)

Appendix 2: Progressive Greying can result in Fancy patterns

An iconic breed of Canary *Serinus canaria* is the London Fancy, distinguished by its absence of melanin in the body feathers, resulting in yellow plumage due to the presence of carotenoid alone, but fully melanised flight and tail feathers (Fig. 32). The breed disappeared in the early 1900s and breeders ever since have unsuccessfully tried to recreate the London Fancy, because the pattern was not caused by Leucism (a mutation common in the species) but by Progressive Greying. London Fancy canaries are fully melanin-pigmented when juvenile, but loss of melanin cells starts almost immediately after the bird has developed this plumage, so after its first incomplete moult the new feathers lack melanin. Canaries, like most passerines, do not moult their flight and tail feathers in their first year, so the typical pattern of the London Fancy was the result of adult feathers (without melanin) and the still present juvenile feathers (with melanin). This pattern lasts just c.8 months until the first complete moult. Afterwards a London Fancy will be (almost) all yellow. Canary breeders in 1800 knew this, but their counterparts in the 20th century did not. Recreating the breed was impossible without the particular mutation for progressive melanin cell loss, which disappeared with the London Fancy from canary aviculture. Recently, however, the mutation spontaneously re-occurred in a stud of canaries in the Netherlands, and together with the mutation the London Fancy is back. The mutation can occur in any species and is recorded in several wild birds (Figs. 33–34).



Figure 32. London Fancy Canary; the typical pattern of dark flight and tail feathers (melanin) and yellow body plumage (no melanin) in this distinctive breed of the domestic Canary *Serinus canaria* is the result of a heritable form of Progressive Greying in which the loss of melanin cells starts shortly after the first, fully melanised juvenile plumage is developed. The flight and tail feathers are still juvenile, whilst the rest of the plumage is adult following the first incomplete moult (© Alois van Mingeroet)

Figure 33. Heritable Progressive Greying in a first-winter Eurasian Siskin *Spinus spinus*, Liverpool, England, January 2016; loss of melanin caused by similar Progressive Greying mutation as the London Fancy Canary (© Steve Young)

Figure 34. Heritable Progressive Greying in a first-winter Blue Tit *Cyanistes caeruleus*, Schaffhausen, Switzerland, January 2019; loss of melanin caused by similar Progressive Greying mutation as the London Fancy Canary (© Stefan Schopper)

Vocalisations, taxonomy and nomenclature of the pied boubous of eastern Africa

by James E. Bradley

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SUMMARY.—A vocal analysis of the duets of pied boubous *Laniarius* spp. across eastern Africa is presented, focusing on birds from coastal Somalia south to Mozambique. Based on the presence or absence of certain note types in duets, and variation in their structure across different populations in this region, forms of duet were found to cluster at both larger and smaller spatial scales. Vocal congruence suggests that taxon *mossambicus* could be conspecific with *sublacteus*, whereas marked differences between these two and coastal Kenyan birds confirm their previously reported genetic distinctiveness. Patterns of vocal variation broadly align with taxonomic divisions already indicated by genetic data and I integrate these to identify and define the ranges of four distinct groups: the Tropical (*major* and *ambiguus*), Ethiopian (*aethiopicus*), Somali (*somaliensis*) and East Coast groups (*sublacteus*, *mossambicus* and extralimital *limpopoensis*). Species rank for birds in coastal Kenya under the name Juba Boubou *L. somaliensis* is also proposed, and vocal data presented here support the findings of Nguembock *et al.* (2008) and Finch *et al.* (2016) that plumage criteria are unreliable indicators of taxonomy in *Laniarius*.

Following the taxonomy of Gill *et al.* (2021), and distributions reported by Fry *et al.* (2000), the pied boubous in eastern Africa are currently thought to comprise three species. The monotypic Ethiopian Boubou *Laniarius aethiopicus* (J. F. Gmelin, 1789) occurs in far eastern South Sudan north to Eritrea and east through Ethiopia to northwest Somalia and northern Kenya at Moyale.

Tropical Boubou *Laniarius major* (Hartlaub, 1848) is represented by three subspecies in the region covered here. *L. m. major* occurs in West and Central Africa east to South Sudan, Uganda, central and western Kenya, north-central Tanzania (Essimngor, Loliondo and Ngorongoro) south to Njombe, extreme north Malawi (where it intergrades with *L. m. mossambicus*) and west to north and north-west Zambia; *L. m. ambiguus* von Madarász, 1904, east of the Rift Valley in northern Tanzania (Mt. Kilimanjaro and Mt. Meru) and Kenya, north to Marsabit and Mt. Kulal; and *L. m. mossambicus* (Fischer & Reichenow, 1880) Zambia (except the north and north-west), Malawi (except the far north), eastern Botswana, Zimbabwe (except the far south-east) and Mozambique.

Finally, the monotypic East Coast Boubou *Laniarius sublacteus* (Cassin, 1851) is found in the lowlands of extreme southern coastal Somalia through coastal Kenya to north-east Tanzania (including the Usambara and North Pare Mountains) to Zanzibar.

However, the genus *Laniarius*, including the taxa mentioned above, has long confounded taxonomists and field workers (Harris & Franklin 2000), and it is only comparatively recently that genetic analyses have shed light on some of the less well understood relationships (Nguembock *et al.* 2008, Finch *et al.* 2016). A key finding has been that intraspecific polymorphism occurs in the genus, making some plumage traits unreliable indicators of genetic affinity and species-level taxonomy. Specifically, Nguembock *et al.* (2008) concluded that divergence may have taken similar form in separate lineages,

resulting in distantly related taxa showing convergent morphology. While resolving some uncertainties, molecular studies also identified issues in need of further study, one of these being the taxonomy of pied boubous in the coastal forests of East Africa. Birds in this region were all considered as *L. sublacteus* (see above) until Nguembock *et al.* (2008) showed that, in fact, two visually identical species were involved: birds from the East Usambara and Rubeho Mountains of north-east Tanzania were referred to *sublacteus* Cassin, 1851 (type locality Eastern Africa?; see Discussion), and found to be possibly allied to extralimital Southern Boubou *L. ferrugineus* (J. F. Gmelin, 1788); and those in the Sokoke Forest, coastal Kenya, were found to be most closely related to *L. major*, and perhaps distantly allied to Turati's Boubou *L. turatii* (J. Verreaux, 1858: type locality Guinea-Bissau; see Bannerman 1939) from West Africa.

Due, however, to concern that the sample from Sokoke may have been contaminated, Nguembock *et al.* (2008) left this apparently distinct population unnamed. Subsequently, however, Finch *et al.* (2016) demonstrated that this population is genetically distinct from north Tanzanian birds, and instead was a close relative of a pied boubou from southern coastal Somalia named *somaliensis* Reichenow, 1905. Whilst *somaliensis* differs in appearance from closely related birds of coastal Kenya only by having white vs. black 'shoulders', it has incorrectly been regarded as a pied morph of the all-black Coastal Boubou *L. nigerrimus* (Reichenow, 1879) (= *L. erlangeri*; see Ash & Miskell 1998) with which it is sympatric in south-coastal Somalia. However, due to uncertainty over whether the type of *sublacteus* may be from the Sokoke Forest region, or from the Usambaras in north-east Tanzania, Finch *et al.* (2016) also declined to assign a name to birds in coastal Kenya. Therefore, while the pied boubou of coastal Kenya is specifically distinct from identical-looking birds in coastal Tanzania, it still bears the same name, *sublacteus*. Meanwhile birds from south-coastal Somalia (*somaliensis*), from the same genetic lineage as those in coastal Kenya, are currently not afforded recognition in any world checklist (Dickinson & Christidis 2014, del Hoyo & Collar 2016, Clements *et al.* 2019, Gill *et al.* 2021).

Meanwhile, the vocalisations of the pied boubou complex have yet to be studied in light of the genetic findings. The well-known duets in *Laniarius* spp. are typically loud and distinctive, involving repeated simple motifs, with each sex's contribution highly synchronised (Fry *et al.* 2000, Harris & Franklin 2000). Duet parts of each sex may be overlapping or antiphonal, and serve to defend a territory. Consistent duetting patterns across all groups involve either: (a) lower or higher bell-like notes from males, and a snarl-like note (hereafter snarl), by females, or (b) slow, monotone whistles and croaking notes by males with snarls by females (pers. obs.). Across the wide geographical area covered here, these duets are sufficiently variable that regional patterns may be detected that provide further insight into pied boubou taxonomy, especially where polymorphism may obscure cryptic diversity. In assigning birds to vocal groups based on their duets, I seek to reconcile these with genetic data and published distributions, to better define the range limits of taxon groupings. Given persisting disagreement, I also suggest a possible revised nomenclature and taxonomy for the group.

Methods

Recordings of pied boubou vocalisations were sourced via correspondence with observers and online at Xeno-canto (www.xeno-canto.org), Macaulay Library (www.macaulaylibrary.org) and AVoCet (www.avocet.zoology.msu.edu). Additional recordings at the British Library but not available online were not consulted. Recordings were analysed from across all of East Africa, but with a focus on coastal southern Somalia south to Malawi and northern Mozambique. Vocalisations of some extralimital taxa were also analysed,

for context. The vocalisations of duetting pairs formed the principal basis of the analysis, to recognise distinct vocal groups and, if possible, allocate taxa to them. While each sex mimics the voice of the other, and is therefore capable of producing duet phrases in solo renditions, there appears to be no evidence suggesting that the sexes reverse their roles during actual duets, and the attribution of sexual identity throughout this paper is inferred based on extensive review of audio recordings, video footage and personal field experience over a period of 30 years in Kenya and Tanzania. In describing repertoires of each group, only the main songs and calls are considered, these being heard 75% or more of the time in the field (pers. obs.). Examples are presented as sonograms, created using Syrinx software (Burt 2006). For my analyses, birds at Sokoke Forest, Kenya are treated as *L. somaliensis*, in line with genetic and morphometric congruence (Finch *et al.* 2016).

Results

Three hundred and sixty-five audio recordings of pied boubou taxa were analysed. Duets recorded from across East Africa were grouped based on various shared characteristics and the presence or absence of certain notes in different populations. For example, snarls comprise the only duet vocalisations by females in some populations while, among the more variable notes delivered by males, some are also specific to certain groups (Table 1). The analysis of vocalisations using these criteria suggests the presence of four main vocal groups in East Africa, with one split into two subgroups (Fig. 6), and a fifth group comprising intergrades, as detailed below. Following each group name, the data in parentheses note the taxa assigned to it and the number of recordings of my overall sample that pertain to each group.

Tropical group (*major* and *ambiguus*; $n = 170$ [northern subgroup], $n = 39$ [southern subgroup]; see Figs. 6–7). *Distribution*.—Recordings from West Africa (Cameroon, Ghana, Ivory Coast), east to Nyankunde, DR Congo, to Uganda and Kenya (Murchison Falls, Mt. Elgon, Tugen Hills, Mt. Kenya, the Aberdares, Nairobi, Chyulu Hills) south through northern and western Tanzania and the Albertine Rift (Kilimanjaro, Arusha, Iringa and Mufindi, Sitebe, Kigoma, Minziro Forest, Kigali, Bujumbura, Goma) to northern Zambia (Kitwe, Mayau, Salujinga) and southern DR Congo (Lubumbashi).

Basic duet.—Two bell-like notes on different pitches; the female initiates with a high note, followed by a shorter and lower note by the male, which typically overlaps with the end of the female note, e.g. *tee-loo*, repeated (Fig. 1a). These form the basis for more excited duets involving multiple notes by each bird (and which may also be initiated by the male?), usually at a faster pace but always on different pitches, e.g. *loo-tee-loo-tee-loo* or *too-too-too-too-lee*.

Variations.—During aggressive territorial displays, the length of the bell-like notes shortens and speed of delivery increases, resulting in duets of multiple *too-too-too* note series without higher notes (Fig. 1b). During particularly aggressive duets the female may also switch to using a snarl, to accompany the bell-like notes of the male, e.g. *too-grrrr-too* or *too-too-too-grrrr*, with the snarl typically delivered at the same time as the male's notes. However, this is not common, with most duets comprising solely bell-like notes. Bell-like notes in duets may be repeated singly or as multiples and, while male and female sometimes overlap, duets are usually antiphonal.

Unique notes.—Multiple *too-too-too* notes delivered during aggressive displays are absent in other groups. In these displays, multiple pairs (up to four; pers. obs.) may engage in a lazy but coordinated routine of bounding from branch to branch on a circular track through the subcanopy of a large tree, while snarls are layered over the multiple bell-like phrases.

TABLE 1

Attributes of duet phrases by pied boubous *Laniarius* spp. in East Africa. Presence or absence of distinguishing characters in duet vocalisations are highlighted. The Tropical group is divided into northern and southern subgroups, with differences between them shown in Fig. 1. * = examples from Zanzibar, where the drawn out flute-like whistle is also used; ** = examples from the Zambezi and Luangwa Valleys, where the croak note and drawn-out flute-like whistle are also used; green = main differences in duet characteristics between the East Coast and other groups; yellow = duet characteristics unique to both the Somali group and southern Tropical subgroup; orange = duet characteristics common to both the Ethiopian and East Coast groups; blue = possible absence of a female snarl in the repertoire of the Somali group. Attribution of sexual identity is inferred based on extensive review of audio recordings, video footage and personal field experience in Kenya and Tanzania.

Sex	Duet note characteristics	Tropical group		Ethiopian group	Somali group	East Coast group		
		(northern) major	(southern) major			<i>ambiguus</i>	<i>aethiopicus</i>	<i>somaliensis</i>
Male	bell-like <i>too</i> notes or <i>too-too-too</i> series	0.8–1.1 KHz absent	0.8–1.0 KHz absent	0.9–1.1 KHz absent	1.0–1.1 KHz absent	absent	absent	absent
	sonar-like <i>too-too-too</i> series	absent	absent	absent	absent	absent	0.9–1.0 KHz*	0.9–1.0 KHz**
	drawn out flute-like whistle	absent	absent	absent	absent	absent	1.4–2.1 KHz	1.7–2.4 KHz
	varying-pitch note	absent	yes	absent	absent	yes	absent	absent
	frog-like croak note	absent	absent	absent	absent	absent	1.0–1.1 KHz	1.0–1.1 KHz
Female	bell-like <i>too</i> notes or <i>too-too-too</i> series	yes	yes	yes	yes	yes	absent	absent
	varying-pitch note	absent	yes	absent	absent	absent	absent	absent
	use of basic snarl note	uncommon	uncommon	uncommon	common	absent?	common	common
	embellished (including doubled) snarl notes	absent	absent	absent	yes	absent	yes	yes



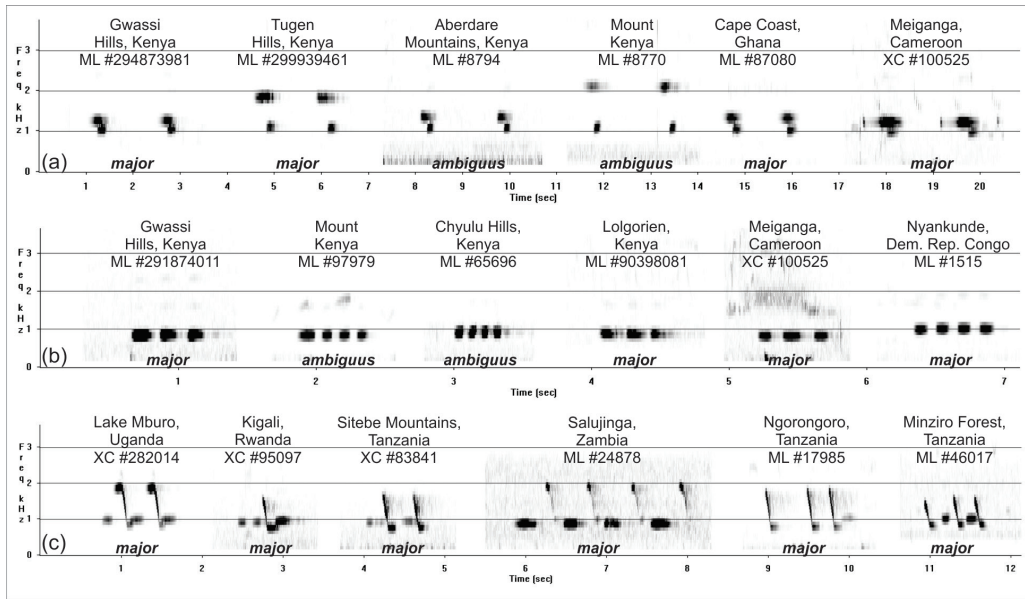


Figure 1. Sonograms of the Tropical group showing (a) variation in the basic *tee-loo* high-low duet (one motif repeated once), (b) rapid, multiple bell-note *too-too-too* calls of Tropical Boubeou *Laniarius major* and *L. m. ambiguus* from West Africa to Kenya (single bird), and (c) varying-pitch notes with gonolek-like quality in duets of *L. major* from south-west Uganda, Zambia, and the Mufindi and Ngorongoro regions of Tanzania. For recording credits see Appendix.

Subgroups.—The Tropical group divides into two subgroups, northern and southern, based on differences in duet structure (Fig. 1) Thus, duets by *L. major* populations from the southern fringes of the Congo Basin, north to the Albertine Rift and east to the Crater Highlands of Tanzania differ from those of *L. major* (and *ambiguus*) elsewhere by the inclusion of a varying-pitch note by either the male (Fig. 1c, examples 2, 3, 5 and 6 from left to right) or female (Fig. 1c, examples 1 and 4) in tandem with bell-like notes by the other sex. This varying-pitch note (which is most similar to that used by the Gabela Bushshrike *L. amboimensis* of western Angola) affords a ‘plonking’ quality to duet phrases, a characteristic perhaps best known among the gonoleks, e.g. *too-k’Yonk-too-k’Yonk-too*. Emphasis is on the low element of this note in the male, and on the high element in the female (like the Somali group).

General comments.—Almost all duets comprise bell-like notes with snarls, by the female, perhaps incorporated into c.20–30% of duets on average. Birds in this group make rich, mellow and reverberating notes characteristic of the evergreen forests of interior East Africa.

Ethiopian group (*aethiopicus*; $n = 32$). **Distribution.**—Recordings from throughout the Ethiopian highlands south to Mt. Marsabit, Kenya; see Figs. 6–7).

Basic duet.—Bell-like note duets are very similar to those of the previous group, but the male (low note) may initiate the duet more frequently than in the Tropical group, wherein the female (high note) typically starts the duet (Fig. 2a). Additionally, duets are repeated largely unvaryingly for extended periods, which is not typical of the Tropical group.

Variations.—Unlike the Tropical group, snarls are much commoner elements in duets, and possibly the most frequent female vocalisation. These are usually delivered over the single or multiple, rich bell-like notes of the male.

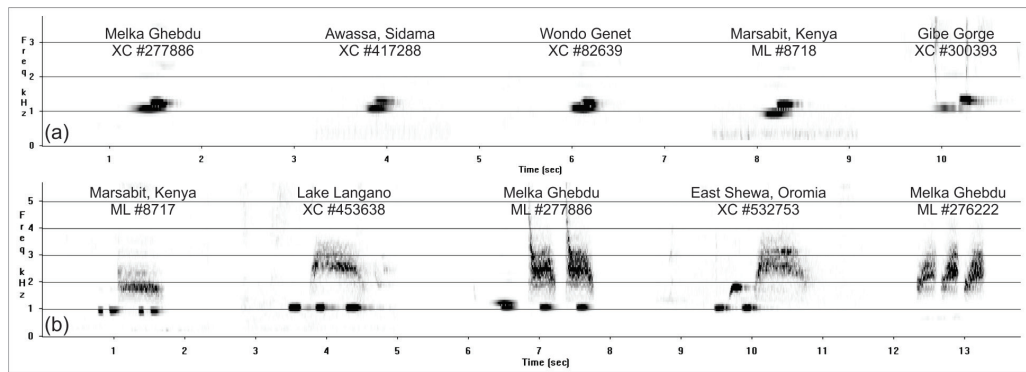


Figure 2. Sonograms of the Ethiopian group showing (a) variation in the basic male-initiated *too-lee* low-high duet, and (b) various snarl notes incorporated into duets or delivered alone by females in the repertoire of Ethiopian Boubou *Laniarius aethiopicus*. Recordings are all from Ethiopia unless labelled otherwise. For recording credits see Appendix.

Unique notes.—Snarls by the female (?) are elaborate in this group, sometimes embellished or doubled over the bell-like notes of the male, or delivered in multiple series by the male alone (Fig 2b). This range of snarls, their frequency of use and combinations in which they are delivered is matched only by subspecies *mossambicus* (see below).

East Coast group (*sublacteus* and *mossambicus*; $n = 95$). *Distribution.*—Recordings from north-east Tanzania (Zanzibar, Saadani National Park, the Usambara and Pare Mountains to Mikumi National Park) south through eastern Tanzania to Mozambique, all of Malawi and Zimbabwe (north of $c.20^{\circ}\text{S}$), eastern and southern Zambia (Luangwa Valley, Kasanka National Park, Lusaka and Zambezi Valley) to north-east Botswana and north-east Namibia (Caprivi); see Figs. 6–7.

Basic duet.—Three unmusical and typically non-overlapping notes (vs. two in other groups) that differ distinctly from those used by all other groups. The typical note of the male, which initiates the duet, is either a distinctive frog-like croak (Fig. 3a) similar to those of Lühder’s Bushshrike *L. luehderi* and Braun’s (Orange-breasted) Bushshrike *L. brauni*, or a slowly repeated, drawn-out flute-like whistle (Fig. 3b), with a similar piping quality to the song of Grey-headed Bushshrike *Malaconotus blanchoti*, and higher pitched than any typical duet note by males in other groups. When incorporated into duets, croaks or whistles are delivered in a double series with female snarls interspersed, e.g. *peeeeeuu-grrrr-peeeeeuu*.

Variations.—A less common variation involves two snarls by the female between the two notes of the male. Also, a distinctive and slowly delivered series of sonar-like *too-too-too* notes with a tinkerbird-like resonance (very similar to Southern Boubou), followed by a snarl from a female. This is infrequently recorded (examples from Zanzibar and the Luangwa Valley). While structurally not dissimilar to some duets in the Tropical group, the sound in the latter variation is entirely different in quality.

Unique notes.—The croak note of the male does not occur in other groups, whilst a commonly used, exaggerated double snarl by the female is shared only with *aethiopicus*. Meanwhile, *mossambicus* (examples from Malawi, Mozambique and Zambia) may engage in a rapidly repeated duet, including a single sonar note or short, inflected whistle (male) and harsh, grating scold (female), e.g. *too-kaa-too-kaa-too-kaa* or *twee-kaa-twee-kaa-twee-kaa*, which is unique.

General comments.—The female is capable of making only groaning snarls in duets and there are no duets, with each sex whistling on a different pitch, unlike in other groups.

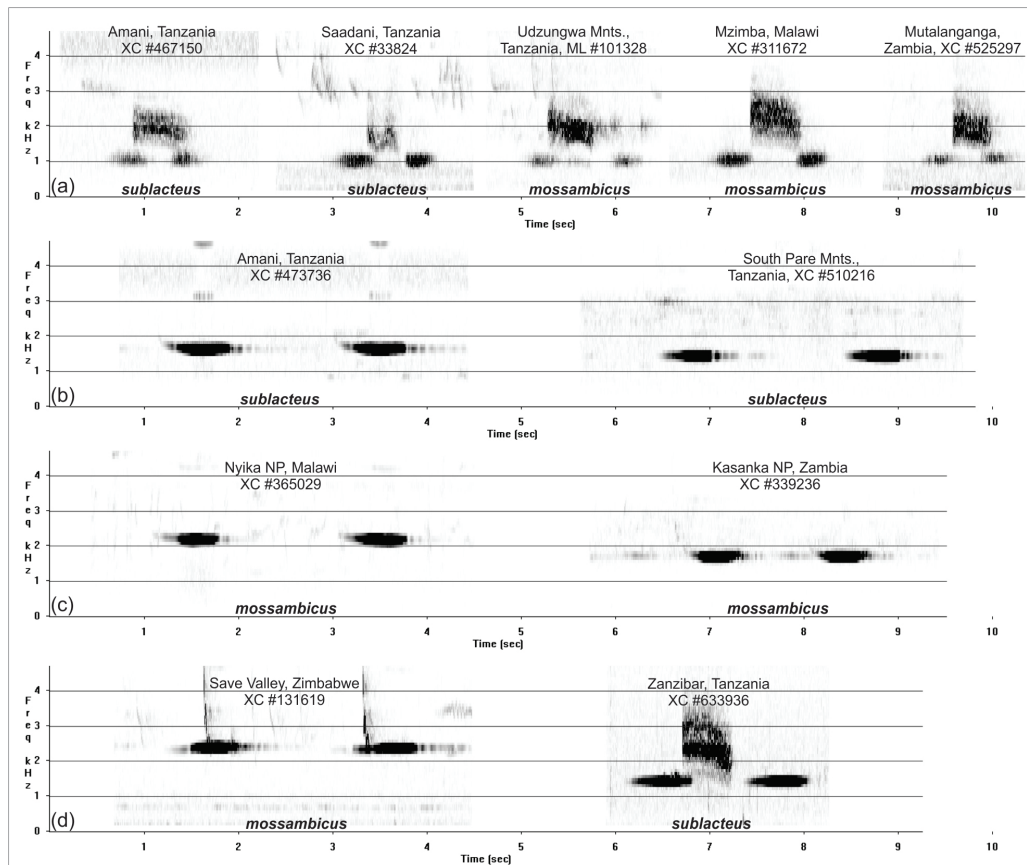


Figure 3. Sonograms of the East Coast group showing (a) variation in the basic croak-snarl-croak duet, and (b–d) the repeated, drawn-out double-monotone whistle that can also be incorporated into a duet (d; Zanzibar) by the addition of a female snarl in the repertoire of East Coast Boubou *Laniarius sublacteus* and *L. m. mossambicus*. For recording credits see Appendix.

