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Comments on the species limits of certain North American birds, part 1

by Oscar Johnson, Shawn M. Billerman, Blanca E. Hernández-Baños, Daniel F. Lane, Pamela C. Rasmussen, J. V. Remsen, Jr., Kevin Winker & R. Terry Chesser

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http://zoobank.org/urn:lsid:zoobank.org:pub:9FE9C2A8-6B09-42BC-92AD-C9C06276FA57

Summary.—Although species limits of North American birds are relatively well delineated, discrepancies among global lists identify species complexes that are subject to differences of opinion. As part of our work with the North American Classification Committee (NACC) of the American Ornithological Society, here we assess species limits in 11 such species complexes of North American birds: Spruce Grouse *Canachites canadensis*, Band-tailed Pigeon *Patagioenas fasciata*, Antillean Mango *Anthracothorax dominicus*, Greenish Puffleg *Haplophaedia aureliae*, Black Oystercatcher *Haematopus bachmani*, Hook-billed Kite *Chondrohierax uncinatus*, Sharp-shinned Hawk *Accipiter striatus*, Elegant Trogon *Trogon elegans*, American Three-toed Woodpecker *Picoides dorsalis*, Golden-olive Woodpecker *Colaptes rubiginosus* and Olive-throated Parakeet *Eupsittula nana*. We update information on the taxonomic history of these species, and recommend revised taxonomic treatments by using published works, analysis of museum specimens and citizen/community science databases. This work can provide a foundation for future taxonomic research in these species complexes.

Although species limits of North American birds are among the best delineated of any animal group, they are nevertheless subject to differences of opinion due to inadequate data and differing interpretations of the available information. Such borderline cases have resulted in numerous discrepancies in taxonomic treatment by different authorities. As part of our work with the North American Classification Committee (AOS-NACC, or NACC) of the American Ornithological Society, which maintains the Checklist of North American birds (https://checklist.americanornithology.org/), here we assess species limits in 11 species complexes that are treated differently by at least one of the major global avian checklists.

This effort was coordinated with the activities of the Working Group on Avian Checklists (WGAC) of the International Ornithologists' Union (https://www.internationalornithology.org/working-group-avian-checklists), who are reconciling incongruences among global avian checklists to produce a unified checklist. As part of this effort, NACC is addressing taxonomic discrepancies among global checklists pertaining to bird species occurring primarily in North America. These discrepancies, and the resulting proposals written for consideration by NACC, primarily concern taxonomic issues for which there is limited published information. The proposals, therefore, are in many cases the best available synthesis of taxonomic work on these species complexes at this time. For cases in which the complex is distributed in both North and South America, proposals were submitted also to the South American Classification Committee (SACC; Remsen *et al*. 2023; https://www.museum.lsu.edu/~Remsen/SACCBaseline.htm). All taxonomic treatments suggested here follow the Biological Species Concept (Mayr 1942). We intend these accounts to serve as a

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foundation for future research on these species complexes, and as such have included in each account a section outlining possible next steps.

This publication is based on NACC proposals that were based primarily on original research by the proposal authors (i.e., on data otherwise largely unpublished) and summaries of historical taxonomic treatments. The primary author of each taxonomic treatment is listed under that species account, but all authors of this manuscript contributed to all species accounts. As signalled by the ‘part 1’ designation, we plan to publish other compilations of proposals and synopses for additional taxonomic issues for which more work is needed, to inspire future research on these species.

Accounts are provided in taxonomic order according to the current AOS checklist (Chesser *et al*. 2024). The proposal number and voting results (passed/did not pass) of each taxonomic proposal are included, along with our views on potentially fruitful avenues of research for the group. These views are frequently informed by comments provided by members of NACC and SACC. Full results and committee member comments on each proposal can be found at the NACC and SACC websites. Future authors can peruse these committee member comments for additional insights into the relevant taxonomic issues.

We made frequent use of citizen science (also known as community science) databases for qualitative analysis of plumage and vocalisations. References to catalogue numbers for specific vocalisations or photographs from Xeno-canto (XC; https://xeno-canto.org/) and Macaulay Library (ML; https://macaulaylibrary.org/) are provided and can be accessed at those websites. We also examined specimens of taxa under consideration in the following collections: Florida Museum of Natural History (UF), Gainesville; Louisiana State University Museum of Natural Science (LSUMZ), Baton Rouge; Museo de Historia Natural “Javier Prado” Universidad Nacional Mayor de San Marcos (MUSM), Lima; and National Museum of Natural History (USNM), Washington, DC.

SPRUCE GROUSE *Canachites canadensis*

Background.—Based on NACC proposal 2022-C-17 ‘Treat *Canachites franklinii* as a separate species from *Canachites canadensis* (Spruce Grouse)’, which did not pass. Proposal author: PCR.

Until 1955, *Canachites canadensis* (Linnaeus, 1758) and *C. franklinii* (Douglas, 1829) were considered separate species based on plumage and structural differences, e.g., the obvious large white spots on the uppertail-coverts and usual lack of a chestnut terminal tail-band in the *franklinii* group, coupled with its nearly truncate-tipped and broader rectrices than in the *canadensis* group, which lacks the white uppertail-covert spots, usually has a distinct chestnut terminal tail-band, and has narrower, rounder-tipped rectrices (Ridgway & Friedmann 1941). Rand (1948) stated that the zone in which intermediates occur is very narrow and that intergradation seemed not to be common even there. Brooks & Swarth (1925) stated ‘Franklin and Spruce grouse are reported as occurring together at the headwaters of the Parsnip and the Big Salmon rivers [the former at least in eastern British Columbia] (F. K. Vreeland, MS)’, which could be taken to suggest sympatry. However, since the 30th supplement of the *Check-list* in 1955, Spruce Grouse has been considered to comprise a single polytypic species (AOU 1955), based on the rationale that intergradation occurs between the *canadensis* and *franklinii* groups (Jewett *et al*. 1953). A note in Jewett *et al*. (1953: 203) stated that ‘There is now abundant evidence that the Franklin grouse is a race of the spruce grouse rather than a distinct species as has always been maintained in the literature. Intergradation between these supposedly distinct species takes place chiefly in north-central British Columbia and western Alberta [see Fig. 1], but tendencies toward chestnut tail tips seem to appear occasionally almost anywhere within the range of