Duets also differ, in particular from *major* (and *ambiguus*), in the near-complete absence of *too-too-too* notes in the male's repertoire, of which the rarely heard sonar-like versions described above are the only examples.

Somali group (*somaliensis*; $n = 30$). *Distribution*.—Recordings from the Kenya coast (Lamu, Witu Forest, Sokoke Forest, Samburu [Taru], Rabai, Mombasa, Ukunda, Msambweni, Shimba Hills, Shimoni); see Figs. 6–7.

Basic duet.—Typically comprises two bell-like notes, and initiated by the female with a unique varying-pitch note, sliding from high to low, to match the low note of the male, e.g. *teeyoo-too* (Fig. 4a). This duet is also commonly given in a three-note series initiated with the low note of the male, e.g. *too-teeyoo-too* (Fig. 4b).

Variations.—Females may also deliver the varying-pitch note in a double series, followed by a single low note by the male, e.g. *teeyoo-teeyoo-too*, while a less common variation comprises a high-pitched whistle by the female (c.2.1 kHz) with an intervening varying-pitch note by the male, e.g. *tee-teeyoo-tee*.

Unique notes.—The varying-pitch note of the female is very distinctive, rendering the duet unique. Also unusual is the apparent absence of a snarl in the female repertoire.

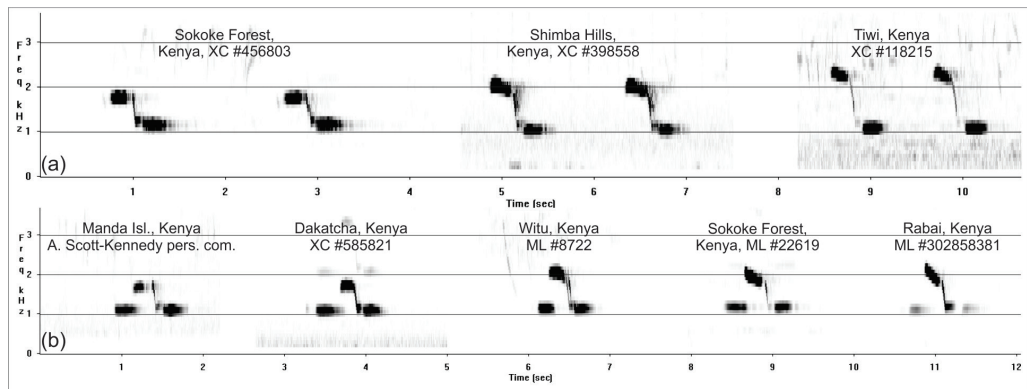


Figure 4. Sonograms of the Somali group showing (a) variation in the basic, yet highly distinctive, two bell-note, female-initiated duet of Juba Boubou *Laniarius somaliensis* from the Kenya coast (single motif repeated once) and (b) the three-note male-initiated version. For recording credits see Appendix.

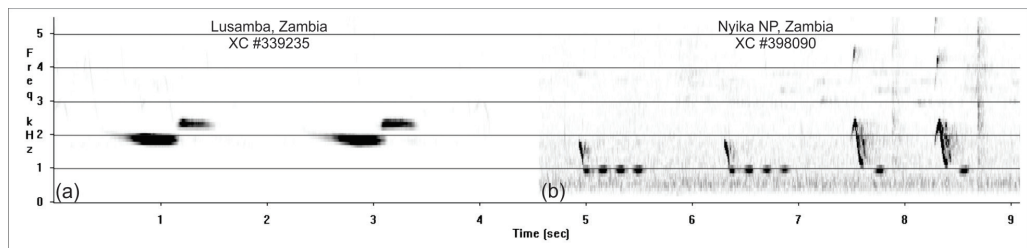


Figure 5. Sonograms of pied boubous *Laniarius* spp. showing two examples of duets from Zambia considered to represent mixed pairings and / or intergrades, with characteristics of both the Tropical (southern subgroup) and East Coast groups. For recording credits see Appendix.

Instead the male may duet with a snarl, the converse of duets in the East Coast group, wherein only females produce snarls.

General comments.—In terms of the sound's quality, which is sharp and deeply resonating, the duet stands apart from those of other groups, especially the East Coast group.

East Coast × southern Tropical intergrades ($n = 3$). A small number of duets from southern Tanzania to northern Malawi and northern Zambia were intermediate between the East Coast group and southern subgroup of the Tropical group, suggestive of interbreeding between them (Fig. 5). In one case (Fig. 5a), high, drawn-out flute-like whistles by the male (characteristic of the East Coast group) were combined with slightly higher flute-like whistles of the female (characteristic of Tropical), while in another (Fig. 5b) a male switched between the gonolek-like varying-pitch note in *too-too too* series (characteristic of the Tropical group) and a phrase consisting of sharp, inflected *twee* and single *too* notes (less common but characteristic of the East Coast group), followed by a hard female scold (also characteristic of the East Coast group), e.g. *kyonk-too-too-too...tweetoo-kaaa*.

Discussion

Vocalisations and taxonomy.—My results are broadly congruent with those of published DNA analyses. The distributions mapped in Fig. 7 integrate the genetic results from Nguembock *et al.* (2008) and Finch *et al.* (2016) with the findings reported here, also taking the literature and previously mapped distributions into account. The vocal evidence

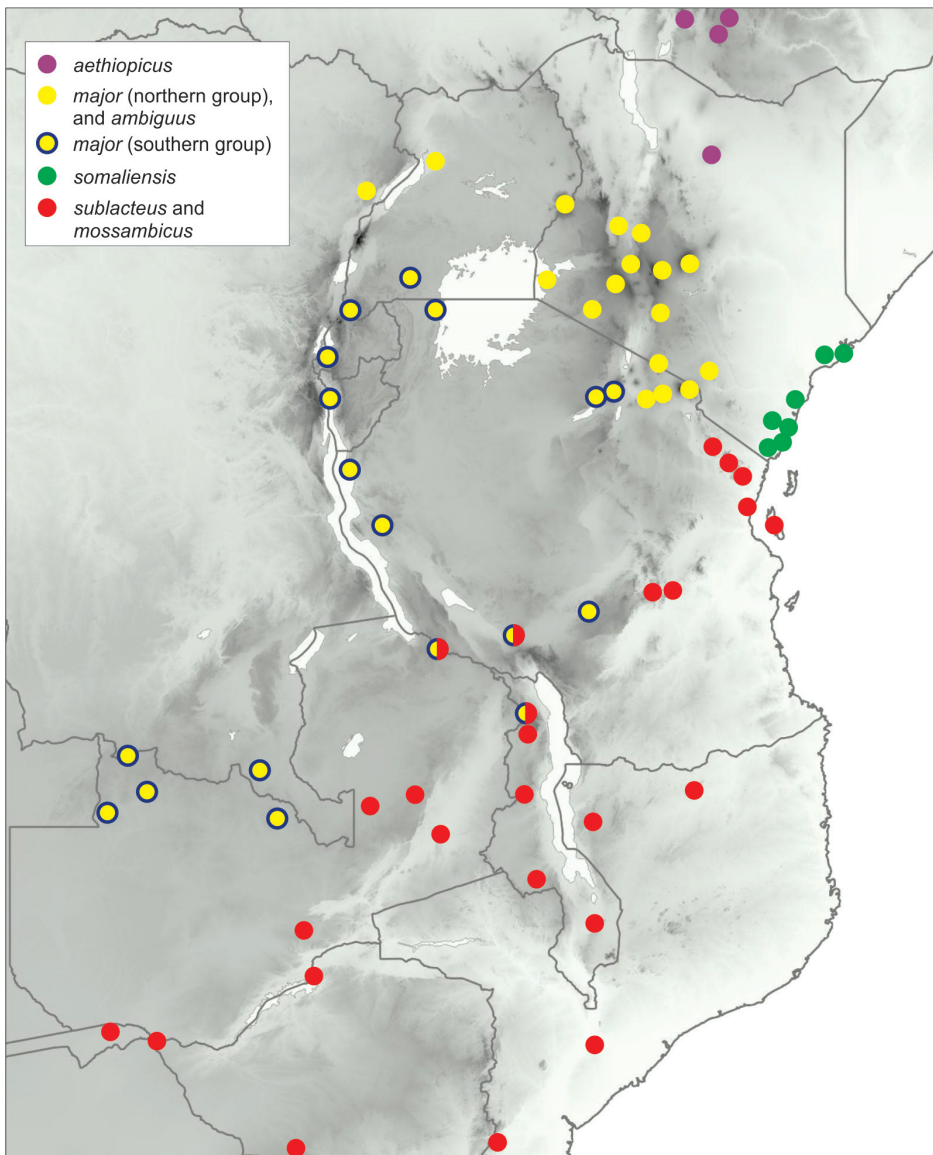


Figure 6. Map showing the locations of audio recordings of pied boubous (*Laniarius* spp.) in East Africa and adjacent regions, allocated to the four distinct groups based on duet type (purple, yellow, green and red markers) and one subgroup (blue and yellow markers) recognised herein. Red and yellow markers denote audio recordings with elements from two different groups, indicating some intergradation.

presented here fully supports the three key findings of genetic studies by Nguembock *et al.* (2008) and Finch *et al.* (2016).

1. Birds referred to *sublacteus* from the Usambara Mountain region in central-east Tanzania are not conspecific with other pied boubous in East Africa (possibly excluding *mossambicus*, which was not sampled by Nguembock *et al.* 2008 but is vocally identical to *sublacteus* and therefore could be conspecific as indicated herein). This is supported by, among other characteristics, the presence of a unique croak note in *sublacteus* (plus *mossambicus*) given by males in duets, and the absence of a whistle from the female repertoire.

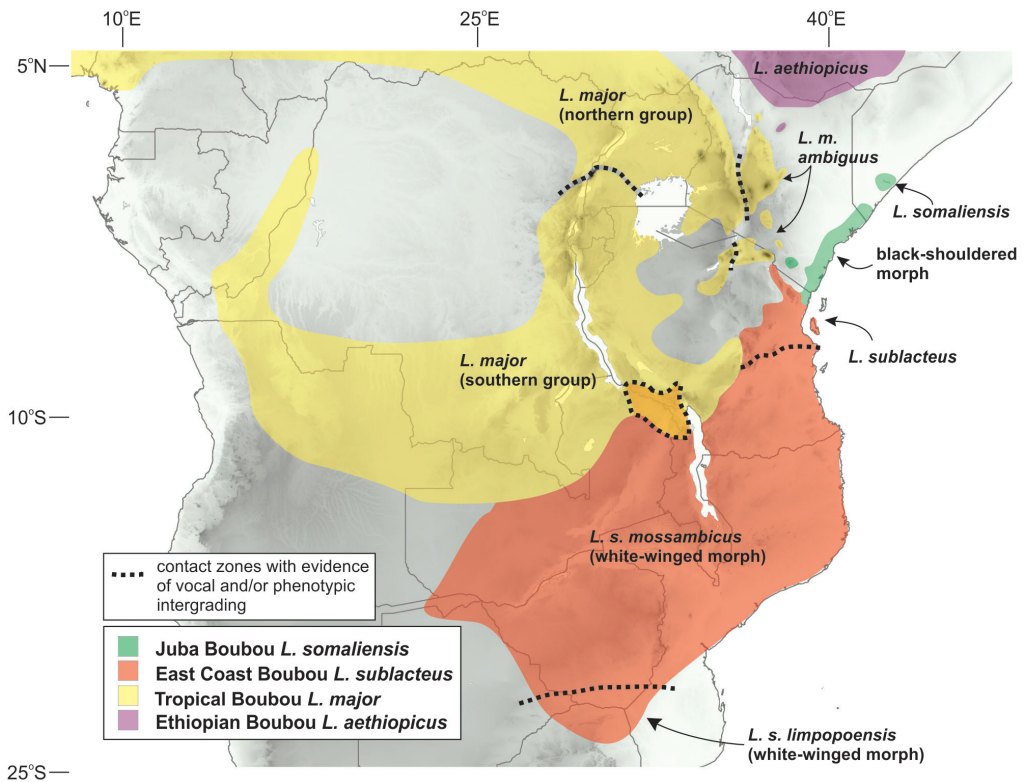


Figure 7. Map showing the distribution of the species and subspecies in the pied boubou complex (*Laniarius* spp.) in East Africa, as inferred from vocal analyses in this study and previous genetic studies (Nguembock *et al.* 2008, Finch *et al.* 2016).

2. Taxon *somaliensis* is a different species from *sublacteus*, despite their identical appearance. Although the latter ranges to areas immediately south of Kenya in north-east Tanzania, populations of *somaliensis* are vocally consistent throughout coastal Kenya from Shimoni and the Shimba Hills north to at least Manda Island, and do not overlap in voice with adjacent *sublacteus* (Fig. 7), but rather utter mellow bell-like notes mixed with sharper varying-pitch notes. While there are no known recordings from southern coastal Somalia (J. Miskell *in litt.* 2020), it is expected that birds there will be vocally consistent with birds on the Kenya coast, as their similar genotype suggests.

3. The relationship between birds in the northern subgroup of the Tropical group and the Ethiopian group is comparatively close relative to that between these forms and both the East Coast and Somali groups. This is reflected in their duet characteristics: the Tropical group uses rich mellow bell-like notes in multiple series, those of the Ethiopian group are similar with a greater use of snarls, whereas neither of these repertoires shows any significant overlap with either the East Coast or Somali groups.

Further attesting to the significance of the vocal evidence presented here concerning the two coastal forms, are the prophetic words of Sclater & Moreau (1933) who were well aware of these vocal differences and their implications. They clearly described the voice of *somaliensis*, from just south of the Kenya / Tanzania border on the coastal plain at Tanga (at the southern limit of its distribution), and that of *sublacteus* in the Usambara foothills, only 60 km inland:

'It is a remarkable fact that the calls of the coast and the mountain birds are different, although there seems to be no morphological distinction between them. The call of the Tanga bird consists of three notes with a magnificent bell-like resonance ... [and it] occurs through the savannah immediately inland, but as soon as the Usambara foothills are reached this ringing intonation is heard no more. Throughout the (Usambara) mountains the Boubou utters a very loud double call, never triple. Each of the two notes is a prolonged uninflected fluting whistle, with no metallic clang. Their notes are as consistently distinct as if they belonged to different species.... The female, with perfect synchronisation, replies with a deep groan. I doubt she is capable of producing the whistle'.

This finding is also in line with common regional species distribution patterns, in that the Tanga-Pangani region of Tanzania comprises a significant biogeographical divide on the east coast of Africa. This marks the southern limit of species typical of the Somali biome, such as Golden Palm Weaver *Ploceus bojeri* and Ethiopian Swallow *Hirundo aethiopica*, as well as the northern limit of species more typical of woodland of the southern tropics such as Böhm's Bee-eater *Merops boehmi* and Piping Cisticola *Cisticola fulvicapilla*.

While the evidence presented here supports the recommendation of Nguembock *et al.* (2008) that species status is warranted for *sublacteus*, it also indicates, unexpectedly, that *mossambicus* (currently treated within *L. major* by all authors and not adequately sampled by Nguembock *et al.* 2008) should be united with it. Based on vocalisations, these two taxa, along with the similar-sounding extralimital *limpopoensis*, appear to comprise three subspecies within one discrete genetic lineage. Finch *et al.* (2016) suggested that *mossambicus* may be specifically distinct from *sublacteus*. That conclusion is not supported here, although vocal evidence does argue strongly that *mossambicus* should be transferred to *sublacteus* from *major*.

In Zambia, Dowsett & Dowsett-Lemaire (1980) and Dowsett *et al.* (2008) noted the unique croak note of birds in the Livingstone area (assigned to *mossambicus*), and which is absent in birds from northern Zambia (which they attributed to *major*), a treatment implying they considered the differences in voice to be dialectical. While there is no vocal evidence of intergradation between these taxa over most of Zambia, both specimen evidence and vocalisations are, however, supportive of it in a small area of northern Malawi and northern Zambia (Nyika National Park) to southern Tanzania (Ufipa to Mbeya) (Fry *et al.* 2000). Some duets from this region are characterised by elements from both taxa (Fig. 5), while a specimen from the Mbeya region was recognised as an intergrade and described as *L. hybridus* Neumann, 1899.

Also unexpected, and not uncovered by previous molecular studies, vocalisations suggest the presence of an unrecognised biogeographic division within *major*. Consistent use of a varying-pitch note in the duets of birds in the south of its range, entirely absent to the north, is suggestive of two discrete lineages. The location of the divide is in south-west Uganda, which also marks that between many species pairs with fragmented subtropical distributions (e.g., Northern *Melaenornis edolioides* and Southern Black Flycatchers *M. pammelaena*, Lesser *Lamprotornis chloropterus* and Miombo Blue-eared Starlings *L. elisabeth*, Northern *Ptilopsis leucotis* and Southern White-faced Owls *P. granti*, or Dark-eyed *Melaniparus leucomelas* and Pale-eyed Black Tits *M. guineensis*). The division between southern *major* and *ambiguus* is similarly evident in the Crater Highlands of northern Tanzania, where birds with a varying-pitch duet meet and possibly intergrade with taxon *ambiguus* of areas east of the Rift Valley, at Essimngor to Mt. Meru. This is suggested by photographs of birds that show the white median coverts of both forms, but with white proximal greater coverts as in *major* (black

in *ambiguus*), and all-black secondaries as in *ambiguus* (two are white in *major*; e.g., see ML 249878891 and ML 291083661). The presence of a varying-pitch note in duets of southern *major* raises the possibility of a relatively close affinity with coastal *somaliensis*, which also has a varying-pitch note. Indeed, some recordings of *major* from northern Zambia are not dissimilar by ear to duets of *somaliensis*.

Nomenclature.—The name East Coast Boubou has been applied to pied boubous of the entire east coast of Kenya and Tanzania by most authors, under the assumption these birds were all one species and referable to *sublacteus* (e.g., Britton 1980). More recently, the same name has again been used in conjunction with *sublacteus*, particularly for birds in north-east Tanzania (i.e. not those birds genetically matching *somaliensis* in coastal Kenya; Nguembock *et al.* 2008). The vocal data presented here support the genetic discovery that north-east Tanzanian birds are not closely related to those in coastal Kenya, and I propose that the English name East Coast Boubou should also include the taxa *mossambicus* Fischer & Reichenow, 1880, and *limpopoensis* Roberts, 1922 (Fig. 7). While Clements *et al.* (2019) currently use Zanzibar Boubou for *L. sublacteus*, East Coast Boubou is preferred here to reflect the extensive distribution of subspecies *sublacteus* and *mossambicus* in coastal Tanzania from the Saadani–Pangani region southwards.

Of importance to the taxonomy and nomenclature of birds of coastal Kenya (see below) is justification for their referral to *somaliensis* here. Finch *et al.* (2016) opted not to assign a name to birds on the Kenya coast although the genetic data pointed to conspecificity with *somaliensis*, because of uncertainty over the type locality of the form *sublacteus*, labelled ‘Eastern Africa’ (Cassin 1851, *vide* Grant & Mackworth-Praed 1944). With the origin and precise type locality of *sublacteus* not considered traceable, several locations in coastal Kenya were posited, apparently arbitrarily (Grant & Mackworth-Praed 1944, 1947). Irrespective of exactly where, it seems likely that coastal Kenya was suggested simply because birds with the phenotype of *sublacteus* had been collected there.

The improbability that the type locality of *sublacteus* is in Kenya can be inferred from details of the 12,500+ bird specimen collection belonging to François Massena, Second Duke of Rivoli, which the Academy of Natural Sciences of Philadelphia acquired in 1844. From this collection, ten specimens were described as new species, three with type localities designated as Zanzibar (Cassin 1851), so at least some material originated there. Collection of birds from what is now Kenya did not commence until Baron von der Decken’s expedition in 1859 (D. A. Turner *in litt.* 2021) and the first specimens known from mainland Tanzania were taken during the expedition of Captain J. H. Speke in 1860 (N. Baker *in litt.* 2021). Therefore, *sublacteus* can have originated only from Zanzibar, which European naturalists visited from the 1820s onwards. It therefore seems justified to refer birds on the Kenya coast to *somaliensis*, and while a genetic study of the *sublacteus* type specimen is planned (B. Finch *in litt.* 2021), the treatment proposed here seems appropriate in the absence of contradictory DNA evidence.

Meanwhile, *somaliensis* was afforded the English name Juba Pied Shrike by van Someren (1932), reflecting its type locality ‘Unterlauf des Ganale’ (i.e. ‘lower course of the Ganale’; Reichenow 1905), generally thought to be the Juba River. To draw much-needed awareness to the conservation plight of the lower Juba’s riverine forests, which are currently experiencing severe levels of deforestation, the name Juba Boubou is proposed here for *L. somaliensis*.

Conclusion

This study, based on vocal differences, supports the findings of Nguembock *et al.* (2008) and Finch *et al.* (2016) that two distinct and unrelated species of pied boubous should be recognised on the East African coast, with the English name East Coast Boubou for

L. sublacteus, as already in use, and Juba Boubou, as recommended here, for *L. somaliensis*. Vocal data also suggest that white-winged *mossambicus* is better aligned with black-winged *sublacteus* than with white-winged *major*, again supporting statements by Nguembock *et al.* (2008) that plumage criteria are unreliable indicators of taxonomic affinity. Meanwhile, vocal evidence also suggests southern populations of Tropical Boubou *L. m. major* are worthy of further taxonomic investigation, based on consistent vocal differences from northern populations.

Future work on this complex in East Africa should seek to ascertain several outstanding details raised by the treatment proposed here. First, DNA comparisons between *sublacteus* and *mossambicus* are needed to test the hypothesis of conspecificity, or if *mossambicus* is better considered specifically. Second, audio recordings of the white-shouldered morph of *somaliensis* in south-coastal Somalia should be obtained and compared with those of the black-shouldered morph of *somaliensis* in coastal Kenya, to test previous genetic findings of conspecificity. Third, DNA comparisons of *major* from the southern (e.g. Zambia to western Tanzania) and northern (west Kenya to Cameroon) parts of its range should test my vocal data, that these birds may comprise two separate lineages.

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Address: 7961 East Saanich Road, Saanichton, British Columbia, Canada, V8M 1T4, e-mail: james_bradley@ymail.com

Appendix: Details of recordings used in the figures. ML = Macaulay Library catalogue number, XC = Xeno-canto catalogue number, NP = National Park.