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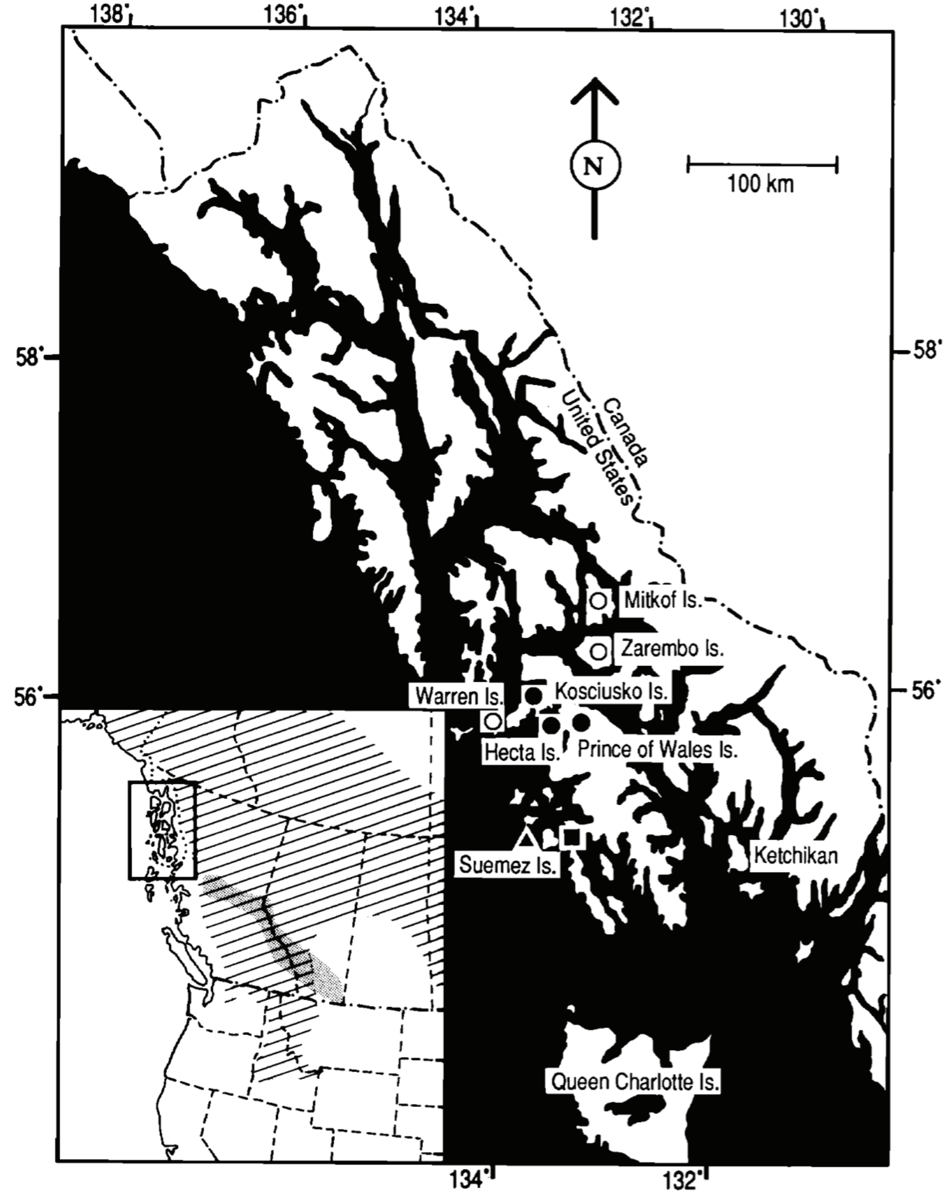

Figure 1. Map showing the distribution of the Spruce Grouse *Canachites canadensis* in western Canada and Alaska, including the range of *C. c. isleibi* and zone of intergradation between the *canadensis* and *franklinii* subspecies groups (inset). Symbols: solid dot = specimen record; open dot = sight record; triangle = bones; square = nest. Adapted from Dickerman & Gustafson (1996). Reproduced by permission from *Western Birds* 27: 41–47, 1996.

franklinii. A large series of specimens in the U.S. National Museum (USNM) shows complete intergradation in all characters between *franklinii* and *canadensis*.'

This variation is not mentioned in Ridgway & Friedmann (1946), which would have been based on much the same USNM material, and these authors (presumably Friedmann, Ridgway being by then deceased) did not indicate uncertainty as to species status of the *franklinii* group, although RTC noted that the identifications of several birds as hybrids were

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made later, in the early 1950s. Furthermore, Short (1967) stated that in many respects the differences between *C. canadensis sensu lato* and Siberian Grouse *Falcipennis falcipennis* (now known not to form a monophyletic group with *Canachites*; Persons *et al*. 2016) are no greater than those between the *canadensis* and *franklinii* groups, and Short (1967) even suggested that *F. falcipennis* might prove to be conspecific with these.

For comparison, it should be noted that Jewett *et al*. (1953) gave a similar though less detailed note regarding Dusky *Dendragapus obscurus* and Sooty Grouse *D. fuliginosus*: 'We have found that the characteristics of the blue grouse of the Pacific Coastal region intergrade completely with those of the Rocky Mountain region and so can see no reason for maintaining them as distinct species. The area of intergradation is in the mountains of northern Okanogan County.' The AOU had previously (AOU 1944) lumped the *D. fuliginosus* group within the *D. obscurus* group in the 19th Supplement, following Peters (1936: 28) without comment, but at that time continued to maintain *C. franklinii* as a species, as did Peters (1936). The split between *D. obscurus* and *D. fuliginosus* enacted in Banks *et al*. (2006) followed a detailed analysis of the phylogeography of the genus (Barrowclough *et al*. 2004), but no such comprehensive analysis has been produced for *Canachites*.

New information.—Gutierrez *et al*. (2000) sequenced five mitochondrial genes (cyt-b, CO-III, ATPase-6, ATPase-8 and ND2) for a phylogenetic study of species and well-differentiated subspecies in the subfamily Tetraoninae. They found 1% sequence divergence between the *franklinii* and *canadensis* groups, and, noting that this is greater than between any species of prairie grouse *Tympanuchus*, they considered that *Canachites* constitutes two species rather than a species with two subspecies groups (they also considered *Dendragapus* to comprise two species). Drovetski (2001) considered his genetic analyses to support the specific status of *C. c. franklinii* as much as for several other taxa of grouse that have been variously treated as species or subspecies, but almost all of which are now treated as species (except Attwater Prairie Chicken *Tympanuchus* [*cupido*] *attwateri*). Barry & Tallmon (2010) found what they considered to be significant genetic variation in mtDNA and nuclear microsatellites between the insular south-eastern Alaska population *C. c. isleibi* on Prince of Wales Island in the Alexander Archipelago (on morphology considered to be a member of the *franklinii* group; see Fig. 2) and both the *franklinii* and *canadensis* groups. They also found *C. c. franklinii* and *C. c. canadensis* to be more closely related to each other than either is to *C. c. isleibi*. This may have been either because their *C. c. franklinii* samples originated from the hybrid zone in British Columbia, or due to incipient divergence of the insular *C. c. isleibi*. However, the apparently intermediate phenotype of *C. c. isleibi* (Fig. 2) also suggests introgression and not necessarily valid subspecific status, which would be consistent with its geographic position near the hybrid zone.

Spruce Grouse was split by del Hoyo & Collar (2014) into *Falcipennis canadensis* and *F. franklinii*, citing 'all-dark *vs* broad orange-buff tips of rectrices (3); bold white (*vs* all-dark) tips of elongate uppertail-coverts (3); thin broken *vs* strong continuous white line across breast (1); broader rectrices (effect size based on published data[163] 1.67; score 1); possession of wing-clap territorial display *vs* none[163] (3); moreover, long zone of hybridisation occurs at boundary, where two taxa inhabit different habitat (*C. c. franklinii* in montane conifers, *C. c. canadensis* in taiga[163]) (2).' Reference 163 is the *Birds of North America* (BNA) account (Boag & Schroeder 1992). The noticeably darker, blacker central underparts of male *franklinii*, apparent in some photographs (e.g., ML 263068381 and ML 184617751) were illustrated in the plate in del Hoyo & Collar (2014) and seem to be obliquely indicated in these authors' character list by the 'thin broken *vs* strong continuous white line across breast'.

Note also that males of the *canadensis* group often nearly lack chestnut tail tips even in the far east of their range; this can readily be seen in photos (e.g., ML 102027511) with

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Figure 2. Watercolour by Mike Ramos showing the upperparts of males of three subspecies of Spruce Grouse *Canachites canadensis*. Left, *C. c. canadensis*. Based on two adults, Museum of Southwestern Biology (MSB) 880, from Thomas Lake, 30 miles north-east of Ely, St. Louis Co., Minnesota, 19 December 1924, and MSB 679, from mile 50 along Richardson Highway, 150 miles north-east of Anchorage, Alaska, 3 September 1961. Middle, *C. c. isleibi*. Based on American Museum of Natural History (AMNH) 830554, an adult, and 830555, an immature, both from Kosciusko Island, about 50 miles south-east of Ketchikan, Alaska, in autumn 1991. Right, *C. c. franklinii*. Based on two adults, Univ. of Washington Burke Museum (UWBM) 36214, from Skull and Crossbones Ridge, Okanogan Co., Washington, November 1981, and UWBM 50206, from Freezeout Ridge, 9 miles west and 7.5 miles north of Conconully, Okanogan Co., Washington, 27 August 1987. Adapted from Dickerman & Gustafson (1996). Reproduced by permission from *Western Birds* 27: 41–47, 1996.

different amounts of chestnut on the two sides of the tail (presumably from different feather generations). Feather wear might account for some of the variation in the amount of chestnut on the tail tips (see, e.g., ML 159178181). A photo of a male from Michigan (ML 383073331) shows small but obvious whitish spots on the uppertail-coverts, but this could represent natural variation within the *canadensis* group rather than intergradation with the *franklinii* group.

RTC examined and photographed some of the extensive USNM series (photos of select specimens shown in Fig. 3) and considered that, at first glance, the interpretation of Jewett *et al*. (1953) seems justified. It does not seem to uphold Rand’s (1948) report of a very narrow hybrid zone in which hybridisation is uncommon.

It is well established that southern *C. c. franklinii* populations usually give a double wing-clap as part of the flight display when descending to the perch, and this initially would appear to support species status for this taxon, but according to Schroeder *et al*. (2021), northern populations of *C. c. franklinii* do not wing-clap. This difference, however, is not mentioned in the original *BNA* account (Boag & Schroeder 1992) cited by del Hoyo & Collar (2014), and it appears to remain unpublished except as included in Schroeder *et*