Taxon (subgroup)	Location	Country	Catalogue	Recordist
<i>aethiopicus</i>	Marsabit	Kenya	ML 8718	Marian McChesney
<i>aethiopicus</i>	Melka Ghebdu	Ethiopia	XC 277886	Andrew Spencer
<i>aethiopicus</i>	Awassa	Ethiopia	XC 417288	Nicolas Martinez
<i>aethiopicus</i>	Wondo Genet	Ethiopia	XC 82639	David Marques
<i>aethiopicus</i>	Gibe Gorge	Ethiopia	XC 300393	Peter Boesman
<i>ambiguus</i>	Chyulu Hills	Kenya	ML 65696	Jennifer Horne
<i>ambiguus</i>	Aberdares	Kenya	ML 8794	Myles North
<i>ambiguus</i>	Mt. Kenya	Kenya	ML 8770	Myles North
<i>ambiguus</i>	Mt. Kenya	Kenya	ML 97979	Ian Sinclair
<i>major</i> (northern)	Gwasssi Hills	Kenya	XC 294873981	James Bradley
<i>major</i> (northern)	Tugen Hills	Kenya	XC 299939461	James Bradley
<i>major</i> (northern)	Cape Coast	Ghana	ML 87080	David Moyer
<i>major</i> (northern)	Meiganga	Cameroon	XC 100525	Hans Slabbekoor
<i>major</i> (northern)	Gwasssi Hills	Kenya	XC 291874011	James Bradley
<i>major</i> (northern)	Lolgorien	Kenya	ML 90398081	Nathan Hentze
<i>major</i> (northern)	Nyankunde	DR Congo	ML 1515	Peter Kaestner
<i>major</i> (southern)	Minziro Forest	Tanzania	ML 46017	David Moyer
<i>major</i> (southern)	Lake Mburo	Uganda	XC 282014	Rolf de By
<i>major</i> (southern)	Kigali	Rwanda	XC 95097	Rory Nefdt
<i>major</i> (southern)	Sitebe	Tanzania	XC 83841	David Moyer
<i>major</i> (southern)	Ngorongoro	Tanzania	ML 17985	Ted Parker
<i>major</i> (southern)	Salujinga	Zambia	ML 24878	Stuart Keith
<i>mossambicus</i>	Mzimba	Malawi	XC 311672	Frank Lambert
<i>mossambicus</i>	Mutulanganga	Zambia	XC 525297	Daniel Danckwerts
<i>mossambicus</i>	Nyika NP	Malawi	XC 365029	Frank Lambert
<i>mossambicus</i>	Kasanka NP	Zambia	XC 339236	Peter Boesman
<i>mossambicus</i>	Save Valley	Zimbabwe	XC 131619	Mark Harper
<i>somaliensis</i>	Sokoke Forest	Kenya	XC 456803	Frank Lambert
<i>somaliensis</i>	Shimba Hills	Kenya	XC 398558	Rory Nefdt
<i>somaliensis</i>	Tiwi	Kenya	XC 118215	Rory Nefdt
<i>somaliensis</i>	Sokoke Forest	Kenya	ML 22619	Stuart Keith
<i>somaliensis</i>	Rabai	Kenya	ML 302858381	James Bradley
<i>somaliensis</i>	Witu Forest	Kenya	ML 8722	Myles North
<i>somaliensis</i>	Dakatcha	Kenya	XC 585821	Colin Jackson
<i>sublacteus</i>	Amani	Tanzania	XC 467150	Peter Ericsson
<i>sublacteus</i>	Saadani NP	Tanzania	XC 33824	Marc de Bont
<i>sublacteus</i>	Zanzibar	Tanzania	XC 633936	Louis Hansen
<i>sublacteus</i>	Udzungwas	Tanzania	ML 101328	David Moyer
<i>sublacteus</i>	Amani	Tanzania	XC 473736	Rolf de By
<i>sublacteus</i>	South Pares	Tanzania	XC 510216	Peter Boesman
<i>major</i> (southern) × <i>mossambicus</i>	Nyika NP	Zambia	XC 398090	Peter Boesman
<i>major</i> (southern) × <i>mossambicus</i>	Lusamba	Zambia	XC 339235	Peter Boesman

Extinct and endangered ('E&E') birds in the ornithological collections of the Musée de la Vallée, Barcelonnette, France, with comments on a Siberian Crane *Leucogeranus leucogeranus* egg

by Christophe Gouraud

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<http://zoobank.org/urn:lsid:zoobank.org:pub:10F43EDD-3605-43D5-B492-E8E278832162>

SUMMARY.—The Musée de la Vallée in Barcelonnette, France, houses two privately assembled ornithological collections totalling 1,405 mounted birds and 1,686 eggs, mostly from the 19th century. According to the current IUCN Red List of threatened species, the mounts and eggs represent 36 and 18 extinct or endangered ('E&E') bird species, respectively. This article concentrates on the specimens of 'E&E' species that deserve special curatorial care. The list includes one extinct and six threatened species. Special mention is made of a Siberian Crane *Leucogeranus leucogeranus* egg that is apparently one of the oldest of this species in the world's collections. In addition to IUCN status, the EDGE score of each species is also specified.

The fundamental role played by natural history museums in the dissemination of knowledge is of ever greater importance in this era of global threats to biodiversity (Collar *et al.* 2003, Bauernfeind *et al.* 2010, Webster 2017, Miller *et al.* 2020). Museum collections provide essential historical data for understanding the spatial evolution and historic demography of birds (e.g. Beissinger & Peery 2007), and are important in the implementation of effective conservation measures for species with declining populations. Ecologists and conservationists need to know 'what is where' in museum collections. Therefore, as suggested by Cooper & Steinheimer (2003), museums should publish catalogues of extinct or endangered ('E&E') avian species. For extinct taxa, museum specimens are irreplaceable and special care is required (Adams *et al.* 2003). The 5,000,000 bird eggs in the world's museums are an invaluable and underused resource (Kiff 2005, Marini *et al.* 2020), but they have enabled decisive discoveries that have improved protection of threatened birds (see, e.g., Ratcliffe 1967, Hickey & Anderson 1968). Therefore lists of eggs belonging to 'E&E' species are also of value.

The Musée de la Vallée, Barcelonnette, France (hereafter MDLV) houses two ornithological collections comprising mounted specimens and eggs, which were thoroughly inventoried between 2012 and 2019 (Gouraud 2012, 2015, 2019). They are briefly presented below.

The ornithological collections of the Musée de la Vallée

The Caire-Chabrand collection was initiated by Joseph-Adolphe Caire (1809–84), also known as the 'abbé des Oiseaux' (Arnaud 1904) whose goal was to possess a pair of all European species, as well as an example of their eggs. Three years before Caire died, his nephew-in-law Emile Chabrand (1843–93) acquired the collection. Chabrand was a passionate naturalist who enriched the collection with birds he traded or collected during his journeys, especially a round-the-world trip in 1882–83 (Chabrand *et al.* 2008). As his

collection grew, in 1886 Chabrand constructed a dedicated repository intended for its public display. After his death in 1893, the collection passed to the municipality. The Caire-Chabrand collection comprises 880 mounts of 487 species, and 1,178 identified eggs from a total of 1,426 representing 318 species (GBIF dataset).

The Berlie collection was started by Pierre Berlie (1832–1914), a teacher near Barcelonnette, and continued by his son Antoine (1864–1934), also a teacher. Like Caire, the Berlies aimed to assemble a collection of European birds and their eggs. The collection remained in the family home until April 2019, when the great-granddaughter of Pierre Berlie reached an agreement with the MDLV's director to deposit the collection in the museum. The Berlie collection holds 525 mounted specimens of 396 species, and 249 identified eggs (from a total of 260) of 102 species (GBIF dataset).

Two manuscript catalogues list the species in the Caire-Chabrand collection. The first, dated 29 September 1881, is the notarial deed prepared when Emile Chabrand acquired the Caire collection¹. This consists of three columns for each species giving (1) the number of mounts, (2) the French vernacular name, and (3) the number of eggs. The second catalogue, dated 1894, was prepared by Pierre Berlie following the death of Emile Chabrand. It comprises different lists of all natural history and ethnological items present in the collection at that time. Non-European species are listed separately (other than a very small number that were included in the European list). A list of c.30 mounts that reached MDLV between 1896 and 1911 completes the catalogue; 16 were located during the recent inventory, including an Andean Condor *Vultur gryphus* (1899) and one of two Egyptian Vultures *Neophron percnopterus* (from 1908) (see Table 1). Pierre Berlie also produced a handwritten catalogue of species in his own collection. Dated 1902, this may be incomplete as it was prepared 12 years before Pierre's death and 32 years before Antoine's. Moreover, some sheets are loose pages and as a result others may have been lost. It contains several lists. The main one appears to be the list of European species; it consists of several columns, with the French vernacular name, the sex, the number of birds, and a price². A second list is dedicated to exotic and non-European species, and gives only the number and sex of specimens of each species.

French vernacular names used in Chabrand's and Berlie's catalogues are sometimes too vague for clear identification. In addition, neither of these catalogues provides information on the collector or the date and locality of collection. Finally, study and comparison of these catalogues with the contents of the collections sometimes show certain inconsistencies (for example, for some species the 1881 list mentions a single egg and the 1894 list none, when there are in fact two in the collection).

Some specimens (both mounts and eggs) bear a label with the species name and sometimes a locality; very few give more detailed information. Both collections have faced several relocations, which explains how labels have been lost, some eggs were broken and shells of different species were mixed, all of which can hinder identification (especially some passerine eggs of the same genus or family). Generally, the eggs of relatively few species can be identified by the appearance of the shell alone. Without original data, identification of eggs to species can be very difficult, if not impossible, and even with them identification can be debated if an adult was not positively observed at the nest (which is not always noted on the labels). Moreover, the authenticity of many eggs supplied by dealers is doubtful. Much caution is therefore required in identification. However, it now seems

¹ Record in the Digne-les-Bains archives under classification no. 2E 22 161.

² No indication is given as to whether this is the price paid to acquire the specimens, or the price at which they were offered for sale. Shortly before his death in 1934, Antoine Berlie sought to part with the collection (Rochon-Duvigneaud 1934: 143). It is not known whether this was already the case in 1902.

TABLE 1

List of the 39 extinct and endangered ('E&E') bird species (mounts and eggs) in the Musée de la Vallée ornithological collections. * in the EDGE score column refers to the 16 species whose EDGE score has been recalculated following changes in their IUCN status since Jetz *et al.* (2014). The taxonomy of Velvet Scoter *Melanitta fusca* and Italian Sparrow *Passer italiae* have also changed since the publication of Jetz *et al.* (2014): the former was previously considered a polytypic species (now split), whereas the latter was considered as a subspecies of either House Sparrow *Passer domesticus* or Spanish Sparrow *P. hispaniolensis*. The EDGE score provided by Jetz *et al.* (2014) for these two species is therefore no longer representative of current taxonomy and is replaced by 'Taxo'.

Family	Species	English name	IUCN (2020)	EDGE score	No. of mounts	No. of eggs
Anatidae	<i>Oxyura leucocephala</i>	White-headed Duck	EN	3.95	3	6
	<i>Clangula hyemalis</i>	Long-tailed Duck	VU	3.59	4	3
	<i>Marmaronetta angustirostris</i>	Marbled Teal	VU	3.44	2	1
	<i>Aythya ferina</i>	Common Pochard	VU	2.44 *	1	3
	<i>Melanitta fusca</i>	Velvet Scoter	VU	Taxo	2	1
Podicipedidae	<i>Podiceps auritus</i>	Horned Grebe	VU	4.32 *	2	1
Columbidae	<i>Ectopistes migratorius</i>	Passenger Pigeon	EX	N/A	1	0
	<i>Streptopelia turtur</i>	European Turtle Dove	VU	3.11 *	4	1
	<i>Goura cristata</i>	Western Crowned Pigeon	VU	4.07	1	0
Gruidae	<i>Leucogeranus leucogeranus</i>	Siberian Crane	CR	5.16	0	1
Otididae	<i>Chlamydotis undulata</i>	African Houbara	VU	4.55	2	0
	<i>Otis tarda</i>	Great Bustard	VU	4.55	1	2
Hydrobatidae	<i>Hydrobates leucorhous</i>	Leach's Storm Petrel	VU	4.45 *	1	1
Diomedidae	<i>Diomedea exulans</i>	Wandering Albatross	VU	3.17	0	1
Procellariidae	<i>Puffinus yelkouan</i>	Yelkouan Shearwater	VU	3.47	1	0
Ardeidae	<i>Agamia agami</i>	Agami Heron	VU	4.24	1	0
Charadriidae	<i>Vanellus gregarius</i>	Sociable Lapwing	CR	5.23	2	1
Laridae	<i>Rissa tridactyla</i>	Black-legged Kittiwake	VU	3.20 *	3	3
	<i>Larus audouinii</i>	Audouin's Gull	VU	2.50 *	1	0
Alcidae	<i>Fratercula arctica</i>	Atlantic Puffin	VU	3.37 *	3	3
Strigidae	<i>Nyctea scandiaca</i>	Snowy Owl	VU	3.65 *	1	0
Cathartidae	<i>Vultur gryphus</i>	Andean Condor	VU	5.19 *	1	0
Accipitridae	<i>Neophron percnopterus</i>	Egyptian Vulture	EN	5.44	2	1
	<i>Clanga clanga</i>	Greater Spotted Eagle	VU	3.20	3	0
	<i>Aquila rapax</i>	Tawny Eagle	VU	3.16 *	1	0
Bucerotidae	<i>Buceros r. rhinoceros</i>	Rhinoceros Hornbill	VU	4.05 *	1	0
Strigopidae	<i>Nestor m. meridionalis</i>	Kaka	EN	5.09	1	0
Cacatuidae	<i>Cacatua s. sulphurea</i>	Yellow-crested Cockatoo	CR	4.61	1	0
	<i>Cacatua moluccensis</i>	Salmon-crested Cockatoo	VU	3.37	1	0
Psittacidae	<i>Amazona v. vittata</i>	Puerto Rican Amazon	CR	4.12	1	0
Tityridae	<i>Iodopleura pipra</i>	Buff-throated Purpletuff	EN	4.50 *	1	0
Laniidae	<i>Lanius meridionalis</i>	Southern Grey Shrike	VU	3.05 *	1	7
Alaudidae	<i>Chersophilus duponti</i>	Dupont's Lark	VU	4.14 *	1	0

Acrocephalidae	<i>Acrocephalus paludicola</i>	Aquatic Warbler	VU	3.44	5	2
Passeridae	<i>Passer italiae</i>	Italian Sparrow	VU	Taxo	1	0
Emberizidae	<i>Emberiza aureola</i>	Yellow-breasted Bunting	CR	4.55 *	0	1
Icteridae	<i>Leistes defilippi</i>	Pampas Meadowlark	VU	3.12	1	0
	<i>Euphagus carolinus</i>	Rusty Blackbird	VU	3.09	1	0
	<i>Xanthopsar flavus</i>	Saffron-cowled Blackbird	EN	3.54 *	1	0
Totals					60	39

possible to extract DNA from even a tiny fragment of shell (Birkhead 2016: 19). Hopefully, the development of molecular techniques will help identify eggs without original data (thereby underlining the importance of preserving unlabelled oological material that is sometimes considered—wrongly—to be ‘scientifically worthless’). Larger eggs at MDLV usually have inscriptions on their shells, whilst smaller eggs are identified on a separate label (some with information, often a number, also on the shell). I systematically tried to confirm the species mentioned on the original inscriptions by comparing their appearance and dimensions with those of eggs of the species in the literature (plates in Cramp *et al.* 1977–94, Walters 1995, Harrison & Castell 2002)³.

Although all continents, except Antarctica, are represented in both of the two collections, the birds and their eggs are of species that predominantly occur in Western Europe. Because the Berlies never travelled abroad, it is probable that exotic or non-European species in their collection were obtained via exchanges or purchases with other naturalists or dealers.

I present here the catalogue of ‘E&E’ bird species, including eggs, in MDLV. According to the Red List of threatened species (IUCN 2021), the MDLV ornithological collections house 60 mounts of extinct and threatened birds comprising one extinct species (a single specimen) and 35 threatened taxa, of which three are Critically Endangered (CR), five Endangered (EN) and 27 Vulnerable (VU). Among eggs, a total of 39 units comprising 18 threatened species, of which three are CR, two EN and 13 VU are held at MDLV (Table 1). From this list, I provide additional information for seven species that meet the following criteria. As with the Baillon collection (Gouraud 2014), I have detailed mounts and eggs of all Critically Endangered species at MDLV because of their small number. In addition to the criteria applied by Adams *et al.* (2003: 341) to the EN and VU categories, I have elected to also detail species with either (1) a restricted geographic range, either Extent of Occurrence or Area of Occupancy (IUCN criterion B), or (2) a small and declining population (IUCN criterion C). Just one species is involved (Buff-throated Purplethroat *Iodopleura pipra*) of which the number of mature individuals is estimated to be fewer than 2,500 and the number of individuals in the largest subpopulation <250 (i.e. IUCN criterion C2a(i), see BirdLife International 2016).

An important parameter for ecologists and conservationists is the ‘originality’ of a species, expressed as a measure of its genetic isolation (measured in My). This parameter, first developed for mammals by Isaac *et al.* (2007), then extended to birds by Jetz *et al.* (2014), combines the global threat level (or extinction risk, i.e. IUCN status) and results in an estimate of a species’ expected loss of evolutionary history per unit of time. The result (termed the Evolutionary Distinctiveness and Globally Endangered, or EDGE, score) ‘incorporates a species value of originality, or irreplaceability, weighted by the urgency of

³ Photos of eggs held in the oological collection at the Zoological Museum, Moscow Lomonosov State Univ. are at <http://www.fotoparus.com/photogallery>, and were used to compare eggs of species that breed in Russia.

action' (Reilly 2018: 108) and is complementary to IUCN status but EDGE species do not include extinct taxa. I have added EDGE scores according to the list prepared by Jetz *et al.* (2014: Table S1). For a consistent assessment of the EDGE scores presented below, note that those calculated by Jetz *et al.* (2014) ranged from 0.58 (species with a low level of threat and low degree of genetic isolation) to 6.83 (species with a high degree of genetic isolation), and a 95th percentile of 3.94 (based on 9,993 bird species; mean = 2.31 and median = 2.13). The IUCN status of 16 species had changed since Jetz *et al.* (2014). I recalculated and updated their respective EDGE scores following equation (1) in Isaac *et al.* (2007: 2).

Photographs of the mounts can be viewed in the respective GBIF database by following the hyperlinks attached to the inventory numbers. Eggs were not photographed, except the Siberian Crane *Leucogeranus leucogeranus* egg for the purpose of this study. The taxonomy and nomenclature of del Hoyo & Collar (2014, 2016) are employed for the Caire-Chabrand and the Berlie collections, and are followed here. IUCN status is that in the IUCN Red List of threatened species website (<https://www.iucnredlist.org>) during the inventory and updated on 15–23 December 2020. I present and discuss data from original labels, where possible, in relation to information provided in the catalogues dated 1881, 1894 and 1902.

Extinct species

COLUMBIDAE

PASSENGER PIGEON *Ectopistes migratorius*

Columba migratoria Linnaeus, 1766

MDLV.2012.0.429; mount, adult male, Caire-Chabrand collection. *Catalogue 1881*.—'Colombe voyageuse'. *Catalogue 1894*.—'Colombe voyageuse'.

Remarks.—This mount bears a Chabrand label that merely states 'Colombe voyageuse', or 'passenger dove'. It is unknown when and where it was collected, and from whom it was obtained. I am confident that it is the bird mentioned in the 1881 catalogue, and therefore collected prior to that date. At least 1,532 skins in museums worldwide were reported in the early 1960s (Hahn 1963) to which at least three more can be added: one in the Baillon collection of La Châtre (Gouraud 2014), another in the ornithological collection of Abbeville museum (pers. obs.), and that mentioned here. The 1902 catalogue mentions a 'Colombe voyageuse' which indicates that another bird was held in the Berlie collection. The whereabouts of the latter is unknown.

Threatened species

GRUIDAE

SIBERIAN CRANE *Leucogeranus leucogeranus* CR / EDGE score: 5.16

Grus leucogeranus Pallas, 1773

MDLV.2015.0.4; egg, measurements 95.53 × 57.45 mm, Caire-Chabrand collection (Fig. 1). *Catalogue 1881*.—Not mentioned. *Catalogue 1894*.—Two mounts (male and female) listed under 'Grue leucogérone / *Grus leucogeranus*' with the comment 'manquant [missing]'. No egg is mentioned.

Remarks.—The only inscription on the egg reads '*Grus leucogeranos*'. It appears twice, once in pencil, and again on a small label pasted on the shell, apparently in different handwriting (Fig. 1). Although no egg is mentioned in the 1881 and 1894 catalogues, it was almost

certainly part of the Caire-Chabrand collection when Emile Chabrand died in 1893. After his death, very few natural history objects were added to the collection (c.30 mounts—and no eggs—between 1896 and 1911). Moreover, this is not the only case where a specimen (mount or egg) is present but not listed in the 1894 catalogue. For example, the 1881 catalogue mentions a single egg of Common Crane *Grus grus*, but the 1894 catalogue none. However, the collection has two, one dated '1853' and which is the egg mentioned in 1881.

Siberian Crane eggs do not appear to be common in world oological collections and the majority appear to have been collected post-1900 (Appendix). Of 93 Siberian Crane eggs reported in collections, 73 were laid in captivity, and according to their labels only 16 are of wild provenance. The other four, including MDLV.2015.0.4, are of unknown origin. Although the *Siberian Crane studbook* gives 1905 as the date of the first captive Siberian Cranes (Kashentseva & Belterman 2009), Lord Lilford had this species in his aviaries as early as 1893 (Lilford 1903: 284). The first eastern and western Siberian Crane nests seem to have been discovered in 1960 and 1981, respectively (P. Tomkovich *in litt.* 2021, *vide* Vorobyev 1963 and Sorokin & Kotyukov 1982, respectively). The origin of any egg said to have been collected in the wild pre-1960 therefore appears questionable and further research is needed.

On his return from the North Cape in 1890, Chabrand made a short stopover in St. Petersburg (24–27 July) and Moscow (28–30 July). During his travels Chabrand frequently visited museums and sometimes met their directors or curators (Homps 2010). He visited the 'Parc zoologique' of St. Petersburg (probably what is now the St. Petersburg Zoo)



Figure 1. Egg of Siberian Crane *Leucogeranus leucogeranus* (MDLV.2015.0.4) showing the two different inscriptions (© Aurélie Béranger / Musée de la Vallée)

on 25 July, and the 'Musée de l'Industrie' in Moscow (where he saw a mammoth, genus *Mammuthus*) on 29 July. Chabrand's diaries⁴ do not specify if he met the curators or directors, or if he obtained specimens or eggs (during this period, Valentin Bianchi was one of the curators at the Imperial Academy of Sciences, St Petersburg; see Appendix). Although the provenance of MDLV.2015.0.4 is unclear, it is reasonable to hypothesise a captive origin. With a laying date prior to 1 September 1893 (and the death of Emile Chabrand), this egg seems to be, if not one of the first obtained, at least one of the oldest in the world's collections. Moreover, in addition to one at Muséum d'Histoire naturelle de Toulouse (Appendix), that in the Caire-Chabrand collection appears to be the second egg known in France (the Paris museum does not possess any eggs of this species; J. Fuchs *in litt.* 2021).

As mentioned in the 1894 catalogue, the two bird specimens are no longer part of the collection, and their whereabouts are unknown.

CHARADRIIDAE

SOCIABLE LAPWING *Vanellus gregarius* CR / EDGE score: 5.23

Charadrius gregarius Pallas, 1771

MDLV.2012.0.275; mount, adult male, Caire-Chabrand collection.

MDLV.2012.0.276; mount, adult female, Caire-Chabrand collection.

MDLV.2015.0.118; egg, measurements 45.51 × 31.38 mm, Caire-Chabrand collection. *Catalogue 1881*.—Two 'Vanneau social [Sociable Lapwing]'; no egg mentioned. *Catalogue 1894*.—Two 'Vanneau social / Vanellus gregarius' (male and female); one egg mentioned.

Remarks.—The mounted male and female bear Chabrand labels that state 'Vanneau social male / Vanellus gregarius Europe / 1881' and 'Vanneau social femelle / Vanellus gregarius Europe / 1881', respectively. The geographical definition of 'Europe' is vague. It is also unknown if 1881 was the year of collection or acquisition, but they were presumably collected before 31 December 1881. The egg bears a handwritten note that states 'Vanneau / social' and a label pasted to its shell inscribed 'Van[ellus]. gregarius Wolga'. The latter suggests that the egg was taken near the Volga River, which traverses three Russian federal districts (Central, Volga and Southern). Because the egg is mentioned only in the 1894 catalogue, and not 1881, it is reasonable to suggest that it reached the Caire-Chabrand collection between these years; the date of collection, however, could be earlier than 1881.