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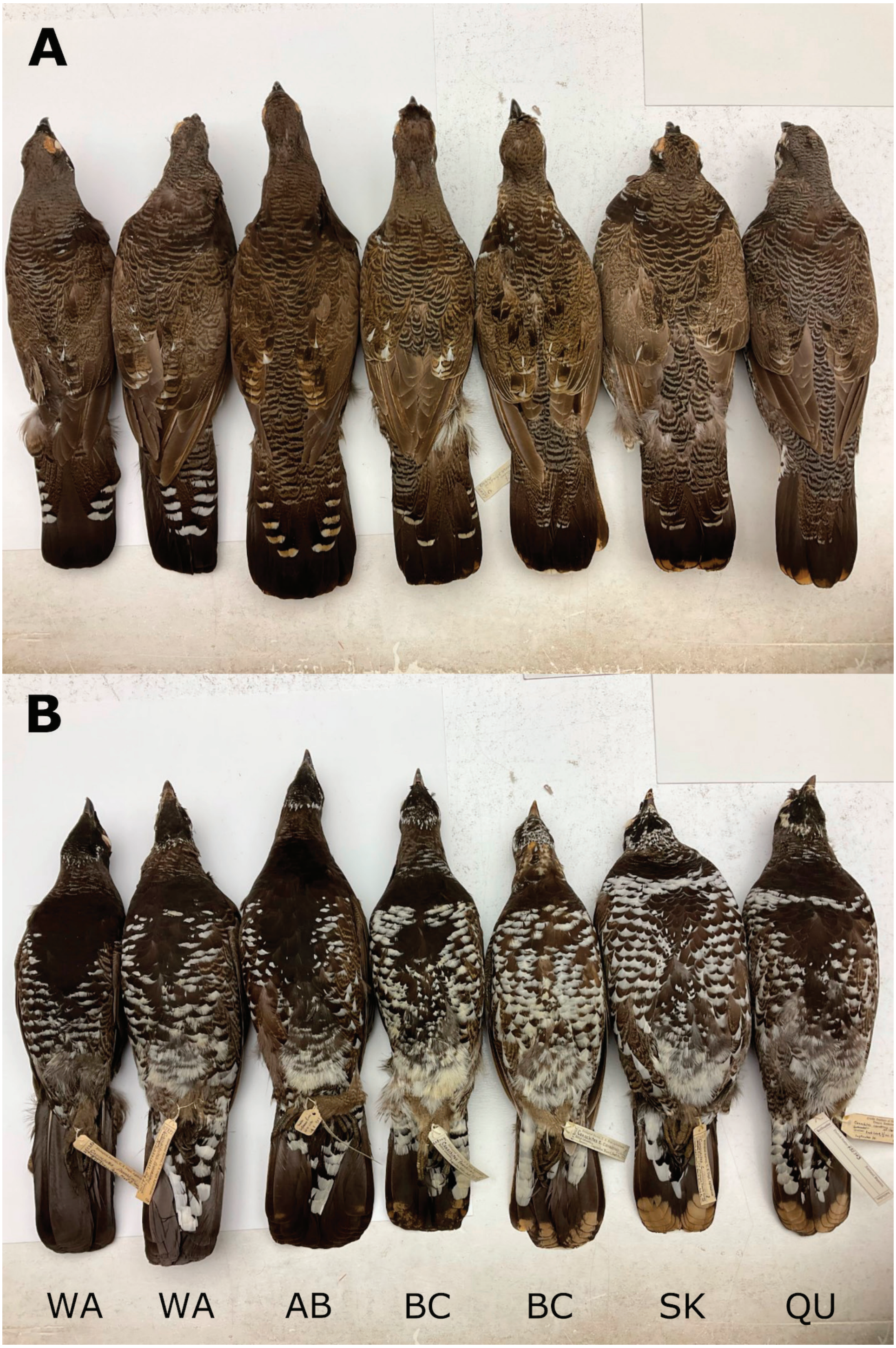

Figure 3. (A) dorsal and (B) ventral photos of select *Canachites* specimens housed at the National Museum of Natural History, Washington, DC, highlighting variation from west to east across North America. WA = Washington (USNM 285383 and USNM 271897), AB = Alberta (USNM 229737), BC = British Columbia (USNM 208064 and USNM 208065), SK = Saskatchewan (USNM 283443), QU = Quebec (USNM 458343) (R. Terry Chesser)

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al. (2021). Birds from the zone of intergradation have been noted to give either single wing-claps or to wing-clap in flights between trees (Schroeder *et al*. 2021).

As for other potential mechanisms for reproductive isolation, there does not appear to be any true song in Spruce Grouse, although the cackle of females can be considered a song (Schroeder *et al*. 2021), and other vocalisations mainly consist of clucks, chick calls, incidental wing noise, male wing-whirrs, stomps, short bouts of drumming, and the double wing-clap of southern *C. c. franklinii*. Reports of a very low-pitched hooting song appear mistaken (Schroeder *et al*. 2021).

Subsequent treatments.—In an initial vote, the WGAC voted to treat Franklin's Grouse as a separate species, so the issue was subsequently addressed by NACC. A follow-up vote by WGAC considering the information in the NACC proposal led to a reversal of the consensus to split *franklinii*. NACC has recognised *Dendragapus obscurus* and *D. fuliginosus* as separate species since 2006 (Banks *et al.* 2006); this treatment, in addition to recognition of three species of *Tympanuchus*, with their low genetic divergences (Galla & Johnson 2015), could be used to argue that *Canachites* should be treated as two species; however, the displays and vocalisations differ substantially among the three taxa treated as species in *Tympanuchus* and also between the two taxa treated as species in *Centrocercus*. Further, a comprehensive phylogeographic analysis (Barrowclough *et al*. 2004) was available for the Blue Grouse complex, whereas no such analysis exists for the Spruce Grouse complex.

Recommendation.—Given the seemingly extensive introgression over a large area suggested by plumage (including the putative subspecies *C. c. isleibi*) and by the observed variation in the wing-clapping display of *C. c. franklinii*, at this time there is not a convincing case to be made that *Canachites* should be accorded the same two-species treatment as *Dendragapus*. We thus recommend that *C. c. franklinii* be maintained as a subspecies of *C. canadensis* for now, but we hope that a comprehensive analysis will soon clarify the picture.

Next steps.—Critical to sorting out species limits in this group is a quantitative analysis of the contact zone between the *franklinii* and *canadensis* groups, to test for assortative mating and the degree of gene flow. This should incorporate analysis of DNA and plumage data, and variation in the wing-clapping display. Committee members were not convinced by comparisons to Dusky and Sooty Grouse, which have differently coloured air sacs on their necks, slightly different songs, and different downy young plumages, all supporting two-species status in that group, whereas similar data are lacking for *Canachites*.

BAND-TAILED PIGEON *Patagioenas fasciata*

Background.—Based on NACC proposal 2022-B-12 'Treat *Patagioenas albilinea* as a separate species from *P. fasciata* (Band-tailed Pigeon)', which did not pass. Proposal author: RTC.

Patagioenas fasciata (Say, 1823) is a widespread species occurring from western Canada south to north-western Argentina. Formerly placed in *Columba*, it consists of two groups (AOU 1998): *P. fasciata*, distributed from Canada south to northern Nicaragua, and *P. albilinea* (Bonaparte, 1854) in highlands from Costa Rica to Argentina. Many sources, such as the IOC (International Ornithological Congress) list (Gill *et al*. 2022) and Howard & Moore (1991), recognise subspecies *monilis*, *fasciata* and *vioscae* (an isolated subspecies in Baja California Sur) within the *fasciata* group, although others, such as Clements *et al*. (2022), separate two additional Central American subspecies from the somewhat variable *fasciata*: *letonai* of Honduras and El Salvador and *parva* of Nicaragua. Three subspecies are consistently included in the *albilinea* group: *crissalis* of Costa Rica and Panama, *roraimae* of southern Venezuela and adjacent Guyana, and *albilinea* from Colombia to Argentina.

The two groups were formerly considered separate species, e.g., by Ridgway (1916) and even Peters (1937), although the latter remarked that 'Perhaps *C. fasciata*, *C. albilinea*,

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and *C. araucana* (Lesson & Garnot, 1827) should be regarded as conspecific.' Hellmayr & Conover (1942) treated the *fasciata* and *albilinea* groups as a single species (*C. fasciata*) with the following explanation: 'The *C. albilinea* group is clearly conspecific with *C. fasciata*, the Costa Rican form being, as far as coloration is concerned, in a way intermediate to the northern races.' Most subsequent sources (e.g., Goodwin 1983, Sibley & Monroe 1990, Gibbs *et al*. 2001, and various regional guides and global lists) have treated Band-tailed Pigeon as a single species; however, del Hoyo & Collar (2014) considered the groups as separate species based on the following evidence:

> [*P. albilinea* is] usually considered conspecific with *P. fasciata*, but [is] separable at species level on account of all yellow *vs* black-tipped yellow bill (2); darker grey underparts generally, with no shading to white on belly (3); wing-coverts as dark grey as mantle, not paler grey with whitish fringes, resulting in a distinct wingband in flight (2); gloss of nape and mantle green *vs* bronze (ns1). Subspecies *crissalis* somewhat intermediate, with undertail-coverts pale greyish-white, wing-coverts intermediate, and occasionally dusky tip to culmen.

Band-tailed Pigeon is currently considered a single species by Dickinson & Remsen (2013), Clements *et al*. (2022) and Gill *et al*. (2022), as well as by NACC and SACC. NACC recently considered a proposal not because of new data, but because the difference in taxonomic treatment brought this issue before WGAC.

Morphology.—Size seems to show only minor variation within *P. fasciata* (Keppie & Braun 2020), despite apparent differences in some of the specimen photos (Figs. 4–6), and is not mentioned in the del Hoyo & Collar (2014) analysis as differing between the two groups. However, plumage varies geographically, with the darkest subspecies in South America (*albilinea* and the similarly dark *roraimae*), somewhat paler subspecies in Costa Rica and Panama (*crissalis*), and still paler, although variable, subspecies to the north (*fasciata* and *monilis*). The subspecies in Baja California Sur (*vioscae*) has the palest plumage, to the extent that the band on the tail is faint or (more often) lacking. Such variation is evident in the photos of mostly male specimens shown in Fig. 4.

The dark vinaceous coloration of *P. f. albilinea* contrasts with the purplish hue of *P. f. crissalis* and the lighter purplish-and-white coloration of subspecies *fasciata* and *monilis*. The variability within *P. f. fasciata* is also evident, especially in the pale individual from Honduras ('*letonai*'), as is the slightly darker colour of *P. f. monilis*. The same patterns are noticeable in the colour of the pileum in Fig. 4B. The green vs. bronze mantle gloss is also conspicuous, although birds from Costa Rica again appear somewhat intermediate. The seemingly discrete difference between the solid yellow bill of the *albilinea* group and the yellow bill with a black tip of the *fasciata* group can be seen in Fig. 4C.

Wetmore (1968), however, noted that bill colour in one of two adult female specimens from Panama (i.e., subspecies *crissalis*, and the only two specimens for which soft parts colours were available) was 'honey yellow, with the tip of the culmen dusky neutral gray' and a grey or dark grey (perhaps even black) bill tip is also noticeable in many photos of *P. f. crissalis* from Costa Rica in the Macaulay Library (many of these are juveniles but some are adults). See, for example, ML 369692871, ML 376900401 and ML 252378571. A dark tip is also visible in photos of several birds from South America, such as an adult (ML 272622831) from Colombia (*P. f. albilinea*).

It is difficult to get a good handle on the variation in contrast of the wing-coverts from Fig. 4C.; these are said to be paler with whitish edgings in the *fasciata* group, creating a band in flight, and to contrast with the darker back and scapulars, but the contrast shows

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Figure 4. (A) Ventral, (B) dorsal and (C) lateral photos of specimens of Band-tailed Pigeon *Patagioenas fasciata* housed at the Louisiana State University Museum of Natural Science (LSUMZ), Baton Rouge, highlighting plumage variation across the distribution of the species. Arranged from left to right are one *albilinea* (Peru; LSUMZ 87230), two *crissalis* (Costa Rica; LSUMZ 63633 and 32187), four *fasciata* (Honduras; Guatemala; two from San Luis Potosí, Mexico; LSUMZ 29022, 65500, 16757 and 10898) and one *monilis* (Oregon; LSUMZ 7996). Note that the rightmost Costa Rican specimen is a female, which tend to be slightly duller than males (© Nicholas A. Mason)

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up better in Fig. 5C. The del Hoyo & Collar (2014) analysis notes that this character, too, is intermediate in *P. f. crissalis*.

Vocalisations.—The typical song differs between the *fasciata* and *albilinea* groups but is largely consistent within them, as noted by Boesman (2015) in his comparison of their vocalisations (https://birdsoftheworld.org/bow/ornith-notes/JN100041). Nevertheless, it is worth exploring variation in songs, particularly in the *crissalis* group.

The song of the *fasciata* group typically consists of 1–2 introductory notes followed by a series of double (bisyllabic or two-note) elements. The pace of the song varies individually, as does the interval between the two notes of each element, but the first note always reaches higher frequency and is shorter than the second, with a quicker rise and fall. This can be seen in the sonogram in Fig. 7A.