CACATUIDAE

YELLOW-CRESTED COCKATOO *Cacatua sulphurea sulphurea* CR / EDGE score: 4.61

Psittacus sulphureus J. F. Gmelin, 1788

MDLV.2012.0.432; mount, adult; Caire-Chabrand collection. *Catalogue 1881*.—No precise mention of the species, but '10 perroquets [10 parrot species]' are mentioned. *Catalogue 1894*.—A 'Cacatua à huppe jaune [Yellow-crested Cockatoo]' is mentioned.

⁴ These consist of two notebooks, which are still in the family archives of Chabrand's descendants and are therefore not at MDLV. They are known as 'Carnets de voyage d'Émile Chabrand, 1890. Private collection, Barcelonnette'. Surprisingly, natural history information is almost absent from these notebooks and there is no mention of the acquisition of any ornithology specimens.

Remarks.—The mount lacks any label or inscription. The plumage matches the nominate subspecies and therefore the bird was probably collected on Sulawesi, Indonesia.

PSITTACIDAE

PUERTO RICAN AMAZON *Amazona vittata vittata* CR / EDGE score: 4.12

Psittacus vittatus Boddaert, 1783

MDLV.2012.0.440; mount, unsexed adult, Caire-Chabrand collection. *Catalogue 1881.*—No precise mention of the species, but ‘10 perroquets [10 parrot species]’ are mentioned. *Catalogue 1894.*—Several parrots listed but their French vernacular names are too vague to link any to this species.

Remarks.—Like the previous mount, this one bears no label. Endemic to Puerto Rico and I believe the bird was collected there, but we cannot exclude the possibility of captive origin (see, e.g., Ghiraldi & Aimassi 2019: 39). The size of the specimen matches the nominate subspecies. This parrot was formerly found throughout the island, but the current wild population is estimated to be fewer than 50 mature birds (BirdLife International 2020).

TITYRIDAE

BUFF-THROATED PURPLETUFT *Iodopleura pipra* EN / EDGE score: 4.50

Pardalotus pipra Lesson, 1831

MDLV.2019.8.254; mount, adult male, Berlie collection. *Catalogue 1902.*—Not found or listed.

Remarks.—The mount bears a Berlie label that states ‘Manaquin / a parents / violets’. The name given on the label is not listed in the 1902 catalogue. The bird was perhaps obtained later but before the deaths of Pierre and Antoine Berlie (in 1914 and 1932, respectively). As this species is endemic to coastal eastern and north-eastern Brazil, the bird was presumably collected there.

EMBERIZIDAE

YELLOW-BREASTED BUNTING *Emberiza aureola* CR / EDGE score: 4.55

Emberiza aureola Pallas, 1773

MDLV.2015.0.654; egg, no measurements taken, Caire-Chabrand collection. *Catalogue 1881.*—Two ‘Bruant auréole [= Yellow-breasted Bunting]’; no egg mentioned. *Catalogue 1894.*—Two ‘Bruant auréole [= Yellow-breasted Bunting]’; no egg mentioned.

Remarks.—The only inscription on the egg reads ‘Bruant [Bunting] / E[mberiza]. aureola’. Like many buntings, eggs of this species show important intraspecific variation in their ground colour as well as in size, number and colour of the markings. The appearance and pattern of MDLV.2015.0.654 match eggs of clutch Q-3762 at the Zoological Museum, Moscow Lomonosov State Univ.⁵ It is unknown when and where the egg was collected, or who obtained it. The two bird specimens mentioned in the 1881 and 1894 catalogues no longer form part of the collection, and their whereabouts are unknown.

⁵ Photo at: http://www.fotoparus.com/photogallery/animals/wild_animals/aves/21_PASSERIFORMES_FRINGILLIDAE_EMBERIZA_aureola/bird.html (accessed 26 April 2021).

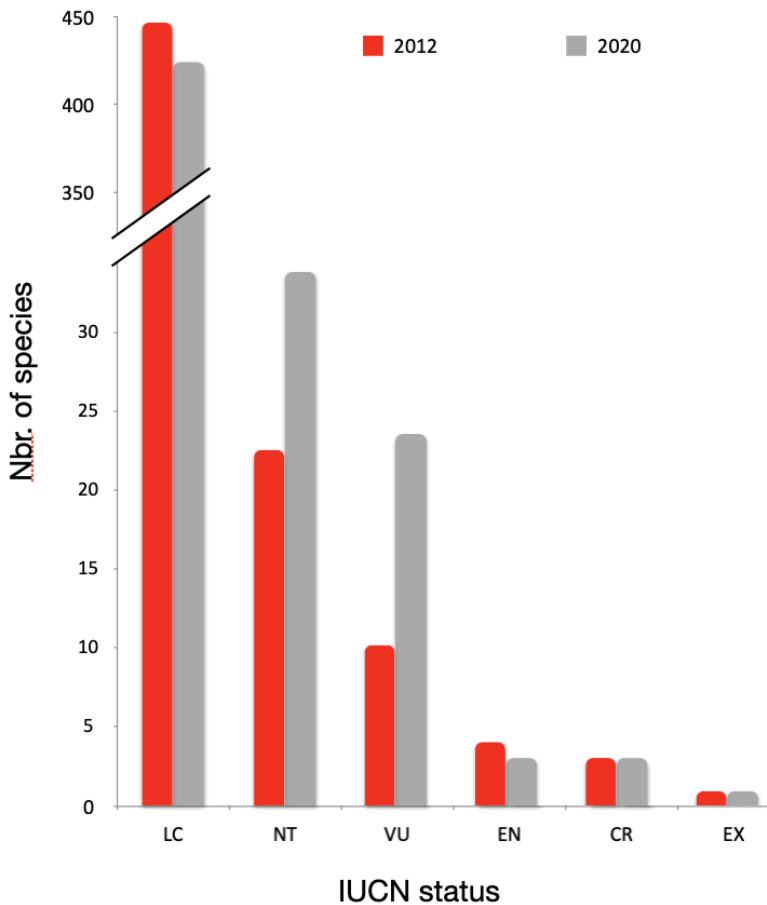


Figure 2. Comparison of the number of bird species in the Caire-Chabrand collection listed in each IUCN Red List category, between 2012 (red bars) and 2020 (grey bars)

Evolution of the list of threatened species at MDLV during 2012–20

Birds are the best-studied taxonomic group and is the only class to have been evaluated in its entirety (52 species lack data and are treated as Data Deficient). In 2020, 14% of the world's extant bird species were threatened, i.e. listed as CR, EN or VU (IUCN 2021, see Summary statistics, Table 1a). There is broad consensus as to the loss of biodiversity globally and the notion of the sixth mass extinction (Barnosky *et al.* 2011, Kolbert 2014, Ceballos *et al.* 2017). Like other large groups, birds are no exception (Inger *et al.* 2015, Rosenberg *et al.* 2019). At the start of the present millennium, 1,186 bird species were threatened and 128 extinct (Stattersfield & Capper 2000). Twenty years later, 1,508 species are classified as threatened and 159 extinct (IUCN 2021, see Summary statistics, Table 3). We can expect to see these changes reflected in museum ornithological collections, leading inevitably to an ever-growing list of species potentially on the verge of extinction or worse. Regular reappraisal of 'E&E' species lists ideally would be necessary.

The inventory of mounted birds in the Caire-Chabrand collection was made in 2012. As expected, eight years later the number of threatened species has increased slightly. Near Threatened (NT) and VU species increased by 11 and 13, respectively, reflecting the

reclassification of 23 Least Concern species (Fig. 2). Finally, the status of one species (Velvet Scoter *Melanitta fusca*) moved from EN to VU in 2015 (see IUCN 2021, Summary statistics, Table 7 [2014–15]).

As the inventories of the Caire-Chabrand oological collection and of the Berlie collection (birds and eggs) were completed in 2015 and 2019, respectively, I judged that the time difference with the present study was not sufficient for a comparison. A reassessment of the IUCN status of species in the MDLV's ornithological collections is planned in 10–15 years.

Recognition of the number of species whose IUCN status has changed over the last decade is certainly much greater in large ornithological collections, which are more likely to contain species otherwise poorly represented in collections worldwide, and is even truer for those rich in endemic or (especially Pacific) island species. In the context of global biodiversity loss, reassessment of the number of threatened species in the world's ornithological collections is another, albeit sad, means of documenting the current ecological crisis.

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Address: Collections ornithologiques du Musée de la Vallée, Villa La Sapinière, 10 avenue de la Libération, 04400 Barcelonnette, France, e-mail: ornithocoll@gmail.com

Appendix

Institutions that hold Siberian Crane *Leucogeranus leucogeranus* eggs. These data are the result of a request sent to museums via the electronic Bulletin for European Avian Curators (eBEAC) mailing list, consequently it may not be an exhaustive or definitive list. Data are presented chronologically. Dates given for wild eggs are either when collected or arrival in collections (see comments). Acronyms: AMNH: American Museum of Natural History (New York, USA); MDLV: Musée de la Vallée (Barcelonnette, France); MHNT: Muséum d'Histoire naturelle (Toulouse, France); NHMUK: Natural History Museum (Tring, UK); Oka: Crane Breeding Center of Oka State Nature Reserve (Russia); SMF: Senckenberg Museum Frankfurt (Frankfurt am Main, Germany); ZFMK: Zoologisches Forschungsmuseum Alexander Koenig (Bonn, Germany); ZMB: Museum für Naturkunde (Berlin, Germany); ZMMU: Zoological Museum, Moscow Lomonosov State Univ. (Russia).

Institution	No. of eggs	Registration no.	Provenance	Date	Comment
NHMUK	1	1941.4.6.885	Wild	May 1868	a
MDLV	1	MDLV.2015.0.4	Unknown	< 1 September 1893	b
NHMUK	1	1925.12.25.4251	Captivity	10 June 1900	c
NHMUK	2	1973.32.294	Wild	June 1904	d
NHMUK	1	1941.3.1.243	Captivity	1907	
NHMUK	1	1941.3.1.244	Unknown	< 1909	
NHMUK	2	1963.9.97	Unknown	< 10 May 1919	
ZFMK	1	N.IV.1.e.α	Captivity	1933	e
ZMMU	2	Q-2038	Wild	2 June 1960	f, g
ZMMU	2	Q-115	Wild	10 June 1961	f
MHNT	1	MNHT.O.406.1	Captivity	< 1963	h
ZMMU	2	Q-2039	Wild	10 June 1965	i
SMF	2	14695	Wild	23 June 1972	j
ZMMU	2	Q-2040	Wild	1 July 1977	k
ZMMU	2	Not registered	Wild	1 July 1977	l
ZMMU	1	Q-2041	Wild	27 June 1979	i
ZMB	2	Not communicated	Captivity	1996	
ZMB	4	Not communicated	Captivity	2000	
ZMMU	1	Q-5850	Captivity	20 April 2002	
ZMB	2	Not communicated	Captivity	2007	
AMNH	4	AMNH EN 17928	Captivity	< 2018	
ZMB	2	Not communicated	Captivity	2020	
Oka	54	Not communicated	Captivity	1988–2021	m

- a. The index card at NHMUK states that this egg was collected in May 1868 at 'Darasun, Dauria' and purchased by Henry Buckley in July 1869. The collecting location does not lie within the species' known breeding range. Because Siberian and Common Cranes *Grus grus* eggs are very similar, this could be an egg of the latter species.
- b. This study.
- c. The index card at NHMUK states that 'This egg may be the Lilford egg figured by Dresser, but it does not agree [with] the egg figured therein' (see Dresser 1905).
- d. The index card at NHMUK suggests these eggs were collected in the wild ('North east Siberia') and given to Maximilian Kuschel by Russian ornithologist Valentin Bianchi. The latter never visited the species' breeding grounds (P. Tomkovich *in litt.* 2021) and therefore obtained them from a third party. The card also states the eggs were taken from 'nests of rushes and reeds', which matches Common Crane rather than Siberian Crane (P. Tomkovich *in litt.* 2021). Dresser (1905) mentioned and depicted what he said was the only wild-taken egg he had ever seen, and which came from Siberia via Bianchi. The breeding range described by Dresser does not correspond with that of Siberian Crane, but rather its migratory stopovers. Moreover, the first Siberian Crane nests appear to have been discovered only in 1960 and 1981, for eastern and western Siberian populations, respectively (Vorobyev 1963, Sorokin & Kotyukov 1982). Identification thus seems doubtful and they could be Common Crane eggs (P. Tomkovich *in litt.* 2021).
- e. Laid in captivity in the Netherlands (breeder F. E. Blaauw) from where Alexander Koenig received it in 1933 (T. Töpfer *in litt.* 2021).
- f. Eggs collected in the wild (west of the lower Indigirka River, Allaikhosky District, Yakutia, Russia). The first clutch collected in the wild (P. Tomkovich *in litt.* 2021, *vide* Vorobyev 1963).
- g. The label states '02.VI.1960 [2 June 1960]' but Vorobyev (1963) clearly referred to 2 July 1960. The month on the label is probably incorrect (P. Tomkovich *in litt.* 2021).
- h. From the Cossaune collection, acquired in 1963 from Jean Sirven (H. Cap *in litt.* 2021).
- i. Eggs collected in the wild (west of the lower Indigirka River, Allaikhosky District, Yakutia, Russia).
- j. Eggs abandoned, and collected (Makatsch 1974: 151). Locality: Bereljach, North Yakutia (Russia). This clutch is still present in the SMF collection (M. Päckert *in litt.* 2021).
- k. Eggs collected in the wild (west of the lower Indigirka River, Allaikhosky District, Yakutia, Russia) and sent to the International Crane Foundation (Wisconsin, USA) for captive-breeding purpose. They proved infertile and were returned to Moscow (P. Tomkovich *in litt.* 2021).
- l. Eggs collected in the wild (west of the lower Indigirka River, Allaikhosky District, Yakutia, Russia) for captive breeding. Eggshells from dead unhatched embryos are present in the collection but not registered (P. Tomkovich *in litt.* 2021).
- m. In addition to whole eggs, the Oka Crane Breeding Center also has many shell fragments collected after hatching (T. Kashentseva *in litt.* 2021, *vide* Zhuchkova & Kashentseva 2002).

Rediscovery of the Blue-necked Tanager *Stilpnia cyanicollis albotibialis* in the Chapada dos Veadeiros, Goiás, Brazil

by Estevão Freitas Santos & Marcelo Kuhlmann

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SUMMARY.—We report a new record of the Blue-necked Tanager *Stilpnia cyanicollis albotibialis* in the Chapada dos Veadeiros, Brazil, which could represent its rediscovery after nearly 100 years without documented records. *S. c. albotibialis* was known only from its holotype, collected at the Chapada dos Veadeiros, in central Brazil, in December 1929 by José Blaser, and held at the Field Museum of Natural History, Chicago. We present behavioural data and comment on the biogeography of this subspecies, as no information concerning its ecology has been previously published.

Tanagers (Thraupidae) represent one of the most diversified group of Neotropical birds, showing a notable richness in morphological, behavioural and ecological traits. For example, the newly erected genus *Stilpnia* (Burns *et al.* 2016), which is broadly distributed in the Neotropics, comprises 14 species.

Blue-necked Tanager *Stilpnia cyanicollis* is polytypic, with seven subspecies generally recognised (Dickinson 2003), principally distributed in the Andean foothills, from north-west Venezuela to western Bolivia, but also in Brazil, across south-east Amazonia, from Mato Grosso to Goiás, Tocantins and southern Pará (Sick 1997, Dornas 2009, Santos *et al.* 2011, Kirwan *et al.* 2015, Andriola & Marcon 2017). Of the seven subspecies, two are locally distributed in the Amazon and Cerrado of central Brazil (*S. c. melanogaster* and *S. c. albotibialis*), the others in tropical forests of the Andean foothills (Marantz & Remsen 1994).

In Goiás state, central-west Brazil, both *S. c. melanogaster* and *S. c. albotibialis* occur. The former ranges east at least to the right bank of the Araguaia River in north-west Goiás, from where numerous recent records are available, for example, at wikiaves.com.br (e.g., G. Barros, WA2341765). This subspecies is locally common in the region, in tall riparian forest, semi-deciduous woodland, and *cerradão* (pers. obs.), a type of dry, low-stature woodland not associated with the presence of water and having a floristic composition similar to the adjacent savanna (Ribeiro & Walter 2008).

In contrast, *S. c. albotibialis* is known definitely only from the holotype, a female collected at 'Veadeiros' (Alto Paraíso de Goiás), on 9 December 1929 by José Blaser, held in the Field Museum of Natural History, Chicago (Storer 1970, Silva 1989, Lopes 2009, Kirwan *et al.* 2015). Blaser's excursion through the Veadeiros appears to have started in October 1929, as evidenced by a Spotted Nothura *Nothura maculosa major* (FMNH 408926) collected on 26 October 1929 at 'Veadeiros, near Cavalcanti'. The type locality of *S. c. albotibialis* lies between 1,000 and 1,200 m above sea level, this subspecies being restricted, until now, to the Chapada dos Veadeiros (Silva 1989). No information concerning its habitat, biology and natural history has been published. Here, we present the first documented record of Blue-necked Tanager for the Chapada dos Veadeiros, Brazil, which appears to represent the rediscovery of *S. c. albotibialis*, nearly 100 years after the holotype's collection.

New record: identification and natural history observations

On 16 December 2020, at c.07.30 h, we observed a single *S. cyanicollis* in a gallery forest of the rio São Miguel (1,035 m), at Fazenda Volta da Serra (14°10'S, 47°44'W), Alto Paraíso de Goiás, Brazil (Fig 1). According to our analysis *in situ* and the photographs we obtained (Figs. 2–4), the bird was identified as *S. c. albotibialis*, following the description of Traylor (1950) and photographs published by Kirwan *et al.* (2015), subsequently supplemented by the original images supplied by M. Hennen.

According to Traylor (1950) [*Stilpnia c. albotibialis*] differs from all other races in having the thighs and tibia white instead of black; in other characters it most nearly resembles *T. c. granadensis* [...], it differs strikingly from the nearest geographical race, *melanogaster*, of southern Matto Grosso in having a blue rather than a black belly and more purple on the throat'.

One of the diagnostic characteristics clearly visible in Fig. 2 is the purple throat, which is lacking in *S. c. melanogaster* (Fig. 4). Additionally, the bluish in the belly was visible when the bird preened on an exposed, high branch, as were the white marks at the base of both thighs during its third visit to a fruiting tree, when we observed it from below. The blue in the belly was much less visible in the shade than when the bird was sunlit. As Kirwan *et al.* (2015) mentioned, these two subspecies of Blue-necked Tanager are not easily separated given brief views in the forest shade. However, the diagnostic features were seen well in the field, and could be confirmed on our photographs, compared to those of the holotype (Fig. 5), and matching the description of Traylor (1950).

Our observation appears to be the first documented record of the subspecies since 1929. However, there is a single undocumented report from the 1980s by R. B. Cavalcanti (*in litt.* 2021) and the late E. O. Willis, in Chapada dos Veadeiros National Park, at the border of a narrow gallery forest. Cavalcanti noted the conspicuous blue head but, although Willis mentioned seeing the white marks on both tibia, they observed neither the purple on the throat nor the blue belly.

S. c. albotibialis is extremely poorly known (Kirwan *et al.* 2015) and nothing has been published concerning its natural history. *S. cyanicollis sensu lato* feeds on a variety of fruits, including Melastomataceae, e.g., *Miconia theaezans* (Camargo & Vargas 2006), *Miconia* sp. (Cañón *et al.* 2012), Primulaceae, e.g., *Myrsine coriacea* (Camargo & Vargas 2006), Araliaceae,

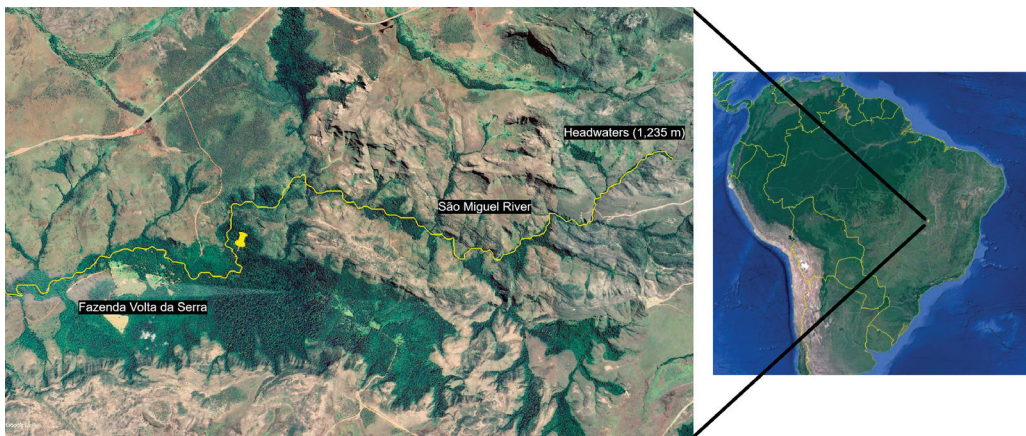


Figure 1. Map showing the rio São Miguel course (yellow line), the boundaries of the Fazenda Volta da Serra, and the area where we recorded *Stilpnia cyanicollis albotibialis* (yellow icon), Chapada dos Veadeiros, Goiás, Brazil (© Google Earth Pro)



Figure 2. Blue-necked Tanager *Stilpnia cyanicollis albotibialis*, rio São Miguel, Chapada dos Veadeiros, Goiás, Brazil, December 2020 (Marcelo Kuhlmann)



Figure 3. Blue-necked Tanager *Stilpnia cyanicollis albotibialis* consuming fruits of *Miconia minutiflora*, rio São Miguel, Goiás, Brazil, December 2020 (Marcelo Kuhlmann)



Figure 4. Blue-necked Tanager *Stilpnia cyanicollis melanogaster*, northern Mato Grosso, Brazil, showing the lack of purple on the throat (Estevão F. Santos)

e.g., *Schefflera morototoni* (Purificação *et al.* 2015) and Urticaceae, e.g., *Cecropia pachystachya* (E. F. Santos pers. obs.).

During the two hours we spent in the area, the bird was observed feeding on fruits of *Miconia minutiflora* (Melastomataceae), a small tree c.6 m tall with bluish-coloured fruits when ripe (Fig. 6), on the bank of the rio São Miguel. The individual spent c.2–3 minutes in the treetop, where there were a greater number of mature fruits, during its first visit. Nevertheless, it was also seen to take immature (green) fruits, but in smaller quantities (Fig. 3). Then, it flew into the gallery forest but, after c.10–15 minutes, returned to feed twice more. Over the three visits, it consumed at least 34 fruits, each of which was briefly mashed before being swallowed. While foraging, it vocalised persistently, giving short, wheezing notes (*tché! tché!*) like the alarm calls of *S. c. melanogaster*.

During our observations, 24 species of birds (including eight tanagers) were seen feeding on fruits of *Miconia minutiflora*; sometimes more than six species fed simultaneously in different parts of the same tree. The *S. c. albotibialis* tended to visit the fruiting tree only in the absence of other birds, and for short periods. It was briefly also observed in the adjacent subcanopy by the river following a mixed flock of tanagers including Hooded Tanager *Nemosia pileata*, Burnished-buff Tanager *Stilpnia cayana*, Black-goggled Tanager *Trichothraupis melanops*, Guira Tanager *Hemithraupis guira*, Blue Dacnis *Dacnis cayana* and Green-winged Saltator *Saltator similis*.

Habitat and biogeography

The headwaters of the rio São Miguel lie at 1,200–1,250 m above sea level, c.14 km west of Alto Paraíso de Goiás. The river drains west and gradually descends via a deep valley, reaching 950–1,000 m in the 'Vale da Lua' downstream. Between these two localities



Figure 5. Holotype of *Tangara cyanicollis albotibialis* (FMNH 75034) collected by José Blaser at Veadeiros, December 1929, in the Field Museum of Natural History, Chicago (Mary Hennen / Field Museum of Natural History)

lies Fazenda Volta da Serra, where we recorded the tanager. This valley is almost entirely dominated by a tall, semi-deciduous forest of c.450 ha, making it one of the largest forested areas in the Chapada dos Veadeiros (L. Jurgeaitis *in litt.* 2020).