The two-note elements have been described as 'a deep, owl-like *whoo-whooo*' (Dunn & Alderfer 2017) and the entire song as 'a deep, slightly hoarse *huh whur* or *wh'hoo*, repeated 3–4×, rarely up to 13× or more, often preceded by a deep *grrrr* and at times followed by a moaning *whorr*, longer series may end with an abrupt *wu't*' (Howell & Webb 1995). The first note reaches a higher peak frequency than does any part of the song of *P. f. albilinea* (Boesman 2015). This song occurs in more northerly populations as well as in birds recorded in the southern part of the distribution in Nicaragua (ML 250647291), Honduras (ML 83901331, XC323712), El Salvador (ML 110064321), Guatemala (ML 211589), Chiapas (XC 334727 and XC 221351) and Oaxaca (ML 153844591 and XC 623976). A recording of subspecies *vioscae* (XC 21480), although largely in the background and somewhat faint, appears also to consist of the typical two-note elements. Individuals of the *fasciata* group also call during display flights, giving a 'grating call' (Dunn & Alderfer 2017).

The song of the *albilinea* group typically consists of an introductory note followed by a series of deep long notes, described as 'deep, mellow cooing, *co' oooh, co' oooh* ...' (Hilty 2003) repeated from two to many times. Schulenberg *et al*. (2007) described this song as 'a low coo with introductory note rising, but other long notes falling: *Woo uh-wooh uh-wooh*.' Boesman (2015) described these elements as monosyllables, but mentioned one exception from Santa Marta, Colombia (XC 236033), that includes a brief 'hiccup' before every note. Although it is not clear whether the two-part descriptions of the elements of the song indicate the presence of a 'hiccup' or simply relate to the rising and falling parts of a monosyllable, the 'hiccup' is present in several additional recordings (e.g., ML 258965901 and ML 257237 from Colombia; ML 129476 from Ecuador). On average, the series of notes given by the *albilinea* group are longer and are delivered more slowly than are those of the *fasciata* group (Boesman 2015). An example, again from Boesman (2015), of the song with monosyllabic elements is shown in Fig. 7B, and one of *P. f. albilinea* with bisyllabic elements in Fig. 7C. Individuals of this group also give a buzzy display-flight call, described as a 'chirping *dzurr*' (Fjeldså & Krabbe 1990).

Seven songs of *crissalis* are available on the Macaulay and Xeno-canto websites. Three consist of the low-pitched series of notes typical of *P. f. albilinea*, described as '*c' cooo c' cooo*' or '*cooOOO cooOOO*' by Stiles & Skutch (1989) and '*co-oooh co-oooh*' by Ridgely & Gwynne (1989). This applies to XC 274341 and ML 165872 from Costa Rica and to ML 172548421 from Panama. Recording XC 274681 is a faster and burrier call but still within the range of variation of the *albilinea* group. The other recording from Costa Rica (ML 51184), however, consists of a partial series of two-note elements that appear to be more similar to those of the *fasciata* group than to the *albilinea* group (although the pace is slower than is typical in the *fasciata* group), and in which the emphatic long note is especially similar to the long notes of some *P. f. fasciata*. The other two recordings from Panama (ML 302869 and ML 302873) sound quite different from either of these: these songs consist of a series of three-note

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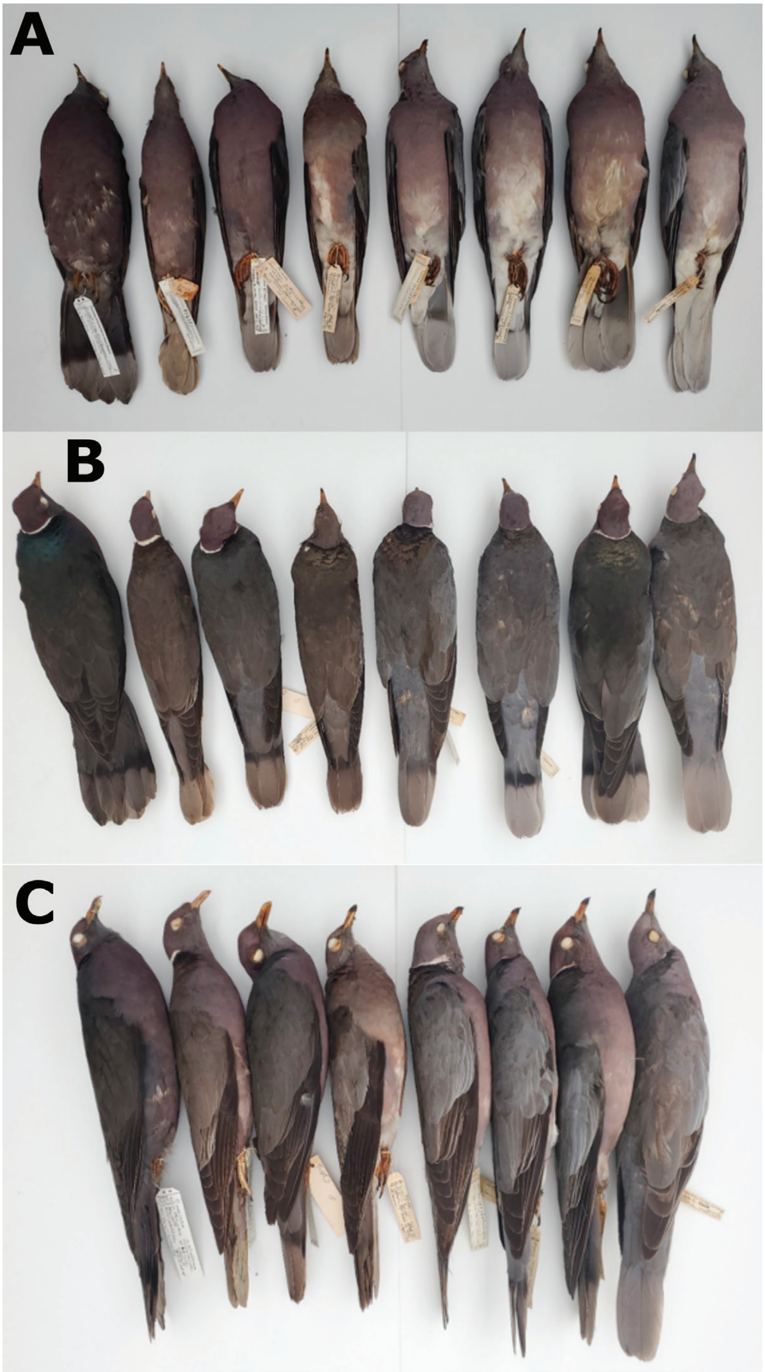

Figure 5. (A) Ventral, (B) dorsal and (C) lateral photos of male specimens of Band-tailed Pigeon *Patagioenas fasciata* at the National Museum of Natural History, Washington, DC. These are also arranged from left to right in roughly south–north order, from *roraimae* to *monilis*, except that this series includes the isolated subspecies *vioscae* at the far right. Included are one *roraimae* from Guyana (USNM 650546), two *crissalis* from Panama (USNM 456382, 470621), three *fasciata* from Guatemala (USNM 396560), Sonora, Mexico (USNM 120760) and Arizona (USNM 299725), one *monilis* from Washington (USNM 365386), and one *vioscae* from Baja California Sur (USNM 203161); note especially the near lack of a tail-band in the specimen of *vioscae* (© Chris Milensky)

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Figure 6. Six specimens of Band-tailed Pigeon *Patagioenas fasciata* from the University of Florida (UF) collection, from left to right showing two from Oaxaca, Mexico (UF 4429, 37587): one ostensibly from Guatemala although the locality is not certain (UF 9060), two from Honduras (UF 4430, 4431; these are *letonai*, if recognised), and one from New Mexico (UF 52967). All are males except the middle two birds, which were not sexed. Note the variability within *letonai* here and in comparison with the skin from LSUMZ in Fig. 4, which illustrates why many, including Hellmayr & Conover (1942), consider this a 'questionable race' (© Andy Kratter)

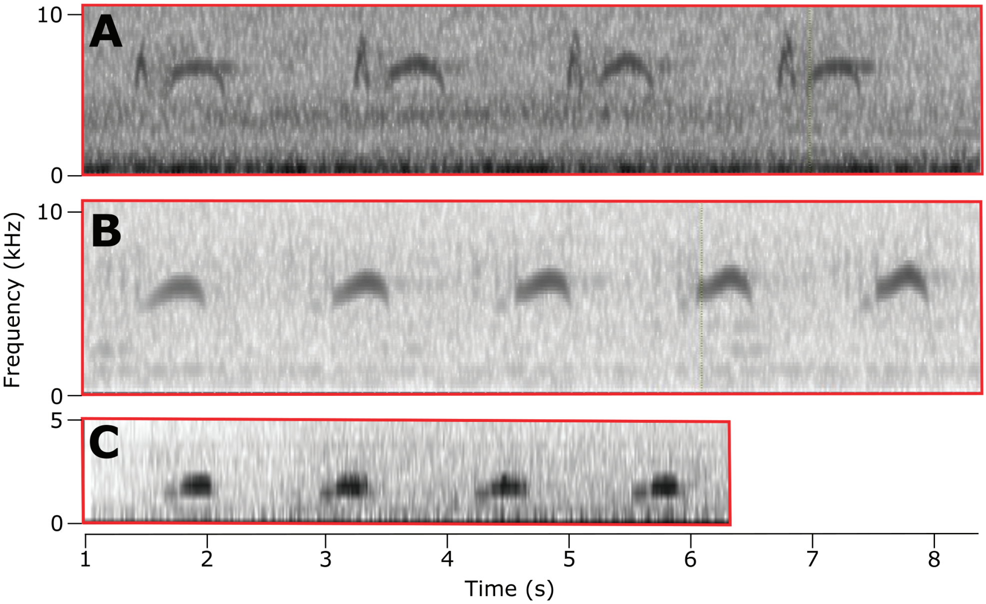

Figure 7. Three sonograms of the primary song of Band-tailed Pigeon *Patagioenas fasciata* showing vocal variation within the species. (A) A bisyllabic song from the northern *fasciata* group (Boesman 2015), (B) a monosyllabic song from the southern *albilinea* group (Boesman 2015), and (C) an example of the *albilinea* group with bisyllabic elements (i.e., with the 'hiccup') from Colombia (XC 529591).

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elements, the second note shorter than the rest, and third note lower and longer, the shorter notes recalling in their brevity the clipped first note of *P. f. fasciata* songs (especially in the last song of ML 302869, in which the first note has a quick rise and fall). These two recordings were made at the same time on the same date by P. Boesman, who put the ID certainty at 80%, presumably because of the unusual nature of the songs compared to those of the *albilinea* group. However, multi-note elements in the pattern 'short-shorter-long' have been noted in other songs of *P. f. crissalis* from Chiriquí, which were described by R. Ward in Ridgely (1976) as '*look for paw-paw*', supporting the identification of these recordings.

Recommendation.—Populations of *P. fasciata* from Nicaragua north to Canada (the *fasciata* group) and in South America (subspecies *albilinea*, and presumably subspecies *roraimae*, which is similarly dark-plumaged but whose voice is apparently unrecorded) appear to differ consistently and diagnosably in morphology and vocalisations, although subspecies *crissalis* of Costa Rica and Panama is intermediate. That *P. f. crissalis* is intermediate in plumage between the *fasciata* and *albilinea* groups seems clear, and it is also intermediate, albeit to a much lesser extent, in the colour of the bill tip; that is, most birds have the all-yellow bill typical of the *albilinea* group, but some have a dusky bill tip. Only seven recordings of *P. f. crissalis* are available: four feature vocalisations that sound like those of the *albilinea* group, but songs in the three other recordings differ from those of both groups and in some characters appear to be more like those of the *fasciata* group. These latter recordings were made in both Costa Rica and Panama, and birds with dusky bill tips also occur in both countries, indicating that these intermediate character states are not restricted to a narrow zone but apparently occur more widely in the range of *P. f. crissalis*.

In our view this information, taken together, raises sufficient doubt concerning species status of the *albilinea* group to recommend that it not be separated from the *fasciata* group, pending further investigation. It is possible that *P.* (*f.*) *fasciata* and *P.* (*f.*) *albilinea* are separate species, but too many questions remain unanswered to endorse species status at this time.