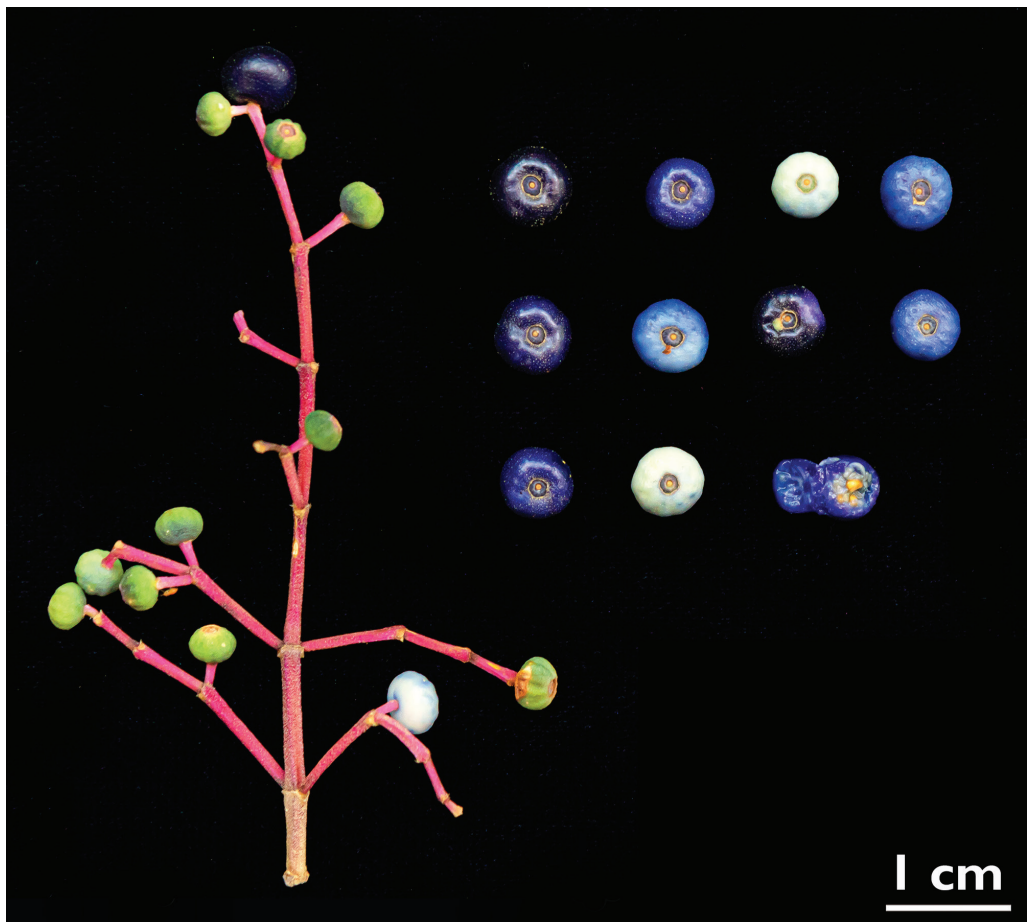


Figure 6. Mature fruits of *Miconia minutiflora* consumed by Blue-necked Tanager *Tangara cyanicollis albotibialis* (Marcelo Kuhlmann)

This forested area, associated with more fertile soils along the rio São Miguel and the adjacent slopes, holds a significant number of other Atlantic Forest taxa (e.g., Lesser Woodcreeper *Xiphorhynchus f. fuscus*, Rufous-breasted Leaf-tosser *Sclerurus scansor*, White-eyed Foliage-gleaner *Automolus leucophthalmus*, Greenish Schiffornis *Schiffornis virescens*), also recorded during our visit. Another example of an Atlantic Forest taxon occurring along the São Miguel is Red-breasted Toucan *Ramphastos dicolorus*, of which nine specimens were obtained by Blaser in January–March 1930, and labelled ‘Rio São Miguel’ (FMNH 75188–197). Other Atlantic Forest species known from the Chapada dos Veadeiros include Chestnut-headed Tanager *Thlypopsis pyrrhocomma* and Grey-hooded Flycatcher *Mionectes rufiventris*, but these taxa seem to occur only in more humid gallery forests around the headwaters of smaller drainages atop the highest plateaux (<1,250 m), not in the valleys and peripheral depressions of, among others, the rio São Miguel (Santos in prep.).

The presence of *S. cyanicollis*, and other Amazonian elements such as Agami Heron *Agamia agami* and Sunbittern *Eurypyga helias* in the São Miguel basin reinforces it as a zone of interchange between regions dominated by Atlantic and Amazonian avifaunal elements (Silva 1996). The relatively large number of Atlantic Forest species can be explained by a suite of factors, including distributional pathways that follow the high drainage of the rio

Tocantins (Santos in prep.), in addition to regular dips in temperature, the region's high elevations and topography, which overall favour the occurrence of such taxa (Silva 1989, Willis 1992, Silva 1996).

Although Blaser did not specify the precise locality where he collected the type of *S. c. albotibialis*, labelling it only 'Veadeiros'—the historical name for the municipality of Alto Paraíso de Goiás—we can speculate that it was collected somewhere near to or in the São Miguel basin, given that he seems to have followed the river's course. Blaser also collected birds at Fazenda Volta da Serra, where we recorded *S. c. albotibialis*, as evidenced by specimens labelled 'Volta da Serra' on 1 January 1930 (e.g., White-naped Jay *Cyanocorax cyanopogon*, FMNH 75011–012). Thereafter, many of his specimens were labelled 'Rio São Miguel', e.g., a *Saltator similis* from 2 January (FMNH 75055).

Conclusions

The probable proximity of the area where Blaser obtained the type of *S. c. albotibialis* to our observations suggests that this tanager is closely tied to forests around Alto Paraíso de Goiás, notably those along high drainages, which occupy a minor fraction of the overall landscape vs. the large area of *cerrado* and grassland.

This could potentially indicate why this subspecies went unseen for so long, despite much field work in the region. As an example, M. Bagno made several visits while compiling an avian inventory at Fazenda Volta da Serra, but did not detect this subspecies (L. Jurgeaitis *in litt.* 2020), and Lopes (2009) mentioned conducting an unsuccessful one-day search of the type locality of *S. c. albotibialis*. Moreover, Chapada dos Veadeiros is regularly visited by birdwatchers who to date have not found the species in the region (e.g., www.ebird.org, www.wikiaves.com.br). Despite this, the Chapada as a whole appears to be only patchily explored by ornithologists, with particular emphasis on the much larger open habitats, whereas forests, often in more remote areas, are only sporadically surveyed.

To date, *S. c. albotibialis* has not been found in areas surrounding the Chapada dos Veadeiros, e.g., in southernmost Tocantins, where detailed field work has been conducted in the last two decades (Pacheco & Olmos 2006, Rego *et al.* 2011, Dornas & Crozariol 2012; T. Dornas *in litt.* 2020). The closest record of *S. cyanicollis sensu lato* to ours, and apparently the only one south-east of Palmas, TO, is represented by a photo taken at São Valério (T. Dornas, WA 3547964), on the right bank of the rio Tocantins, c.250 km to the north. This individual resembles *S. c. melanogaster*, due to, among other traits, the uniformly blue throat. Thereafter, additional records, also matching the *melanogaster* phenotype, only begin to appear in the environs of Palmas and in north-west Tocantins. The rather 'insular' population of *S. c. albotibialis* in north-east Goiás needs to be further investigated, especially taxonomically.

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The case for splitting the Square-tailed Drongo *Dicrurus ludwigii*: a review of the phenetic evidence

by Lincoln D. C. Fishpool, Françoise Dowsett-Lemaire & Robert J. Dowsett

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SUMMARY.—The validity of recent changes in the taxonomic treatment of the Square-tailed Drongo *Dicrurus ludwigii* is assessed via analyses of morphological, morphometric, acoustic and distributional evidence. In addition to confirming the characters already recognised to distinguish West and Central African *sharpei* from the *ludwigii* group, we report previously undocumented but notable differences in voice and tail morphology. The occurrence of a hitherto unrecognised population of *sharpei* in south-east DR Congo, inferred from recent molecular studies, is confirmed, whilst evidence of the close approach of the two taxa in north-west Angola, within c.60 km of each other, further supports their distinctiveness. The proposal to separate *sharpei* itself into two species—with populations west of the Niger River recognised as *occidentalis*—is, however, not supported by vocal data, whilst differences in bill size, the sole known physical discriminant, are here found to be much more modest than previously reported, perhaps attributable to the larger sample sizes used in this study. Thus, on phenetic evidence, *occidentalis* merits no more than subspecific status.

In his revision of the taxonomy of Square-tailed Drongo *Dicrurus ludwigii* (A. Smith, 1834), Clancey (1976) recognised five subspecies, which he divided into two ‘broad groupings’. The first, his *ludwigii* group, comprised four subspecies: nominate, *muenzneri* Reichenow, 1915, *tephrogaster* Clancey, 1975, and *saturnus* Clancey, 1976. His accompanying map showed that the first three were distributed—almost parapatrically—along the East African coast, from the Eastern Cape of South Africa to the Limpopo River (nominate), with *tephrogaster* north of the Limpopo, penetrating inland as far west as southern Malawi and eastern Zimbabwe, and reaching northern Mozambique, where it was replaced northwards by *muenzneri*, ranging from the Ruvuma River in southern Tanzania via coastal Kenya to southern Somalia. The distribution of *saturnus*, disjunct from the other three, was mapped as extending across southern DR Congo west to central Angola. Here it approached the sole member of Clancey’s second lineage: *sharpei* Oustalet, 1879, of north-west Angola to Cameroon, thence east to western Kenya and west to Senegambia (Clancey 1976). This treatment subsequently found wide acceptance in global and regional handbooks and checklists, including Pearson (2000), Hockey *et al.* (2005), Rocamora & Yeatman-Berthelot (2009), Dickinson & Christidis (2014) and del Hoyo & Collar (2016).

As Clancey (1976) pointed out, *ludwigii* and *sharpei* had previously been treated as separate species: Sclater (1930) had considered them to be distinct as, by implication, did Bates (1930) and Bannerman (1939). The decision to reduce *sharpei* to a subspecies of *ludwigii* was made by MacDonald (1946), on the basis that they were ‘clearly very closely related’ and as they were ‘contiguous in distribution, [*sharpei*] should be regarded as a race’. The only comparative information given was that *sharpei* was ‘generally duller than the nominate race’ (MacDonald 1946). In his revision of the family Dicruridae, Vaurie (1949) endorsed this view and it is the one that has, until recently, prevailed.

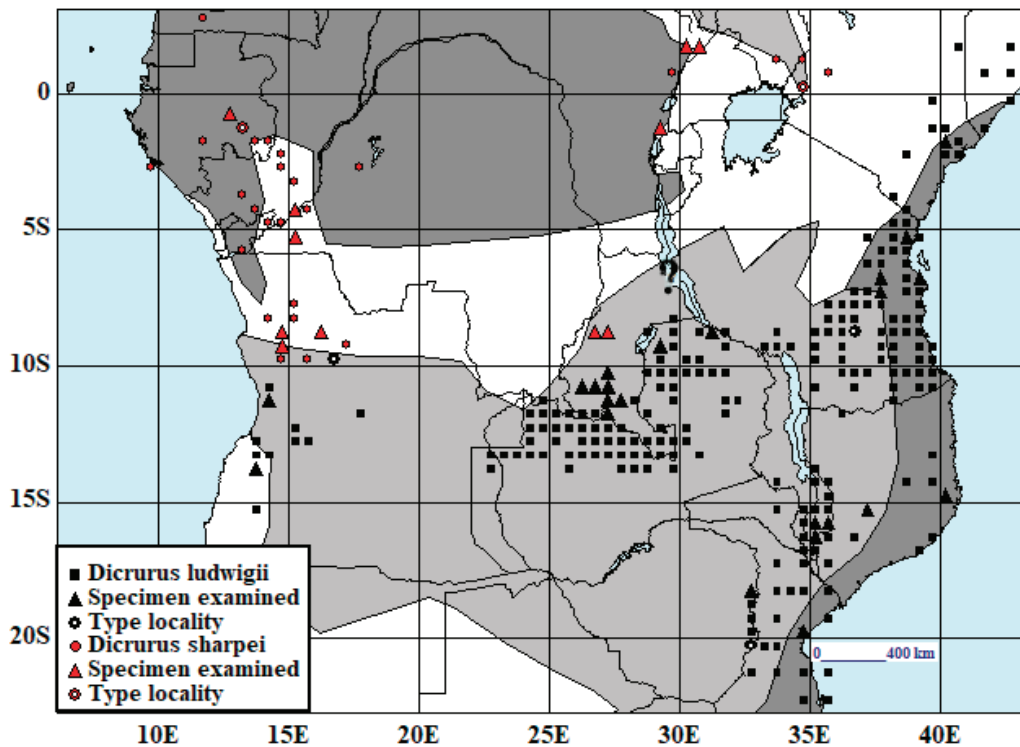


Figure 1. Map showing the distribution in south-central Africa of the Square-tailed Drongo taxa *Dicrurus ludwigii* and *D. sharpei*. For the area of contact in Angola, triangles represent both specimens checked by LDCF and sound-recordings (by M. S. L. Mills) whose identities have been confirmed by FD-L. Shading represents: the Guineo-Congolian and East Coast regions (dark grey), Zambezian region and tip of the Sudanian (medium grey) with transition zones and parts of other regions in white. See text for explanation of '?' on Lake Tanganyika.

The characters by which Clancey (1976) distinguished the two groups are listed in Table 1. While some had, as shown, previously been reported by Vaurie (1949), others Clancey (1976) recorded for the first time and were sufficient to prompt him to speculate that 'this form [i.e. *sharpei*] may in fact not be conspecific with the taxa of the *D. ludwigii* group'. This possibility has since been echoed by Pearson (2000), Rocamora & Yeatman-Berthelot (2009) and del Hoyo & Collar (2016).

As indicated in Table 1, Clancey (1976) reported sexual dimorphism in size in *ludwigii* and for the three characters measured—wing, culmen and tail lengths—he presented the supporting data separately for males and females; however, for *sharpei* they were combined, as he considered the sexes to be of similar size (Table 2). His measurements also suggested that, at least for wing length, *sharpei* averaged larger than *ludwigii* (Table 2). By contrast, with the exception of wing length in male *muenzneri* (on the basis of just four specimens), size differences between taxa in the *ludwigii* group were, at most, modest (Table 2).

The same adjective is applicable to the other differences described by Clancey (1976) between members of the *ludwigii* group, which consisted mainly of the degree of saturation and distribution of glossiness on the body plumage, with *tephrogaster* the palest overall and somewhat greener, less blue-black than the others, and in which the difference in male and female plumage was most obvious. This may explain why, in contrast to wide acceptance of Clancey (1976) by subsequent global and continental treatments, a number of contemporary, geographically more focused studies recognised only *ludwigii* and *sharpei*.

TABLE 1
Differences between *Dicrurus (ludwigii) sharpei* and other taxa included within *D. ludwigii*, as reported in previous studies and found in this study.

Character	Condition		Source			
	<i>D. ludwigii</i> group ¹	<i>D. (l.) sharpei</i>	Vaurie (1949)	Clancey (1976)	Fuchs <i>et al.</i> (2017, 2018)	This study
Intensity of colour of overall plumage	less saturated, paler	more saturated, darker	-	yes	-	yes
Metallic sheen of upper- and underparts	more intense and greenish or steely blue	less intense and purplish or violaceous	yes	yes	yes	yes
Colour of tips of axillaries and underwing-coverts	white in females and subadult males; black in adult males	black in all cases	yes	yes	yes	yes ³
Sexual dimorphism in plumage	belly black in males, sooty or lead grey in females	none	yes	yes	-	yes
Sexual dimorphism in size	males average larger than females	none	(yes) ²	yes	-	no ⁴
Shape of tail	more furcate or lyrate	more parallel-sided and square-ended	-	yes	-	yes
Shape of outer vane of outermost rectrix (r5)	narrows subterminally, broader at the tip	+/- uniform width throughout	-	-	-	yes
Shape of tip of r5	outer and inner vanes meet at an acute or subacute angle	outer and inner vanes meet at an obtuse angle	-	-	-	yes
Width of r5	averages larger	averages smaller	-	-	-	yes
Main song type	jumble of 'whipped' notes, with V-shaped structure	rolled <i>tchre</i> notes, often alternating with various sharp notes	-	-	-	yes

¹Includes the nominate subspecies, *muenzneri*, *tephrogaster* and *saturnus*—see text.

²Vaurie (1949) published measurements which indicated some sexual dimorphism in *ludwigii* but did not discuss this.

³One specimen of *sharpei* found for which this was not true—see text.

⁴Sexual dimorphism occurs in *sharpei* but only in wing length *cf. ludwigii*—see text and Tables 3–4.

These include Zimmerman *et al.* (2001), Stevenson & Fanshawe (2002), Dowsett-Lemaire & Dowsett (2006), Dowsett *et al.* (2008) and Chittenden *et al.* (2016).

Understanding of this complex has, with the publications of Fuchs *et al.* (2017, 2018), changed significantly. The principal taxonomic implications of their findings, which were based largely on molecular evidence, involved the reinstatement of species status to *sharpei* on the basis of substantial genetic divergence between it and the *ludwigii* lineage, a case reinforced by the finding that *sharpei* is in fact more closely related to Shining Drongo *D. atripennis* than to *ludwigii*. In corroboration, Fuchs *et al.* (2017, 2018) simply referred to, and confirmed, the morphological differences between *sharpei* and *ludwigii* reported by Vaurie (1949)—not those by Clancey (1976). In addition, their studies demonstrated an unexpected but marked genetic difference between samples of *sharpei* from either side of the Niger River in Nigeria. These results were supported by hitherto unrecognised differences in bill morphology, whereby culmen length and the width and depth of the bill of the western populations proved to be significantly larger than in those to the east (Table 2). Although based on small sample sizes, these differences were considered sufficient to merit splitting *sharpei* at species level. Thus, those populations west of the Niger River to Senegambia, and also including, tentatively, those north of the Benue River in Nigeria, were separated as a

TABLE 2
Selected mensural data for Square-tailed Drongo *Dicrurus ludwigii sensu lato* and Shining Drongo *D. atripennis* from previous studies. Measurements in mm.
Taxonomy follows named source.

Taxon	Clancey (1976)				Fuchs <i>et al.</i> (2018)							
	Sex	Statistic	Wing	Tail	Culmen	Taxon	Sex	Statistic	Wing	Culmen	Bill width	Bill depth
<i>D. l. sharpei</i>	M+F	Mean	108	88.8	21.6	<i>D. sharpei</i>	M+F	Mean	106.1	20.9	6.4	5.8
		Range	105.5–111.0	86–91	20.5–23.5			Range	103–108	20.0–21.8	5.8–7.1	5.3–6.6
		SD	2.24	1.6	0.9			SD	1.2	0.5	0.5	0.4
<i>D. l. ludwigii</i>	M	Mean	103.5	89.1	21.4	<i>D. occidentalis</i>	M+F	Mean	106.6	22	7.1	6.4
		Range	101.5–107.5	86.0–93.5	20–22			Range	104–110	21.8–23.9	6.5–7.4	6.2–6.7
		SD	2.02	2.54	0.63			SD	1.7	0.7	0.3	0.1
<i>D. l. tephrogaster</i>	F	Mean	99	85.7	20.7	<i>D. l. ludwigii</i>	M+F	Mean	100.6	22.3	6.5	6.5
		Range	96.0–101.5	82–90	20–22			Range	99–102	21.6–22.7	6.3–6.8	6.4–6.7
		SD	1.66	2.56	0.72			SD	1.1	0.4	0.2	0.1
<i>D. l. muenzneri</i>	M	Mean	103.2	89.9	22.2	<i>D. l. muenzneri</i>	M+F	Mean	103.9	21.8	6.5	6.3
		Range	100–107	87.5–93.0	20–24			Range	95–115	20.7–23.5	6.1–6.9	5.7–6.8
		SD	2.01	1.79	1.05			SD	5.3	0.6	0.2	0.2
		Mean	12	12	12			Mean	28	29	27	27



TABLE 2 CONTINUED
 Selected mensural data for Square-tailed Drongo *Dicrurus ludwigii sensu lato* and Shining Drongo *D. atripennis* from previous studies. Measurements in mm.
 Taxonomy follows named source.

		Clancey (1976)				Fuchs <i>et al.</i> (2018)			
F	Mean	98.7	85.8	21.1					
	Range	95.0–103.5	82.0–88.5	20–22					
	SD	3.16	2.11	0.62					
	<i>n</i>	12	12	12					
M	Mean	109	88.5	21.5		Mean	106.5	21	6.8
	Range	104–112	86–91	21–22		Range	106.5–118.5	22.2–24.8	6.3–7.4
	SD	3.46	2.38	0.58		SD	2.3	0.7	0.3
	<i>n</i>	4	4	4		<i>n</i>	22	22	18
F	Mean	99.8	83.5	20.5					
	Range	96–105	80.0–87.5	19.0–21.5					
	SD	3.02	2.62	0.87					
	<i>n</i>	7	7	7					
M	Mean	106.2	89.7	21.6					
	Range	103.5–110.0	85.5–93.0	20.5–23.0					
	SD	2.18	2.88	0.78					
	<i>n</i>	10	10	10					
F	Mean	99.9	85.9	21.1					
	Range	98.0–104.5	82.0–91.5	20–22					
	SD	2.14	2.36	0.78					
	<i>n</i>	10	10	10					

¹Data shown only for populations from Nigeria eastwards



new species, *D. occidentalis* (Fuchs *et al.* 2018: 115), with use of the name *sharpei* restricted to populations east and south of the Niger River (Fuchs *et al.* 2018). An additional conclusion, that *saturnus* (DR Congo to Angola and Zambia) should be considered a subspecies of *sharpei* rather than *ludwigii* (Fuchs *et al.* 2017), was subsequently reversed after more samples were analysed (Fuchs *et al.* 2018). Finally, with some minor qualification, Fuchs *et al.* (2018) advocated the recognition and retention of the four subspecies that comprise the *ludwigii* group *sensu* Clancey (1976). These findings have been adopted by Clements *et al.* (2019), Gill & Donsker (2019) and Winkler *et al.* (2020).

Prompted by the fact that justification for separating *sharpei* from *ludwigii* by Fuchs *et al.* (2017) relied almost exclusively on molecular data and because of the arresting assertion in Fuchs *et al.* (2018) that the new taxon *occidentalis* was the most distinct morphologically of any 'in the *D. ludwigii*-*D. atripennis* complex', we present a study of the morphological basis for these interpretations, based on examination and measurement of specimens of *ludwigii*, *sharpei* and *atripennis*. We also include an analysis of vocal data, a potential source of information not mentioned by Fuchs *et al.* (2017) and mentioned but not explored by Fuchs *et al.* (2018). We also note that Fuchs *et al.* (2018: 127) included mensural data for a specimen of *sharpei* from Ogooué, Gabon (MNHN ZO 1878-90), without recognising it to be the holotype—collected at Doumé on the Ogooué River in November 1876 by Alfred Marche (Oustalet 1879: 97; see also Marche 1882 for details of his travels).

We do not comment on the genetic results of Fuchs *et al.* (2017, 2018). Neither do we attempt a re-assessment of the validity of races of the *ludwigii* group; we accept the status quo but, given the small differences between these taxa, they are here treated collectively except where, because of their geographical proximity in parts of their ranges and the findings of Fuchs *et al.* (2017, 2018), it is necessary to consider the relationship between *saturnus* and *sharpei*.

In the following, unless indicated otherwise, '*ludwigii*' refers to the *ludwigii* group *sensu* Clancey (1976), i.e. comprising *muenzneri*, *tephrogaster*, *saturnus* and the nominate subspecies. We use *sharpei sensu stricto* for those populations of *sharpei* east of the Niger River, and *occidentalis* for those west and north of it; when meaning the form as a whole, i.e. prior to the work of Fuchs *et al.* (2018), *sharpei* is used unqualified. Use of *ludwigii sensu lato* indicates *ludwigii* plus *sharpei*.

Methods

In all, 197 specimens were assessed and measured: 86 *sharpei*, 66 *ludwigii* and 45 *atripennis* held in NHMUK, Tring, and RMCA and RBINS, Brussels (acronyms explained in Acknowledgements). The *sharpei* material comprised 60 specimens of *sharpei sensu stricto* from east of the Niger (11 from Nigeria, 14 Cameroon, one Republic of Congo, 29 DR Congo, three Sudan, two Angola) and 26 *occidentalis* (nine Nigeria including one from north of the Benue River, three Ghana, two Liberia, eight Sierra Leone, one Guinea, two Guinea-Bissau, one The Gambia); the *ludwigii* skins included 14 identified as nominate (one Mozambique, 13 South Africa), 14 *tephrogaster* (five Malawi, five Mozambique, four Zimbabwe), 12 *muenzneri* (one Kenya, 11 Tanzania) and 26 *saturnus* (two Angola, 22 DR Congo, two Zambia). The *atripennis* material came from Liberia (18), Nigeria (15) and Cameroon (12).

Mensural data, all collected by LDCF, comprised length of folded wing (unflattened chord, using a metal wing rule with a perpendicular stop at zero), length of tail (from point of insertion to tip of r5, the outermost rectrix), culmen length (from point of insertion on the skull to tip), bill width and depth at the distal end of the nares (all measured using Vernier callipers accurate to 0.1 mm) and max. width of the outer rectrix, r5, which was measured,

with the specimen placed ventral side up, by reading from a piece of graph paper (1 mm scale) positioned beneath the distal portion of the feather.

Tarsus length was not measured as neither Vaurie (1949) nor Clancey (1976) assessed it and because Fuchs *et al.* (2018) did not find it informative. Depth of the tail fork (the distance between the tips of r1 and r5), which has sometimes been used to assess differences in tail shape and proportion, was also excluded. Although Vaurie (1949) measured it, he noted that ‘...there is no character that shows so much variation’; nor was it used by Clancey (1976) or Fuchs *et al.* (2018). Unsexed individuals were excluded from the analyses (see below), as were immatures with pointed tips to their rectrices, such that the structure of r5 was unmodified (see below), as both Vaurie (1949) and Clancey (1976) cautioned that this age group averaged smaller in wing and tail measurements than their respective adults. However, those with pale margins to the feathers of the breast, belly and / or undertail-coverts (other indicators of immaturity) were retained if tail shape was adult in form.

The data were analysed for statistically significant differences using Student’s *t* tests and, for those results which were significant, the effect size or magnitude of the differences were assessed using Cohen’s *d*.

The material used for the voice analysis came from published sources (Stjernstedt 1989, Gibbon 1991, Chappuis 2000), xeno-canto.org (XC) and unpubl. recordings by FD-L and M. S. L. Mills (deposited at the British Library). Sonograms were prepared by N. K. Krabbe using CoolEditPro. The distribution map was prepared using DMAP (<http://www.dmap.co.uk>).

Results

Morphology.—This study confirmed all of the plumage differences between *ludwigii* and *sharpei* (Table 1) reported by Clancey (1976), although one of the 86 specimens of *sharpei* (NHMUK 1911.5.31.455, a female from Bitye, Dja River, Cameroon) does possess white tips to the underwing-coverts. This individual is not in adult plumage as the undertail-coverts and some belly feathers are also white-tipped and it is greyish, not black, ventrally, although the tail is adult in structure.

In addition, the difference in tail shape proved to be attributable to a number of structural modifications not hitherto documented. These are that in *sharpei* the outer vane of r5 is mostly either of uniform width throughout its length or widens only slightly towards the tip, whilst the inner and outer vanes meet at the apex, allowing for the blunt or rounded tip, at an obtuse angle. In many (not all) specimens, the angle is sufficiently wide as to make it appear square-tipped. By contrast, in *ludwigii* the outer vane of r5 is, in most cases, perceptibly narrower over much of its length than it is distally, and the tip is more sharply angled, such that it is acute or almost so (Figs. 2a,b, 6a,b). These features, coupled with the fact that the rachis of r5 in *sharpei* is straight or curves outwards to only a limited degree—in *ludwigii* it is more conspicuously outcurved (Fig. 3)—explain the contrast in overall tail shape. Consequently, the tail of *ludwigii* has been variously described as being more forked, fishtail-shaped, furcate, lyrate or lyre-shaped than that of *sharpei* (Clancey 1976, Pearson 2000, Rocamora & Yeatman-Berthelot 2009), such that only the latter can really merit the vernacular epithet ‘Square-tailed’ (Fig. 3).

We also confirm the statement by Fuchs *et al.* (2018) that *sharpei sensu stricto* and *occidentalis* cannot be distinguished using plumage: we were unable to find any diagnostic characters.

Mensural data and the results of our statistical tests are summarised in Tables 3–5. These support Clancey’s (1976) finding that male *ludwigii* average larger than females: wing, tail and culmen lengths were all greater in males ($p < 0.01$) (Tables 3 and 5). By contrast, our data

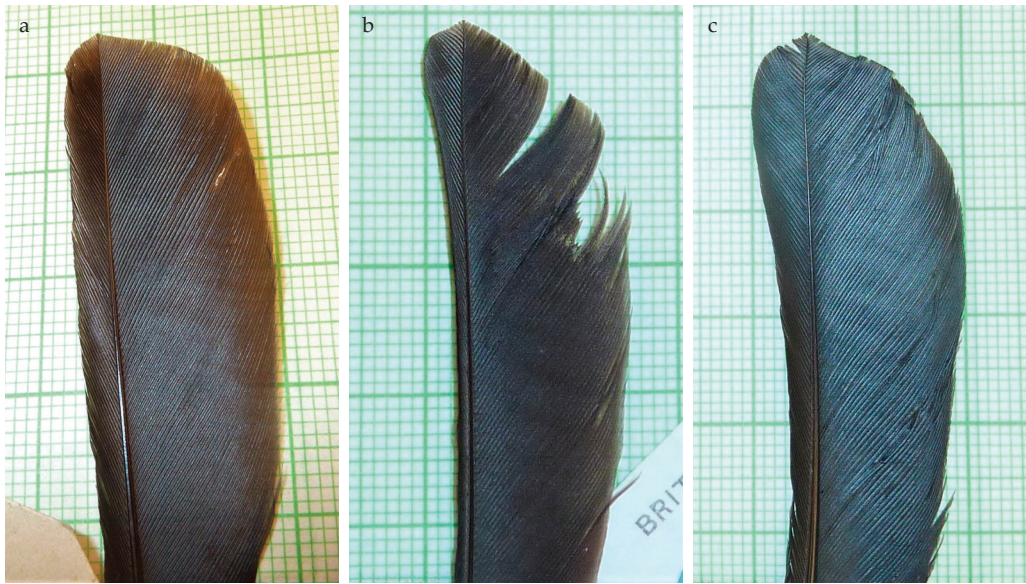


Figure 2. Ventral views of the distal portion of outermost rectrix (r5) of Square-tailed Drongo *Dicrurus ludwigii* taxa and Shining Drongo *D. atripennis*: (a) *sharpei* (NHMUK 1966.16.5812, Bamenda, Cameroon); (b) *ludwigii saturnus* (NHMUK 1957.37.453, Chingoroi, Angola); (c) *atripennis* (NHMUK 1977.20.3042, Mt Nimba, Liberia). See text for discussion of details of structure. Scale in mm (L. D. C. Fishpool, © Natural History Museum, London)

do not fully support his view that the sexes of *sharpei* are ‘virtually alike’ in size; we found male wing length to be greater ($p < 0.01$). No such differences were, however, recorded for the other parameters. Moreover, power tests indicated that for the differences in mean tail and culmen lengths (Table 3) to be assessed (80% chance) as statistically significant ($p < 0.05$), sample sizes of 2,536 and 547, respectively, would be required. This suggests that, unlike *ludwigii*, there is indeed no difference between the sexes in these parameters in *sharpei*. For *atripennis*, the only significant difference ($p < 0.05$) found was in the width of r5 (Table 5). Power analysis in this case found that sample sizes of 80, 14,819 and 131, respectively, would be needed for differences in mean wing, tail and culmen lengths (Table 3) to qualify (80% chance) as significant ($p < 0.05$), indicating that for wing length there is perhaps some uncertainty over this result.

Comparisons of male *sharpei* and *ludwigii* revealed highly significant differences ($p < 0.00001$) in wing length and width of r5, with *sharpei* having longer wings (mean 105.9 versus 101.2 mm) but narrower outer tail feathers (mean 14.86 vs. 16.06 mm). There was also a difference ($p < 0.05$) in culmen length (mean 20.86 [*sharpei*] vs. 21.27 mm) (Tables 3 and 5). Comparable differences in wing length and width of r5 were found for females, but not in culmen length; females, however, showed a difference ($p < 0.05$) in tail length (mean 91.57 [*sharpei*] vs. 89.71 mm). The effect sizes of the differences in wing length and width of r5 were broadly comparable between the sexes and mostly larger than those within the sexes of either taxon (Table 5); in all cases, however, Cohen’s d was < 2 (i.e. with a difference in mean of less than two standard deviations) and, on the basis of the scale used by Tobias *et al.* (2010), the magnitude of these differences therefore qualify as ‘minor’ (see Discussion).

The differences between both sexes of *atripennis* and *sharpei* in all parameters measured, except bill width, were both highly significant ($p < 0.00001$) and with effect sizes that mostly qualify under the Tobias *et al.* (2010) criteria as ‘medium’, whilst for width of r5 it is ‘major’ (Tables 3 and 5). Given how much larger *atripennis* was found to be than *sharpei*, it was not



Figure 3. Ventral views of tails of Square-tailed Drongo *Dicrurus ludwigii* taxa to show differences in structure. Left: *sharpei* (NHMUK 1954.59.179 [top] and 1966.16.5802, Okposi and Abeokuta, Nigeria). Right: nominate *ludwigii* (NHMUK 94.8.16.117 [top] and 94.8.16.114, both Durban, South Africa) (L. D. C. Fishpool, © Natural History Museum, London)

considered necessary to test for differences between *atripennis* and *ludwigii* since the latter, as shown, averages smaller than *sharpei*.

Summary morphometric data for *sharpei sensu stricto* and *occidentalis* are shown in Table 4. Tests between the sexes demonstrated that in *sharpei sensu stricto* there were differences ($p < 0.05$) in wing length and width of r5, and although no corresponding differences were found for *occidentalis* (Table 5), this may be attributable to insufficient sample sizes, at least for wing length. Power tests indicated that sample sizes of 39 and 139, respectively, would be required for the differences in recorded mean wing length and width of r5 in *occidentalis* (Table 4) to be detected (80% chance) as statistically significant ($p < 0.05$). Because, however, no significant differences were found in bill dimensions, the sole reported morphological discriminant between the two, data for the sexes were pooled in subsequent analysis—Fuchs *et al.* (2018) did not separate the sexes. Tests between *occidentalis* and *sharpei sensu stricto* showed that, using the full dataset of the latter, *occidentalis* is larger in bill width and depth ($p < 0.01$) and in culmen length ($p < 0.05$) (Tables 4–5); for each, however, the effect size of these differences was < 2 or ‘minor’. Moreover, because the Niger River in Nigeria forms the boundary between the two taxa, it was considered more informative to restrict analysis of the *sharpei sensu stricto* dataset to those specimens from eastern Nigeria and Cameroon, and thus closest geographically to *occidentalis*. So constrained, the difference between the

TABLE 3
Summarised mensural data for *Dicrurus ludwigii*, *D. (l.) sharpei* and *D. atripennis* from this study.
Measurements in mm.

Taxon	Sex	Statistic	Wing	Tail	R5 width ³	Culmen	Bill width	Bill depth
<i>D. ludwigii</i> ¹	M	Mean	101.17	93.15	16.06	21.27	7.2	6.37
		SD	2.79	3.02	0.91	0.77	0.34	0.28
		Max.	107	100.9	18	22.8	7.9	7.0
		Min.	95	88.8	15	19.9	6.4	5.8
		<i>n</i>	36	31	35	36	35	32
	F	Mean	98.36	89.71	15.68	20.57	7.27	6.4
		SD	2.32	3.95	0.89	0.44	0.36	0.31
		Max.	102	100.2	18	21.5	7.9	7.3
		Min.	94	83.1	15	19.6	6.5	5.9
		<i>n</i>	22	22	22	22	22	22
<i>D. (l.) sharpei</i> ²	M	Mean	105.89	91.77	14.86	20.86	7.22	6.29
		SD	2.92	2.87	0.80	0.78	0.46	0.36
		Max.	112	98.3	17	22.0	8.2	7.1
		Min.	100	86.5	14	18.4	6.2	5.5
		<i>n</i>	44	41	43	43	43	41
	F	Mean	103.87	91.57	14.62	20.73	7.33	6.34
		SD	3.24	2.05	1.05	0.76	0.41	0.27
		Max.	109	95.8	17	22.4	8.1	7.0
		Min.	97	86.7	13	19.4	6.6	5.8
		<i>n</i>	31	30	29	27	29	28
<i>D. atripennis</i>	M	Mean	111.36	101.3	20.82	23.3	7.28	7.24
		SD	3.86	3.69	1.4	0.79	0.38	0.29
		Max.	121	109.8	23	25.3	7.9	7.7
		Min.	105	94.5	19	21.9	6.5	6.6
		<i>n</i>	22	22	22	22	22	22
	F	Mean	109.64	101.19	19.5	22.97	7.45	7.34
		SD	3.23	3.08	1.76	1.09	0.35	0.32
		Max.	116	106	22	24.6	8.2	8.0
		Min.	104	95.3	16	21.1	6.8	6.7
		<i>n</i>	22	20	20	22	22	21

¹Includes the nominate subspecies, *muenzneri*, *tephrogaster* and *saturnus*—see text

²Includes *D. occidentalis*

³Max. width of the outermost rectrix, r5

two populations is limited to bill depth ($p < 0.01$) (Tables 4–5), with *occidentalis* again larger. The effect size remains minor, whilst in all cases the extent of overlap in bill measurements in the two populations is considerable.

TABLE 4

Summarised mensural data for *Dicrurus sharpei* and *D. occidentalis* from this study. Taxonomic treatment follows Fuchs *et al.* (2018). Measurements in mm.

4a. Sexes separated								
Taxon	Sex	Statistic	Wing	Tail	R5 width ¹	Culmen	Bill width	Bill depth
<i>D. occidentalis</i>	M	Mean	106.09	90.76	14.64	21.24	7.51	6.55
		SD	3.01	2.45	0.92	0.50	0.27	0.39
		Max.	110	93.5	17	22	7.9	7.1
		Min.	101	86.6	14	20.5	7.0	5.7
		<i>n</i>	11	11	11	11	11	11
	F	Mean	104.00	91.06	15.00	20.90	7.40	6.37
		SD	3.50	2.57	1.25	0.86	0.33	0.18
		Max.	108	94	17	22.4	7.9	6.6
		Min.	99	86.7	13	19.4	7.0	6.0
		<i>n</i>	10	10	10	9	10	10
<i>D. sharpei</i>	M	Mean	105.82	92.14	14.94	20.73	7.12	6.19
		SD	2.93	2.96	0.76	0.82	0.47	0.31
		Max.	112.00	98.30	17.00	21.80	8.20	6.80
		Min.	100	86.5	14	18.4	6.2	5.5
		<i>n</i>	33	30	32	32	32	30
	F	Mean	104.05	91.96	14.39	20.55	7.27	6.31
		SD	3.09	1.69	0.92	0.59	0.45	0.33
		Max.	109	95.8	17	21.5	8.1	7.0
		Min.	97	89.6	13	19.7	6.6	5.8
		<i>n</i>	20	19	18	17	18	17
4b. Sexes combined								
<i>D. occidentalis</i>	M + F	Mean	105.09	90.86	14.77	21.07	7.47	6.47
		SD	3.26	2.39	1.07	0.67	0.3	0.31
		Max.	110	94	17	22.4	7.9	7.1
		Min.	99	86.6	13	19.4	7.0	5.7
		<i>n</i>	22	22	22	21	22	21
<i>D. sharpei</i>	M + F	Mean	105.04	91.96	14.72	20.64	7.18	6.24
		SD	3.17	2.62	0.85	0.76	0.46	0.31
		Max.	112	98.3	17	21.8	8.2	7.0
		Min.	97	86.5	13	18.4	6.2	5.5
		<i>n</i>	54	50	51	50	51	48
All material	M + F	Mean	104.91	91.34	14.52	20.93	7.41	6.19
		SD	3.33	1.66	0.84	0.6	0.44	0.31
		Max.	112	94.6	17	21.8	8.2	6.9
		Min.	97	89	13	19.8	6.6	5.7
		<i>n</i>	23	20	23	22	23	22

¹Max. width of the outermost rectrix, r5



TABLE 5

Results of Student's *t*-test comparisons and effect size statistics for mensural data between samples of *D. ludwigii*, *D. (l.) sharpei* and *D. atripennis*. **Emboldened, italicised *p*-values indicate the result is significant at *p*<0.01.** *Italicised *p*-values indicate the result is significant at *p*<0.05.* Remainder not significant. Effect size statistic (Cohen's *d*) given only for comparisons with a significant *p*-value.

Comparison	Statistic	Wing	Tail	R5 width ¹	Culmen	Bill width	Bill depth
<i>D. ludwigii</i> ²							
Males vs. females	<i>t</i> -value	3.945	3.596	1.531	3.838	-0.712	-0.385
	<i>p</i> -value	0.0002	0.0007	0.1315	0.0003	0.4793	0.7019
	Cohen's <i>d</i>	0.705	0.978		1.116		
<i>D. (l.) sharpei</i> ³							
Males vs. females	<i>t</i> -value	2.812	0.331	1.096	0.672	-1.02	-0.603
	<i>p</i> -value	0.0063	0.742	0.2767	0.5036	0.3113	0.5488
	Cohen's <i>d</i>	0.655					
<i>D. atripennis</i>							
Males vs. females	<i>t</i> -value	1.61	0.104	2.695	1.153	-1.614	-1.131
	<i>p</i> -value	0.115	0.9178	0.0102	0.2555	0.114	0.2643
	Cohen's <i>d</i>			0.83			
<i>D. (l.) sharpei</i> vs. <i>D. ludwigii</i>							
Males	<i>t</i> -value	7.335	-1.973	-6.176	-2.334	0.248	-1.005
	<i>p</i> -value	<0.00001	0.5247	<0.00001	0.0222	0.8048	0.3183
	Cohen's <i>d</i>	1.653		1.336	0.529		
Females	<i>t</i> -value	6.815	2.21	-3.808	0.875	0.57	-0.732
	<i>p</i> -value	<0.00001	0.0317	0.0004	0.386	0.5712	0.4676
	Cohen's <i>d</i>	1.955	0.591	1.089			
<i>D. atripennis</i> vs. <i>D. (l.) sharpei</i>							
Males	<i>t</i> -value	6.437	11.353	21.807	11.922	0.475	10.488
	<i>p</i> -value	<0.00001	<0.00001	<0.00001	<0.00001	0.6361	<0.00001
	Cohen's <i>d</i>	1.598	2.883	5.227	3.108		2.906
Females	<i>t</i> -value	6.388	13.297	10.038	8.445	1.134	11.857
	<i>p</i> -value	<0.00001	<0.00001	<0.00001	<0.00001	0.2625	<0.00001
	Cohen's <i>d</i>	1.784	3.677	3.367	2.384		3.378
<i>D. sharpei</i> ⁴							
Males vs. females	<i>t</i> -value	2.087	0.241	2.275	0.821	-1.076	-1.234
	<i>p</i> -value	0.0419	0.8107	0.0274	0.4155	0.2874	0.2235
	Cohen's <i>d</i>	0.588		0.652			
<i>D. occidentalis</i> ⁴							
Males vs. females	<i>t</i> -value	1.471	-0.271	-0.764	1.096	0.828	1.377
	<i>p</i> -value	0.1575	0.7894	0.4542	0.2873	0.4181	0.1846
<i>D. sharpei</i> vs. <i>D. occidentalis</i>							
Males and females	<i>t</i> -value	-0.0667	1.685	-0.201	-2.225	-2.712	-2.787
	<i>p</i> -value	0.947	0.9642	0.8409	0.0294	0.0084	0.0069
	Cohen's <i>d</i>				0.6	0.747	0.742
<i>D. sharpei</i> (Nigeria and Cameroon only) vs. <i>D. occidentalis</i>							
Males and females	<i>t</i> -value	-0.181	0.663	-0.99	-0.769	-0.4222	-2.907
	<i>p</i> -value	0.8573	0.5113	0.328	0.4462	0.675	0.0059
	Cohen's <i>d</i>						0.886

¹Max. width of the outermost rectrix, r5²Includes the nominate subspecies, *muenzneri*, *tephrogaster* and *saturnus*—see text.³Includes *D. occidentalis*⁴*Sensu* Fuchs *et al.* (2018)

Vocalisations.—Drongo vocalisations are rather varied and include some soft babbling whistles that can be produced by both sexes in all African species; these presumably have no territorial context. By contrast, the louder calls or songs used in territorial advertisement or defence are more species-specific.

The most frequent song types of *ludwigii* consist of a rapid jumble of ‘whipping’ notes, V-shaped in structure, throughout the distribution of the group (Fig. 4a, H, J and K). These songs can be preceded, or alternated, with typical hard downward *kjiup* notes (Fig. 4a, I) or double *kji-tup*, or other similar hard whistles, also given when leading a mixed-species flock. The sonogram of *ludwigii* in Maclean (1985: 476) illustrated a similar song type. Another, less frequent motif consists of a short, fast jumble of grating notes: a good example can be heard on XC 365934 from southern Malawi, or XC 516540 from Tanzania.

By contrast, in both *sharpei sensu stricto* and *occidentalis* the most frequent song motifs are noticeably different and consist of some hard, slightly rolled *tchre* notes repeated 2–3 times, either given without other notes or, very often, alternating with a sharp note of rather different structure (Fig. 4a, A–F), a loud *kiup* (Fig. 4a, A), or *ueerr* (B), *peek* (C–D), rolled *prurr* (E) or double *kjup*, *kjup* (F). It is striking how similar these songs are either side of the Niger River—they are common to both *sharpei sensu stricto* and *occidentalis* (Fig. 4a, C–D, from Benin and Cameroon, respectively). These sharp notes and also liquid trills *tu-lu-lu-lu-lu* (not illustrated but part of the same recording from Benin, and heard in a recording from northern Angola made by M. S. L. Mills) can also be given in isolation. One motif of both *sharpei* and *ludwigii* is shown in Fig. 4b at a slower timescale to illustrate more clearly the differences in structure.

Both *sharpei* and *ludwigii* can also produce a more complex motif of contrasting notes (that is, with different frequencies in alternation), an example of which is shown for the former in Fig. 4a, G (Togo, by the same bird that produced B), and for the latter in Fig. 4a, L, from South Africa. The latter includes a few *tchre* notes, of a structure slightly different from similar notes in *sharpei*, showing harmonic overtones. Another example of this type of motif in *ludwigii* can be heard on XC 280252, also from South Africa. We have yet to find a motif with *tchre* notes from further north in its range.

A further important difference between the two taxa is the occasional incorporation of imitations of other species in the vocal repertoire of *ludwigii*, whereas to our knowledge this does not occur in *sharpei* (pers. obs.; N. Borrow & R. Demeijer *in litt.* 2020). The most frequent extra-specific motif reproduced by *ludwigii* is the *kwip* call of African Goshawk *Accipiter tachiro*. Vernon (1973) also mentioned imitations of Common Bulbul *Pycnonotus barbatus*, but these must be infrequent and we have not identified any other extra-specific renditions in the songs of *ludwigii*. The goshawk calls have been heard or tape-recorded at least in Zambia, Malawi (pers. obs.; see also XC 365934, with one ‘goshawk’ note at the end), Tanzania (e.g. XC 26822, plus several recent recordings by L. A. Hansen, including XC 516540) and South Africa (XC 280256). S. Keith (*in Fry et al.* 2000) wrote of a recording from Tanzania that *ludwigii* produced a ‘brief ‘twit’ extremely like the ... ‘chit’ made by African Goshawk ... possibly an imitation’. A comparison of sonograms shows these, in fact, to be perfect imitations, with, as in the original motif, many harmonic overtones (FDL pers. obs.).

Commercially published recordings of *sharpei* are limited to those on Chappuis (2000). Unfortunately, most of the cuts therein were of misidentified *atripennis*: thus all five sequences from southern Ivory Coast are typical of the varied repertoire of *atripennis*, as also are two from north-east Gabon (from Makokou: C. Érad *in litt.* 2020). Aside from the soft babbling whistles (cut 9), which could be given by any of these drongo species, all these motifs are outside our experience of *sharpei*, especially the monotonous repetitions of *fu* or *fee* notes, reminiscent of a malaconotid bush-shrike. Cut 3, from south-west Senegal

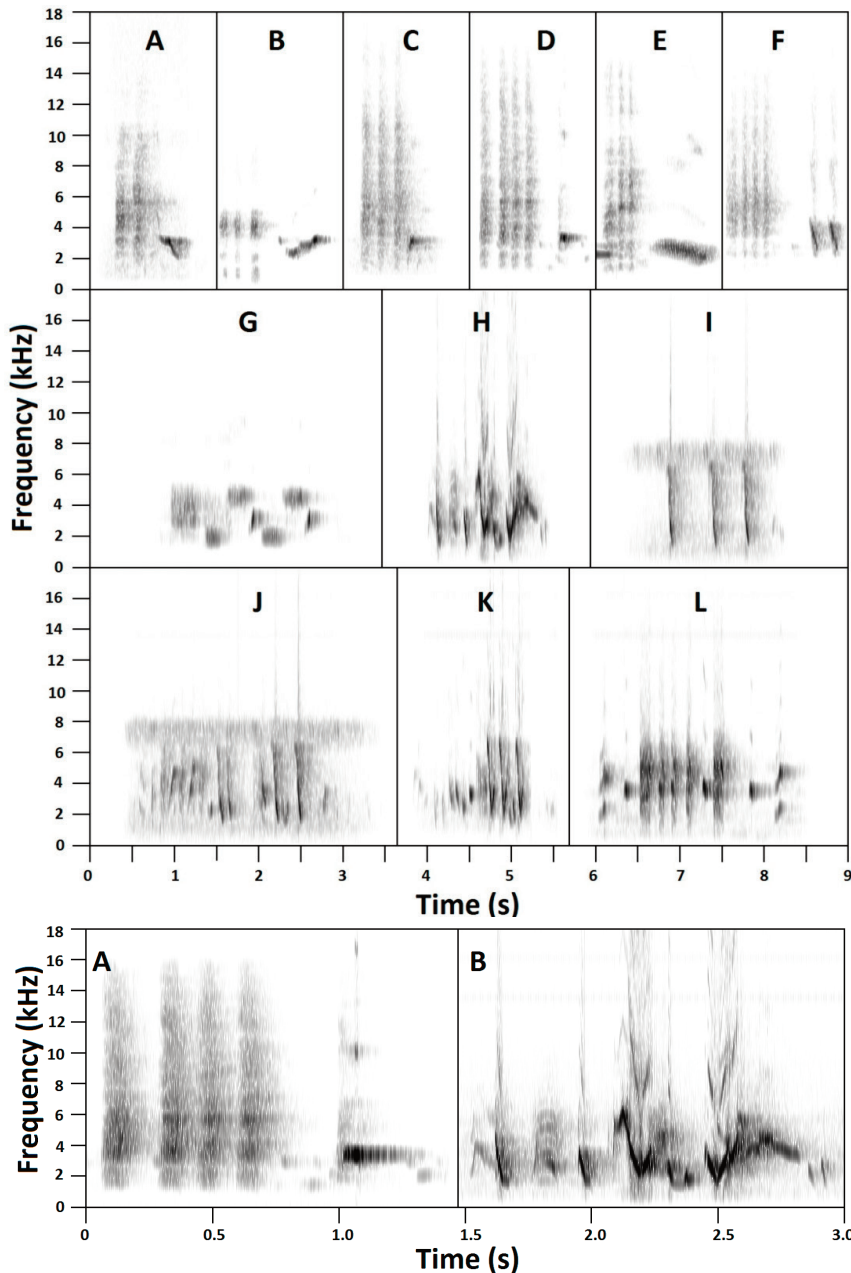


Figure 4a (upper three rows). Sonograms of characteristic vocalisations of Square-tailed Drongo *Dicrurus ludwigii* taxa. A–G: *sharpei* (A–C, G *occidentalis*, D–F *sharpei sensu stricto*—see text). A = Zinguichor, Casamance, Senegal (B. Piot, XC 453789, xeno-canto.org); B = Assoukoko, Togo (F. Dowsett-Lemaire, unpubl.); C = Gbèba, Benin (F. Dowsett-Lemaire, unpubl.); D = Mankon Forest near Bamenda, Cameroon (M. Nelson, XC 99707); E–F = Kakamega, Kenya (E by J. Bradley, XC 101207, F by M. S. L. Mills, 104-003, unpubl.). G = Assoukoko, Togo (F. Dowsett-Lemaire, unpubl.). H–L: *ludwigii*. H = *saturnus*, Ndola, Zambia (Stjernstedt 1989); I–J = *muenzneri*, Witu Forest, Kenya coast (F. Dowsett-Lemaire, unpubl.); K–L = nominate, Mapelane in KwaZulu-Natal and Dweza in Transkei, South Africa (Gibbon 1991).

Figure 4b (bottom row). Sonograms of vocalisations of Square-tailed Drongo *Dicrurus ludwigii* taxa at a slower timescale to illustrate structure more clearly. A (= D in Fig. 4a): *sharpei sensu stricto*—four hard *tchre* notes followed by a sharp *peek*; B (= H in Fig. 4a): *ludwigii saturnus*—jumbled V-shaped, 'whipping' notes (see text).



Figure 5. Ventral views of Square-tailed Drongo *Dicrurus ludwigii tephrogaster* to show sexual dimorphism in colour of the underparts. Male above, female below. (NHMUK 1911.5.30.500 [top] and 1911.5.30.499, both Chirinda Forest, Zimbabwe) (L. D. C. Fishpool, © Natural History Museum, London)

(Casamance)—i.e. *occidentalis*—is, on the other hand, typical of *sharpei*, with hard repeated *tchre* notes alternating with loud, rolled *ruee* notes. Cut 1 (unknown locality in Gabon, a recording by Chappuis) is also rather typical of *sharpei*.

Distribution.—The range of *ludwigii sensu lato* in south-central Africa is shown in Fig. 1 and includes all records traced by the authors that could confidently be attributed to either *sharpei* or *ludwigii*, with provenances of specimens examined by LDCF indicated. Records are mapped at the scale of half-degree (30 × 30 minute) squares (localities and supporting references available from the authors on request). The ‘?’ on Lake Tanganyika refers to the Mpala specimen discussed below.

It is apparent that in the area shown *ludwigii* is essentially confined to the Zambezan and East Coast regions, whilst *sharpei* is found on the margin of the Guineo-Congolian region and in its transition zones with the Sudanian and Zambezan regions. The two approach each other closely in south-east DR Congo and, especially, northern Angola.

Examination of material in RBINS revealed that the series of 20 specimens from Upemba National Park (c.08°45’S, 26°45’E), Katanga, DR Congo, collected by de Witte and attributed by Verheyen (1953) to nominate *ludwigii*, are in fact all *sharpei* (Fig. 6a); morphologically and mensurally they are entirely consistent with other *sharpei* specimens examined. This discovery considerably extends the known range of *sharpei* in DR Congo to the south-east of the country (Fig. 1) and, as discussed below, explains some results of the molecular study of Fuchs *et al.* (2017, 2018). In the same collection there is, moreover, a female specimen (RBINS 51078) of *sharpei*, correctly labelled by Verheyen, collected, also by de Witte, on 26 July 1954 in Virunga (=Albert) National Park, DR Congo, which appears hitherto not to have been reported. The precise locality is given as ‘Ababiba, riv. Affl. Malibonge s/af Lue, altitude 1,420 m’. Ababiba is near Buhima, itself close to Rumangabo at 01°20’S, 29°22’E (Fig. 1).

A specimen, attributed to nominate *ludwigii*, reputedly from Mpala (06°45’S, 29°31’E) (Schouteden 1971: 186), shown by a ‘?’ on Fig. 1, was collected by Emile Storms, but its provenance may be doubted. Dubois (1886: 148) listed two *Dicrurus* in the Storms collection,

'*atripennis*' and '*divaricatus*' (i.e. a form of *adsimilis*). Schouteden indicated that he had not seen the specimen, although Hartlaub (1886: 146) had stated that Storms' specimens were deposited at RMCA. No such specimen that might be *ludwigii sensu lato* has been traced in either of the Belgian collections (RMCA, RBINS). Chapin (1954: 4) wrote that *ludwigii* was reported as far north as north-east Marungu, but Dowsett & Prigogine (1974: 30) were unable to find details. It is possible this was in reference to the Storms specimen. It is known that Storms met Richard Böhm and Paul Reichard at Mpala (Schouteden 1971: 3), but there is no reason to suppose there was confusion over who collected this specimen, and it is not mentioned in the Böhm collection detailed by Matschie (1887). It is apparent from Fig. 1 that *ludwigii sensu lato* is not known in this region of south-east DR Congo, although it does occur in northern Zambia as close as the Lofu River, Lake Tanganyika (NHMUK; Neave 1910: 260).

That Fuchs *et al.* (2018) reported haplotypes of both *sharpei* and *saturnus* from north-west Angola is, however, not surprising since, as they said, Clancey's type of *saturnus* came from Cangandala, Malanje Province, and 'Clancey (1976) considered *sharpei* to occur' in N'Dalatando, Cuanza Norte. We confirm that there are two *bona fide* specimens of *sharpei* (NHMUK 1910.5.6.1546–1547) from N'Dalatando (09°18'S, 14°54'E), collected by William Ansoorge, which form part of this study. The holotype of *saturnus* (type locality: Maubi River, Cangandala, Malanje: 09°47'S, 16°41'E, Clancey 1976) remains in Durban Natural Science Museum (D. Allan *in litt.* 2021) together with a second specimen, clearly *saturnus*, which Clancey would have also examined. This originates from the rio Cacongo (= Cacungun), Cangandala, Malanje (09°25'S, 16°21'E). The latter is little more than 60 km south of the nearest *sharpei*, from 40 km north of Calandula (08°54'S, 16°05'E)—a confirmed sound recording by M. S. L. Mills—and a series of specimens labelled Calandula (09°06'S, 15°53'E) in the Field Museum of Natural History (FMNH), Chicago. Additional nearby *sharpei* are from Luhanda, 5 km north of Quela (09°16'S, 17°02'E; FMNH 220969, a G. Heinrich specimen), the rio Lutete (09°31'S, 15°45'E)—named Pungo Andongo in Dean (2000)—whence a specimen identified by Stresemann (1937: 53) was collected by Rudolf Braun (Fig. 1) and 10 km south of Quibaxe (08°34'S, 14°35'E). The last, together with a record of *saturnus* from Kumbira forest (11°08'S, 14°17'E), derives from acoustic evidence provided by M. S. L. Mills.

Thus, in both south-east DR Congo and north-west Angola, the ranges of *sharpei* and *saturnus* approach each other closely (Fig. 1). This is consistent with the statement by Fuchs *et al.* (2018) that the two 'appear to be parapatrically distributed' in Angola and south-east DR Congo, although we have no evidence that this is also the case in Zambia, as they suggested.

Discussion

Our study confirms all of the differences between *ludwigii* and *sharpei* documented by Clancey (1976), with the partial exception of the lack of sexual dimorphism in size within *sharpei*, a discrepancy which may be attributable to the larger sample size here (86) vs. his 11 (Tables 2–3). Although this dimorphism in *sharpei* is restricted to wing length, the scale of the difference, as measured by Cohen's *d*, was comparable to that of *ludwigii* (Table 5). That *sharpei* does show such dimorphism brings it into line with almost all other members of the Dicruridae, wherein males average larger than females (Vaurie 1949, Rocamora & Yeatman-Berthelot 2009); our finding that there was little mensural difference between the sexes in *atripennis*, including wing length, is therefore notable (Table 5) although, as indicated above, larger sample sizes are desirable to confirm this. However, the occurrence of sexual dimorphism in plumage colour in *ludwigii* (Fig. 5) appears exceptional, if not



Figure 6. Ventral views of the distal portion of outermost rectrix (r_5) of specimens of Square-tailed Drongo *Dicrurus ludwigii* taxa from south-east DR Congo, showing similarities of structure to Fig. 2a and 2b, respectively: (a) *sharpei* (RBINS 26640, Mubale, 08°33'S, 27°21'E, Parc National de l'Upemba, DR Congo); (b) *ludwigii saturnus* (RBINS 68484, Kipopo, 10°40'S, 27°28'E, DR Congo). Scale in mm (L. D. C. Fishpool)

unique, in the family (Rocamora & Yeatman-Berthelot 2009), although female *atripennis* are less extensively glossed below than males (Pearson 2000, Rocamora & Yeatman-Berthelot 2009; pers. obs.).

The contrast in overall tail shape between *ludwigii* and *sharpei*—more or less parallel-sided and square-ended in *sharpei* vs. increasingly divergent distally and with a notch at the tip in *ludwigii* (Fig. 3)—is a consequence of a combination of characters. These include the fact that the outermost rectrix of *ludwigii* shows a greater degree of outward curvature, a wider tip, a sharper angle where the inner and outer vanes meet, and by the subterminal reduction in the width of the outer vane. Each character is inconspicuous and/or subtle but, in sum, they amount to a significant divergence in tail structure. Indeed, in structure—if not dimensions (Tables 3, 5)—the tail feathers of *sharpei* are closer to those of *atripennis* than they are to *ludwigii* (Fig. 2a–c), which is consistent with the finding of Fuchs *et al.* (2017, 2018) that *sharpei* and *atripennis* are sister taxa.

Analysis of vocal repertoires of the various taxa shows that *ludwigii* is clearly distinct from *sharpei*—not only in the structure of motifs and notes, but also in the occasional presence of imitations of calls of African Goshawk, whereas *sharpei* never imitates. In contrast, *sharpei sensu stricto* and *occidentalis* have very similar, even identical, motifs either side of the Niger River.

As mentioned above, Fuchs *et al.* (2017), in making their case to re-elevate *sharpei* to species level, used Vaurie (1949) as authority for the characters which distinguish it morphologically from *ludwigii*; it is unclear why the additional points (Table 1) noted by Clancey (1976), and repeated in the subsequent literature, were ignored. Moreover, Fuchs *et al.* (2017) misquoted Vaurie (1949) by saying ‘...individuals of the subspecies *saturnus* and *sharpei* have white tips (or at least some traces) on the axillaries and on the small feathers along the ventral edge of the metacarpus, whereas they are generally absent in the subspecies *ludwigii*, *muenznerii* [*sic*] and *tephrogaster* (Vaurie 1949)’. In fact, Vaurie (1949) said the converse: ‘In *sharpei*, according to my specimens, the white is completely absent in both immature and adult plumage.’ Our results support Vaurie’s interpretation, while the presence (confirmed here) of white tips to the axillaries in specimens of *saturnus*—undescribed at the time of Vaurie’s study—is indicative of its affinities with the *ludwigii* group, rather than *sharpei*.

As also previously noted, placement of *saturnus* was revised between the two studies by Fuchs *et al.* (2017, 2018). In the former, analysis of a single sample of the taxon, from south-east DR Congo, placed it in a clade with *sharpei*, whereas the later study included samples from seven *saturnus* specimens, two from DR Congo, two from Zambia and three (including the type) from Angola. Whilst genetic analysis recovered the Zambian and Angolan material in the *ludwigii* clade, the two DR Congo samples again aligned with *sharpei*. Their decision to revert to treating *saturnus* as a subspecies of *ludwigii* was influenced by placement of the sample from the type specimen.

The novel implication remained meanwhile that *sharpei* was, on molecular evidence, present in south-east DR Congo. Fuchs *et al.* (2017, 2018) did not, however, draw any explicit inferences from the plumages of specimens concerned. The finding here that the population in Upemba, south-east DR Congo is, on morphological grounds, indeed *sharpei*, *contra* Verheyen (1953), confirms their suspicion (Fig. 1, 6a). The two specimens sampled by Fuchs *et al.* (2018) in fact form part of the de Witte series documented by Verheyen (1953), one of which appears as Fig. 6a (Mubale, 08°33’S, 27°21’E). However, Clancey (1976) was also correct in stating that the range of *saturnus* included DR Congo. He examined material from Kambove (10°52’S, 26°37’E), which is in far south-east Katanga, near Lubumbashi, but it is unclear how many specimens were involved, possibly only one, as there is just one from DR Congo in NHMUK, and that is from Kambove. We confirm that this specimen is indeed *saturnus*, not *sharpei*, as is a series of some 20 specimens in RMCA and RBINS from the general area of Lubumbashi (Fig. 1, 6b). Other localities in Schouteden (1971: 186–187), away from the Upemba area (*sharpei*), and considered to represent *saturnus*, range from Tenke (10°36’S, 26°07’E) east to St Hubert (11°29’S, 27°36’E). The nearest known locality of *saturnus* to Upemba seems to be Lukonzolwa (08°47’S, 28°38’E), on Lake Mweru, to the east of the easternmost *sharpei* specimens at Mubale. Although mentioned by Schouteden (1971), this specimen is not housed in Belgium. It was collected by Michele Ascenso (Salvadori 1907) and it is implied that his specimens were identified by Ogilvie-Grant & Reichenow. Elter (1986: 183) showed it to be in the Museo Regionale di Scienze Naturale, Turin, under the name *luwigi* (*sic*), with coding that indicates it is indeed the Ascenso specimen. The distance between the two localities is 140 km.

The putative difference in iris colour between *sharpei* and *ludwigii* reported by Stevenson & Fanshawe (2002)—orange-red in *sharpei*, scarlet-red in nominate—is not supported by specimen label data. These describe the irides of both variously to be red, orange-red, blood-red, crimson, ruby, orange-vermilion etc. although only for *ludwigii*, in some specimens, are they said to be orange, without a modifier.

Notably, we did not find the major differences in bill measurements reported by Fuchs *et al.* (2018) between *sharpei sensu stricto* and *occidentalis* (Tables 2, 4, 5). While we found the bill dimensions of *occidentalis* averaged larger than those of *sharpei* (Table 4)—the statistical significance of which (Table 5) is discussed above—in line with the trends reported by Fuchs *et al.* (2018), the scale of these differences was much more modest. Thus, the differences between the means of culmen, bill width and depth in *occidentalis* and *sharpei sensu stricto* given by Fuchs *et al.* (2018) were, respectively, 1.1, 0.7 and 0.8 mm: the equivalent figures here, for *sharpei sensu stricto* specimens from eastern Nigeria and Cameroon alone, are 0.14, 0.06 and 0.28 mm; and while (for the same populations) the overlap in the range in culmen lengths reported here is considerable, Fuchs *et al.* (2018) found there to be almost none (Tables 2 and 4). The reason for this may be attributable to disparity in sample sizes, smaller in Fuchs *et al.* (2018)—see Tables 2 and 4.

The accurate and consistent location of the point of measurement of bill width and depth—the distal end of the nostril—proved not to be straightforward, for the reasons given by Vaurie (1949): ‘The frontal feathers in all drongos are dense and extend to a greater or lesser degree over the upper mandible, the nostril being generally well concealed’. Apart from in specimens lacking some feathering in this region, as a consequence of collection, skin preparation and subsequent handling etc., locating the leading edge of the nostril took some practice and persistence: the data used here came from re-measurement of all specimens after several ‘rehearsals’.

In seeking to explain their novel discovery of putative differences in bill size, Fuchs *et al.* (2018) wrote ‘Clancey (1976)...had access to several specimens from within the range of *D. occidentalis*, but he did not measure bill length, but instead examined variation in plumage and tail length’. This is, however, partly incorrect: Clancey (1976: 99) gave measurements of 11 specimens of *sharpei*, including bill length, and while it is not clear exactly how many of these were *occidentalis* (he reported examining 15 skins in all), the list of localities he provided made it apparent that several specimens from either side of the Niger River must have been involved. Both Clancey (1976) and Fuchs *et al.* (2018) refer to a specimen from Anara Forest, Kaduna, Nigeria (10°42′N, 07°38′E) and as this skin, in NHMUK—whose material Clancey (1976) used—was confirmed as a ‘verified specimen’ of *occidentalis* by Fuchs *et al.* (2018), it seems clear that the same specimen was involved. No differences in bill size were reported by Clancey (1976).

Fuchs *et al.* (2018) noted that Clancey (1976) examined variation in tail length—and indeed shape—which they did not, nor did they state why they did not (Fuchs *et al.* 2017, 2018). As mentioned above, Fuchs *et al.* (2018) claimed their ‘...new species of drongo was overlooked by taxonomists despite *D. occidentalis* being the morphologically most differentiated species in the *D. ludwigii*-*D. atripennis* complex’. Even if our study had confirmed the reported differences in bill morphology shown by *occidentalis*, it would be hard to sustain such an assertion, given the differences in tail structure and dimensions between *sharpei* and *ludwigii* described and illustrated here.

The assertion becomes even more untenable when *sharpei* and *atripennis* are compared. Apart from the fact that the plumage of *atripennis* is much more highly glossed than it is in *sharpei* and *ludwigii* (Pearson 2000, Rocamora & Yeatman-Berthelot 2009; pers. obs.), it is clear from Tables 3 and 5 that for all parameters measured, except bill width, the magnitude

of the differences between *atripennis* and *sharpei* dwarfs those between *occidentalis* and *sharpei sensu stricto*. The statement that ‘the most reliable biometric measurements to discriminate *D. atripennis* from any *D. ludwigii* population are bill depth and wing length’ (Fuchs *et al.* 2018) also demands reconsideration in light of the differences in tail dimensions reported here (Tables 3 and 5).

Nor can we agree with the claim that their ‘... data ... clearly enable diagnosis of a discreet (*sic*) set of characters that render *D. occidentalis* distinct from other drongo specimens collected throughout the geographical range of each of the other taxa’ (Fuchs *et al.* 2018). The only ‘character’ by which *occidentalis* can safely be distinguished from *sharpei sensu stricto* in the field, or indeed in the hand, is geographical location.

Del Hoyo & Collar (2016) assessed the case for species status of *sharpei* using the system of scoring proposed by Tobias *et al.* (2010). They gave it—together with *saturnus*, on the basis of the results published by Fuchs *et al.* (2017), subsequently reversed in Fuchs *et al.* (2018)—a total of five points. They also noted that ‘vocal differences not apparent in limited samples available’, an observation which the larger number of samples available to our study has contradicted.

To achieve species status using the system of Tobias *et al.* (2010) a threshold of seven is required. Scores are awarded for differences in plumage, size and voice (but not genetic composition), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in 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. Species status cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two biometric characters (assessed for effect size using Cohen’s *d* where 0.2–2.0 is minor, 2–5 medium, 5–10 major and >10 exceptional) and one behavioural or ecological character (allowed 1) may be counted (hence ‘ns’ with a number in square brackets is used where a difference is identified and judged for its strength, but ‘no score’ is allowed).

On the basis of the revised morphological differences reported here (Table 1), we score *sharpei* as differing from *ludwigii* as follows. Rachis of r5 only weakly outcurved, its outer vane of +/- uniform width throughout or only slightly widened distally, the tip with an obtuse angle vs. rachis more strongly outcurved, outer vane conspicuously narrower subterminally than distally, tip sharply angled (+/- acute) (3); breast and belly black in both sexes vs. breast and belly black in males, sooty or lead grey in females (1); violet-purplish vs. bluish-green gloss (1); all dark (both sexes and immatures) vs. white-tipped underwing-coverts and axillaries in females and subadult males (1) [ns]; longer vs. shorter winged in both sexes (effect size males 1.65, females 1.95) (1); narrower vs. wider tip to outermost tail feather (effect size males 1.34, females 1.09) (1). Total eight.

On plumage and mensural characters alone therefore, the score passes the threshold for species status. If acoustic differences are included (not scored formally but at least 2), together with the possibility that the two forms approach parapatry (a max. separation of 60 km in north-west Angola), which would attract a further score of 3, then the threshold is far exceeded. On the other hand, using the same system the differences between *occidentalis* and *sharpei sensu stricto* (Nigeria and Cameroon only) score no more than 1 for a deeper vs. shallower bill (effect size 0.89) (Table 5), with a possible further 3 for claimed parapatric separation at the Niger River: sample sizes in Fuchs *et al.* (2018) are, however, too small to confirm or refute the existence of such a divide.

Thus, the range and extent of the plumage, morphometric and vocal differences between *sharpei* and *ludwigii* described here, combined with the molecular evidence

provided by Fuchs *et al.* (2017), are, we consider, easily sufficient to justify species status for *sharpei*. On the other hand, judged solely on the phenetic evidence, which boils down to differences in bill size from *sharpei sensu stricto*—there being none in plumage or voice—*occidentalis* should be considered no more than a weakly defined subspecies of *sharpei*.

Fuchs *et al.* (2018) used the phrase ‘... areas where the Western Square-tailed Drongo and Shining Drongo co-occur ...’ In our experience however, *atripennis* is never found syntopically with *occidentalis* or indeed *sharpei sensu stricto*, since they have different habitat requirements, a point made briefly in Fishpool *et al.* (2010) and one which we hope to explore more fully in a forthcoming publication, taking the opportunity to rectify a number of misidentifications in the literature revealed as a result of mapping their respective distributions, part of which appears as Fig. 1.

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- Addresses:* Lincoln Fishpool, 12 Mountain Street, Chilham, Canterbury, Kent CT4 8DQ, UK, e-mail ldcfishpool@gmail.com. Françoise Dowsett-Lemaire and Robert Dowsett, Le Pouget, Sumène 30440, France.

Molecular divergence among Yellow-spotted Barbet *Buccanodon duchaillui* populations suggests unrecognised diversity

by Brooks C. Hall, Lucas H. DeCicco, Isaac N. Rush,
Emily N. Ostrow & Robert G. Moyle

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SUMMARY.—Recently described vocal variation within the monotypic Yellow-spotted Barbet *Buccanodon duchaillui* has been used to suggest the presence of two allopatric species separated by the Dahomey Gap in western Africa. Using mitochondrial and nuclear DNA sequences from two genes, we investigated molecular patterns of divergence across the species' range, in light of the published vocal variation. We found support for a genetic break at the Dahomey Gap, but also identified much deeper divergence among other populations in the eastern part of the species' range. Deep genetic divergence, and geographic variation in the species' vocalisations, suggest a greater degree of diversity in this species than currently recognised.

Yellow-spotted Barbet *Buccanodon duchaillui* occurs in forested regions of tropical Africa, from Sierra Leone east across the Congo Basin to Kenya (Short *et al.* 2020). The western and eastern populations are separated by the Dahomey Gap, a dry forest-savanna break within otherwise contiguous lowland tropical rainforest (e.g., Salzmann & Hoelsmann 2005, Demenou *et al.* 2016, Dowsett-Lemaire & Dowsett 2019). The species was described by Cassin in 1855 based on specimens taken along the Mondah (Moonda) River in Gabon. Subsequently, subspecies *ugandae* was described from the western base of the Ruwenzori Mountains in Uganda based on its lack of yellow spotting on the back (*vide* Chapin 1939; Reichenow, 1911, *Wiss. Ergebn. Deutsche Zentral-Afr. Exped.* III: 278); subspecies *gabriellae* was described from specimens taken in Pangala, 'French Congo', c.80 miles north-west of Brazzaville, based on multiple plumage differences including 'the feathers of the forehead bright scarlet-vermilion instead of crimson' compared to the nominate (Bannerman 1924); and subspecies *bannermani* was described by Serle (1949: 52) from the 'Highlands of the Bamenda Division, British Cameroons' and differentiated by its 'larger size' vs. the nominate. See Fig. 1 for mapped type localities of these subspecies. Chapin (1939: 507) considered *ugandae* invalid 'as yellow spots are not always wanting on the upper back of Uganda birds', but affirmed that subspecies *gabriellae* was valid due to the light red coloration of the crown patch. White (1965) considered *bannermani* to be invalid and Short & Horne (1988, 2001) treated the species as monotypic for no given reason, thereby subsuming *gabriellae*, but noted that 'Birds at higher elevations are larger than lowland birds' (Short & Horne 1988: 442). The species is currently usually treated as monotypic (e.g., Dickinson & Remsen 2013, Gill *et al.* 2020, Short *et al.* 2020). Differences in the vocalisations of the western and eastern populations were first noted by Borrow & Demey (2001). Boesman & Collar (2019) investigated this variation using the number of notes, length of longest note, pace of notes, and acceleration. Following criteria published by Tobias *et al.* (2010), they concluded that western and eastern populations should be recognised as separate species: Western Yellow-spotted Barbet *B. dowsetti*, occurring west of the Dahomey Gap, and Eastern

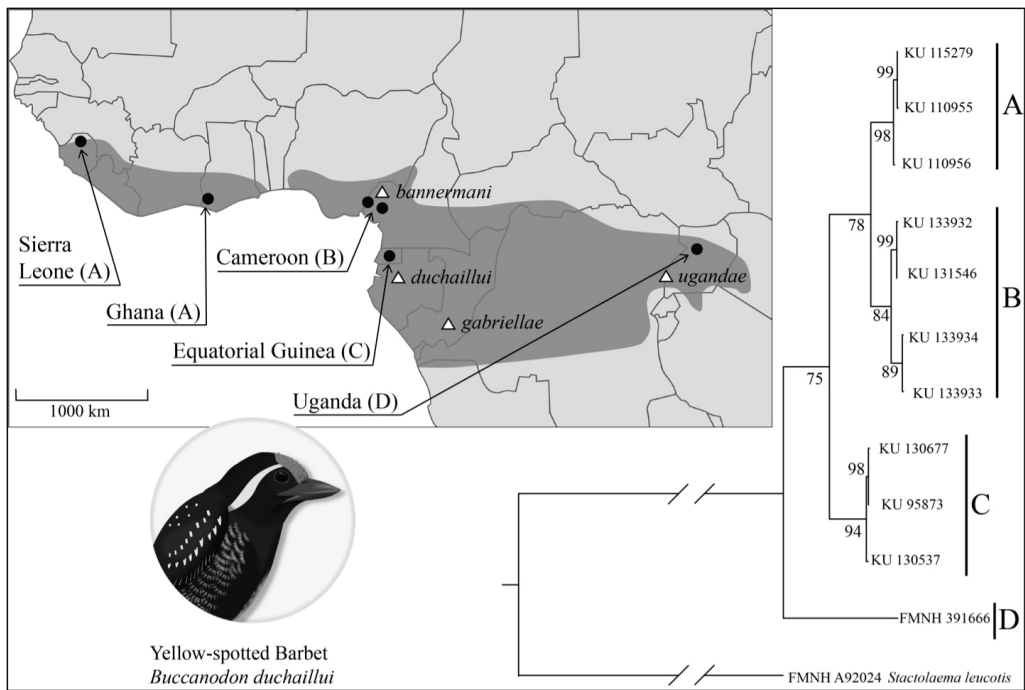


Figure 1. Upper left, distribution (in dark grey) of Yellow-spotted Barbet *Buccanodon duchaillui* including sampling locations (black circles), phylogenetic clade identity (A–D), and approximate type localities of the four described subspecies (white triangles) none of which is currently considered valid. Right, phylogenetic relationships estimated using maximum likelihood methods among the sampled populations, bootstrap support values less than 100 are presented at nodes, and clade labels correspond to sampling location labels on the map.

Yellow-spotted Barbet *B. duchaillui*, to the east of it. Gill *et al.* (2020) did not accept the newly proposed species *B. dowsetti*, citing the need for further work, including genetic analysis.

Using DNA sequence data, we investigated patterns of genetic divergence within the Yellow-spotted Barbet to determine if these patterns matched those in vocal variation outlined by Boesman & Collar (2019). Based on Boesman & Collar's (2019) conclusions and previously recognised biogeographic patterns across the Dahomey Gap, we hypothesised that molecular evidence would support differentiation between western and eastern populations.

Methods

We used 11 specimen-vouchered tissue samples of *B. duchaillui* housed at the Univ. of Kansas Natural History Museum, Lawrence, USA (KU) and the Field Museum of Natural History, Chicago, USA (FMNH) from across the species' distribution: one sample from Sierra Leone, two from Ghana, four from Cameroon, three from Equatorial Guinea, and one from Uganda (Table 1). Samples from Sierra Leone and Ghana came from the range of the proposed western species and the eight remaining samples from that of the proposed eastern species (following Boesman & Collar 2019; Table 1). We used a White-eared Barbet *Stactolaema leucotis* (blood sample, FMNH A92024, GenBank AY279277.1) from Kenya as an outgroup sample.

We extracted genomic DNA using a manual magnetic bead-based protocol (<https://github.com/phyletica/lab-protocols/blob/master/extraction-spri.md>) based on Rohland

TABLE 1

Samples of Yellow-spotted Barbet *Buccanodon duchaillui* used in this research. All specimens are from the Univ. of Kansas Natural History Museum, Lawrence, except for the specimen from Uganda which is housed at the Field Museum of Natural History, Chicago. GenBank numbers refer to archived sequence data for the mitochondrial gene cytochrome *b*.

Catalogue no.	Tissue no.	GenBank no.	Country	Locality
115279	19785	MZ396059	Sierra Leone	Outamba-Kilimi National Park (09°40'30"N, 12°10'37"W)
110955	15577	MZ396061	Ghana	Ankasa Wildlife Reserve (05°16'55"N, 02°38'24"W)
110956	15677	MZ396060	Ghana	Ankasa Wildlife Reserve (05°16'55"N, 02°38'24"W)
133932	34708	MZ396055	Cameroon	Nlonako (04°54'37"N, 09°58'48"E)
131546	32372	MZ396056	Cameroon	Korup National Park (05°04'16"N, 08°51'36"E)
133934	34710	MZ396057	Cameroon	Nlonako (04°54'40"N, 09°58'48"E)
133933	34709	MZ396058	Cameroon	Nlonako (04°54'40"N, 09°58'48"E)
130677	8663	MZ396053	Equatorial Guinea	Monte Alen National Park, Rio Lobo (01°34'16"N, 10°23'17"E)
95873	8695	MZ396054	Equatorial Guinea	Monte Alen National Park, Rio Lobo (01°34'16"N, 10°23'17"E)
130537	8497	MZ396052	Equatorial Guinea	Monte Alen National Park, Monte Alen (01°39'43"N, 10°17'24"E)
391666*		AJ279290.1	Uganda	Budongo Forest, Nyakafunjo Nature Reserve (01°42'32"N, 31°31'34"E)

*from Moyle (2004)

TABLE 2

Average pair-wise molecular distances among sampled populations of Yellow-spotted Barbet *Buccanodon duchaillui*.

	Sierra Leone	Ghana	Cameroon	Equatorial Guinea	Uganda
Sierra Leone	0.0%	0.3%	4.3%	6.5%	10.1%
Ghana	—	0.3%	4.2%	6.5%	10.3%
Cameroon	—	—	0.8%	6.7%	9.7%
Equatorial Guinea	—	—	—	0.2%	8.8%
Uganda	—	—	—	—	0.0%

& Reich (2012), and eluted DNA from beads using 1X TE buffer. We amplified the mitochondrial gene cytochrome *b* (*cytb*) using primers L14841 (Kocher *et al.* 1989), H4a (Harshman 1996), barbCBL (Moyle 2004) and barbCBH (Moyle 2004). We also amplified the nuclear region Beta Fibrinogen intron 7 (β -fibint7) using the primers FIB-B17L and FIB-B17U (Prychitko & Moore 1997). We amplified both genes using a touch-down type polymerase chain reaction protocol (DeCicco *et al.* 2020). Amplified DNA was sequenced by Genewiz. Consensus sequences have been uploaded to GenBank (Table 1).

We used Geneious (Kearse *et al.* 2012) to trim, align, and create consensus sequences. Multi-sequence alignments were made using MAFFT (Katoh *et al.* 2002) in Geneious. We identified codon partitions and models of evolution using Partition Finder 2 (Lanfear *et al.* 2016) based on AICc scores. We estimated phylogenetic relationships using maximum likelihood methods in RAxML (Stamatakis 2014) run for 1,000 bootstrap replicates with previously identified by-codon partitions and the General Time Reversible + Gamma model of sequence evolution. We also used MrBayes (Huelsenbeck & Ronquist 2001) running four chains for one million generations, sampling every 1,000 generations with a burn-in of 0.25 using previously identified optimal partitions and models of sequence evolution.

We calculated uncorrected pair-wise molecular distances among clades identified in our phylogenetic analysis in PAUP* (Swofford 2003).

Results

We obtained complete gene sequences for both *cytb* and β -fibint7 for all 12 samples used. Because the β -fibint7 DNA sequence data provided almost no informative signal for phylogenetic analysis or in a haplotype network, we present results only from our *cytb* data. Using *Stactolaema leucotis* as the root, phylogenetic analyses placed the Ugandan sample of *B. duchaillui* as sister to all other populations, and the Equatorial Guinea samples in a clade sister to the Cameroon, Ghana and Sierra Leone samples. The Cameroon samples were in turn sister to the Ghana and Sierra Leone birds (Fig. 1). Bootstrap support was moderate to high ($\geq 75\%$) for all nodes in the phylogeny. Genetic divergence in *cytb* was generally low within labelled clades ($< 1\%$) but substantial between clades. For example, the single sample from Uganda was 8–10% divergent from all other samples (Table 2). Divergence between clade C and clades A and B was *c.*6.5%. Divergence across the Dahomey Gap, the putative geographic division between *B. duchaillui* and *B. dowsetti*, was 4.2%.

Discussion

Our results, based on the mitochondrial *cytb* gene, highlight a genetic break congruent with the vocal differences noted by Boesman & Collar (2019), consistent with their taxonomic suggestion to treat these populations as two species. However, our results also suggest a more complex evolutionary history for the Yellow-spotted Barbet than simply a Dahomey Gap split and a more complex pattern of molecular divergence than indicated by vocal variation alone, despite largely congruent sampling of vocal and genetic data. Genetic and vocal divergence across the Dahomey Gap has been reported in other bird species, but this pattern is variable among species (e.g., Fuchs & Bowie 2015, Kirschel *et al.* 2020).

Given this complexity, it is difficult to align our results directly with the simple Dahomey Gap split in vocal variation. We find it noteworthy that Boesman & Collar (2019) found the same vocal dialect in all sampled populations east of the Dahomey Gap, populations among which we found up to 10% average pair-wise molecular divergence. This clearly suggests that vocal and genetic variation in this species are decoupled. Denser genetic sampling east of the Dahomey Gap would be valuable to determine more precisely where genetic breaks occur in an otherwise apparently continuous distribution. Such sampling would also provide the ability to assess if this system follows expectations under Pleistocene rainforest refugia hypotheses (see Diamond & Hamilton 1980, Mayr & O'Hara 1986); however, the sampling to date suggests that this system may align with patterns expected under isolation in the three proposed Pleistocene refugia.

Both the vocal analysis provided by Boesman & Collar (2019) and our results suggest greater diversity within this species than previously thought. Discordance between the geographic patterns presented by vocal variation and that of genetic variation are not unexpected (e.g., Nwankwo *et al.* 2018). The complexities of this system presented jointly by the vocal (Boesman & Collar 2019) and molecular variation suggest that this taxon merits further research. How the vocal and genetic variation in a broader sense fit with the described, but not recognised subspecies, is beyond the scope of this note. Additional, denser genetic sampling is required to fully address this question. Clearly, due to the described plumage variation, particularly in subspecies *gabriellae*, there is probably cause to recognise more geographic forms, especially if genetic variation supports some of the described patterns in plumage or vocal variation. We believe a more thorough analysis of taxonomic history,

plumage variation and genetic variation, the latter with denser geographic screening, is required to make adequate taxonomic suggestions. We hope that the information presented here, in conjunction with that in Boesman & Collar (2019), provides some insight into the previously unrecognised diversity within the Yellow-spotted Barbet.

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Addresses: Brooks C. Hall, Dept. of Ecology and Evolutionary Biology, Biodiversity Institute and Natural History Museum, Univ. of Kansas, Lawrence, KS 66045, USA, e-mail: brookshall312@outlook.com. Lucas H. DeCicco, Dept. of Ecology and Evolutionary Biology, Biodiversity Institute and Natural History Museum, Univ. of Kansas, Lawrence, KS 66045, USA, e-mail: lucas_decicco@ku.edu. Isaac N. Rush, Dept. of Ecology and Evolutionary Biology, Biodiversity Institute and Natural History Museum, Univ. of Kansas, Lawrence, KS 66045, USA, e-mail: Isaac.rush16@gmail.com. Emily N. Ostrow, Dept. of Ecology and Evolutionary Biology, Biodiversity Institute and Natural History Museum, Univ. of Kansas, Lawrence, KS 66045, USA, e-mail: emily.ostrow@ku.edu. Robert G. Moyle, Dept. of Ecology and Evolutionary Biology, Biodiversity Institute and Natural History Museum, Univ. of Kansas, Lawrence, KS 66045, USA, e-mail: moyle@ku.edu

The correct name of the antpitta clade

by Jimmy Gaudin, Laurent Raty & George Sangster

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Antbirds, which currently constitute three families, were formerly placed in the single family Formicariidae (Wetmore 1930, Peters 1951, Morony *et al.* 1975), until Sibley & Ahlquist (1990) showed that typical antbirds (Thamnophilidae) and ground antbirds and antpittas (Formicariidae) are not sister groups. More recent phylogenetic analyses have further clarified relationships among antbirds, and have shown that the ground antbirds (*Formicarius*, *Chamaeza*) and antpittas form distinct clades that are also not sister taxa (Irestedt *et al.* 2002, Chesser 2004, Rice 2005a,b, Moyle *et al.* 2009, Harvey *et al.* 2020). The antpitta clade is well supported and comprises the genera *Grallaria*, *Grallaricula*, *Myrmothera*, *Hylopezus* and *Cryptopezus* (Rice 2005a,b, Moyle *et al.* 2009, Carneiro *et al.* 2019, Harvey *et al.* 2020).

Several recent works have used the family-group name Grallariidae for the antpitta clade (Irestedt *et al.* 2002, Moyle *et al.* 2009, Ohlson *et al.* 2013, Dickinson & Christidis 2014, Fjeldså *et al.* 2020). This name was introduced at subfamily rank by Sclater (1890) (not Sclater & Salvin 1873, as listed by Bock 1994). Bock (1994) correctly pointed out that because the genus name *Hypsibemon* Cabanis, 1847, was synonymised with *Grallaria* Vieillot, 1816, prior to 1961, and Hypsibemoninae Sundevall, 1872, has been replaced by Grallariidae, the latter name takes precedence from 1872. Nevertheless, the family-group name Myrmotherinae MacGillivray, 1839, predates Grallariinae P. L. Sclater, 1890 [1872], by several decades. Myrmotherinae cannot be regarded as a 'nomen oblitum' (*sensu* ICZN 1999, Art 23.9.1) because it was used as a valid subfamily name in Cory & Hellmayr (1924), Zotta (1938) and Schwartz (1957). Thus, the correct name of the antpitta clade is Myrmotheridae. We have traced the erroneous use of Grallariidae for the antpitta clade to Lowery & O'Neill (1969), who appear to be the first to have re-used this name (as Grallariinae).

Phylogenomic analyses have shown that the antpitta clade (Myrmotheridae) is sister to a clade consisting of the tapaculos (Rhinocryptidae Wetmore, 1926; not Wetmore 1930, as listed by Bock 1994), the ground antbirds (Formicariidae G. R. Gray, 1840), and the ovenbirds and woodcreepers (Furnariidae G. R. Gray, 1840) (Oliveros *et al.* 2017, Feng *et al.* 2020, Harvey *et al.* 2020), although some previous studies (e.g., Rice 2005b, Moyle *et al.* 2009) had found the antpittas to be sister solely to the tapaculos. The latter two clades were combined by Moyle *et al.* (2009) in the superfamily Grallarioidea. The genus *Rhinomya* Geoffroy Saint-Hilaire, 1832, was synonymised with *Rhinocrypta* G. R. Gray, 1841, prior to 1961, and Rhinomyadae d'Orbigny & Lafresnaye, 1837, has been replaced by Rhinocryptidae. The latter thus takes precedence from 1837, and is senior to both Myrmotherinae and Grallariinae. The superfamily consisting of the tapaculos and the antpittas, if recognised, should therefore be called Rhinocryptoidea Wetmore, 1926 [1837].

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Addresses: Jimmy Gaudin, 34, avenue Antoine de Saint-Exupéry, 17 000 La Rochelle, France, e-mail: jimmy.gdn.lr.taxo@gmail.com. Laurent Raty, 38, avenue de la Chapelle, 1200 Brussels, Belgium, e-mail: l.raty@skynet.be. George Sangster, Naturalis Biodiversity Center, Darwinweg 2, PO Box 9517, 2300 RA Leiden, the Netherlands, e-mail: g.sangster@planet.nl



A family name for the Crested Shrikejay *Platylophus galericulatus*

by Jimmy Gaudin, George Sangster & Murray D. Bruce

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Platylophus galericulatus (Cuvier, 1816) is a lowland forest bird found in southern Thailand, Peninsular Malaysia, Borneo, Sumatra and Java. Its taxonomic placement has long puzzled systematists (e.g. Amadon 1944, Goodwin 1976). Comparisons of feather tracts and osteology led some to believe that it does not belong to the crows (Clench 1985, Hope 1989). Nevertheless, from the 1940s until recently *Platylophus galericulatus* was universally classified as a crow (Wolters 1977, Sibley & Monroe 1990, Clements 2007, Dickinson & Christidis 2014, Gill *et al.* 2021).

Recent molecular phylogenetic studies of Corvidae have shown that *Platylophus galericulatus* is neither a true shrike (Laniidae) nor a corvid (Corvidae), and placed the species as the sister of the true shrikes (Jønsson *et al.* 2008, Aggerbeck *et al.* 2014, Oliveros *et al.* 2019); in a polytomy with two major clades that include Corvidae, Laniidae and several other groups (Jønsson *et al.* 2011); sister to *Eurocephalus* outside Laniidae and Corvidae (Jønsson *et al.* 2016, Fuchs *et al.* 2019); or sister to the birds-of-paradise (Paradisaeidae; Stervander *et al.* 2020). In rank-based taxonomy, it seems best to place *Platylophus galericulatus* in its own family.

Winkler *et al.* (2015), Oliveros *et al.* (2019), Irham & Kurniawan (2020) and Stervander *et al.* (2020) used the name Platylophidae, but this is a *nomen nudum* because no such name has been validly introduced. The 'Platylophidae' account in Winkler *et al.* (2015) listed *P. galericulatus* as its sole species and provided a description that might be construed as a diagnosis. However, these authors did not explicitly indicate the name as intentionally new, and it does not meet ICZN (1999) Art. 16.1. Oliveros *et al.* (2019), Irham & Kurniawan (2020) and Stervander *et al.* (2020) merely used the name 'Platylophidae' and did not make the name available.

The name Lophocittidae was listed by Bock (1994) as a family-group name based on *Lophocitteae* Kaup, 1855. The latter name is derived from the genus *Lophocitta* G. R. Gray, 1841, which is a junior synonym of *Platylophus* Swainson, 1832. However, Kaup's *Lophocitteae* and four other new family-group names attributed to Kaup (1855) by Bock (1994) were proposed as 'Hauptgenera' (i.e. *Cisseae*, *Cyanocitteae*, *Cyanocoraceae*, *Keropieae*). Kaup used his 'Hauptgenera' as divisions of a subfamily¹. Consequently, Lophocitteae is a genus-group name rather than a family-group name.

Because no family-group name for *P. galericulatus* is available, we propose:

Platylophidae new family

Type genus: *Platylophus* Swainson, 1832

Diagnosis: Differs from Corvidae, Laniidae and *Eurocephalus* by a combination of (i) vestigial nasal bristles, (ii) long upstanding crest, (iii) white crescent on the sides of the neck,

¹ Kaup's philosophical approach to classification and the number five also supported the English Quinarian theory of classification, promoted by several ornithologists in the first half of the 19th century, but the methodology proved unpopular and Kaup was one of its last adherents (Bruce 2003: 24–25).

(iv) buff spots at the tips of the feathers of the underparts and wing-coverts in juveniles, and (v) only six feather tracts and 50 feathers on the back (vs. 8–13 feather tracts and 114–198 feathers in Corvidae, 8–10 feather tracts and 126–129 feathers in Laniidae; Clench 1985).

Remarks: *Platylophus galericulatus* has been called ‘Crested Jay’ (e.g. Sibley & Monroe 1990, Madge & Burn 1994, Clements 2007, Dickinson & Christidis 2014), ‘Crested Shrikejay’ (Winkler *et al.* 2015) and ‘Jay Shrike’ (Eaton *et al.* 2016). The evidence of its phylogenetic relationships argues against the names Crested Jay and Jay Shrike because it is neither a jay nor a shrike. We believe the English name Crested Shrikejay is appropriate because it captures both the most pronounced morphological feature of the species and the ambiguity of its phylogenetic position (compare ‘Cuckooshrike’ for some members of Campephagidae).

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Addresses: Jimmy Gaudin, 34, avenue Antoine de Saint-Exupéry, 17 000 La Rochelle, France, e-mail: jimmy.gdn.lr.taxo@gmail.com. George Sangster, Naturalis Biodiversity Center, Darwinweg 2, PO Box 9517, 2300 RA Leiden, the Netherlands, e-mail: g.sangster@planet.nl. Murray D. Bruce, P.O. Box 180, Turramurra, NSW 2074, Australia, e-mail: m.d.bruce@hotmail.com