Next steps.—Additional sampling and analyses of vocalisations of *P. f. crissalis*, and genomic data encompassing *P. f. crissalis* and populations to the north and south would be especially helpful in determining the taxonomic status of *P. f. albilinea*. Quantification of phenotypic, vocal and genomic differences among populations is of high priority. Committee members raised concerns about the apparent intermediacy of subspecies *crissalis* in Costa Rica and Panama, and the apparent high degree of plumage variation in *P. f. letonai* and *P. f. parva* of Honduras, El Salvador and Nicaragua. Studies of subspecies *letonai*, *parva* and especially *crissalis* would be of particular interest to species limits in the group. Differences in vocalisations are important in species recognition in Columbidae, and these data are lacking from many populations of *P. fasciata*. Analysis of the distinctive rapid shallow-fluttering display flights might also be informative.

ANTILLEAN MANGO *Anthracothorax dominicus*

Background.—Based on NACC proposal 2022-C-4 'Treat *Anthracothorax aurulentus* as a separate species from *A. dominicus* (Antillean Mango)', which passed. Proposal authors: OJ & BEHB.

Anthracothorax dominicus (Linnaeus, 1766) is a species with two fairly well-differentiated subspecies; *A. d. dominicus* of Hispaniola and *A. d. aurulentus* (Audebert & Vieillot, 1801) of Puerto Rico. Both sexes of these subspecies differ in colour pattern. Both taxa have the throat metallic green, but *A. d. dominicus* is otherwise wholly black ventrally whereas *A. d. aurulentus* has the flanks green and the belly fuscous-grey, with the black restricted to a patch on the chest (Kirwan *et al*. 2020). In females, *dominicus* has a purplish base to the tail, whereas in *A. d. aurulentus* this area is largely brownish grey (Kirwan *et al*. 2020). Unique

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amongst *Anthracothorax*, females are pure white below, with only the young males having the black ventral stripe typical of continental species of *Anthracothorax* (Kirwan *et al*. 2020).

The two taxa were considered separate species (e.g., Ridgway 1911, Wetmore 1916, Cory 1918) until treated as a single species without comment by Peters (1945). Later authors have largely considered the two conspecific (AOU 1983, Raffaele 1989, Bond 1993, Raffaele *et al*. 1998, Dickinson 2003, Dickinson & Remsen 2013, Kirwan *et al*. 2020), although del Hoyo & Collar (2014) split the two (see below).

Under his account for *A. aurulentus*, Ridgway (1911) noted the following differences vs. *A. dominicus*: 'Similar to *A. dominicus* but decidedly smaller; adult male with black of under parts confined to chest and breast, and middle rectrices usually much more coppery bronze; adult female with basal portion of lateral rectrices light greyish, or partly so, instead of more than basal half wholly chestnut-rufous, black of subterminal portion brightly glossed with bluish green, and under parts more extensively and uniformly greyish, the sides without green spotting or inter-mixture.'

New evidence.—No recent publications. Del Hoyo & Collar (2014) considered *aurulentus* as a separate species from *dominicus* based on the following rationale:

> hitherto treated as conspecific with *A. dominicus*, but differs on account of (in male) blue-black not covering all of underparts below throat but just breast to mid-belly, with flanks green and lower central underparts to vent dark brownish-grey (3); (in male) central rectrices bronzy green *vs* glossy blackish-blue (2); (in female) outer tail dull brownish-grey, shading to darker subterminal tips and white tips *vs* violaceous-rufous, cutting sharply to blackish broad subterminal tips and white tips (3); markedly smaller size, although bill length virtually identical (effect size for wing –4.15, tail –5.63; score 3). Monotypic.

Although this account indicates that lateral rectrices of female *A. d. aurulentus* are pale greyish or greyish brown basally (Fig. 8), RTC noted that 50% of specimens of female *A. d. aurulentus* at USNM (ten of 20) showed purple (or occasionally chestnut) at the base of the rectrices—although, as noted by Ridgway (1911), never as extensively as in *A. d. dominicus* (Fig. 9).

Photos in Macaulay Library readily distinguish males of the taxa, especially ML 176320171, ML 176615901, ML 241371311 and ML 397356871 of male *A. d. dominicus*, and ML 184585191, ML 184585211, ML 287874871 and ML 303680591 of male *A. d. aurulentus*.

Figure 8. Tails of females of the two taxa in Antillean Mango *Anthracothorax dominicus*, showing the differences between *aurulentus* (left) and *dominicus* (right); note the more extensive chestnut coloration at the base of the tail in *dominicus* (Paul Donald, © Trustees of the Natural History Museum, London)

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Figure 9. Three female Antillean Mango *Anthracothorax dominicus aurulentus* (USNM 238818, 231785 and 238281) showing some purple coloration at the base of the tail (R. Terry Chesser)

TABLE 1
Mensural measurements of two subspecies of *Anthracothorax dominicus*. Data from Arendt *et al*. (2004) and Kirwan *et al*. (2020). All measurements in mm except for mass.

Taxon	**Sex**	**Wing length**	**Tail length**	**Bill length**	**Tarsus length**	**Mass**
A. d. dominicus	Males	62–72 (64.8 ± 3.4, *n* = 3)	N/A	N/A	N/A	6.0–8.2 g
	Females	59–67 (64.0 ± 2.7, *n* = 10)	35.3–36.4 (35.9 ± 0.7, *n* = 3)	18.0–25.3 (24.0 ± 2.1, *n* = 3)	5.1–7.3 (6.2 ± 1.6, *n* = 3)	4.0–7.0 g
A. d. aurulentus	Males	57.3–69.0 (61.6 ± 2.0, *n* = 47)	22.7–36.4 (32.0 ± 3.7, *n* = 47)	21–27 (23.2 ± 1.4, *n* = 47)	2.3–7.3 (5.4 ± 1.0, *n* = 47)	4.8–7.2 g
	Females	50.7–63.5 (57.9 ± 2.5, *n* = 60)	22.9–34.7 (32.0 ± 2.0, *n* = 60)	20.8–27.3 (24.5 ± 1.3, *n* = 60)	4.4–7.3 (5.6 ± 0.7, *n* = 60)	4.0–6.4 g

Based on data from Arendt *et al*. (2004), Kirwan *et al*. (2020) listed some morphometric differences between *aurulentus* and *dominicus* (Table 1). They stated that '*aurulentus* has shorter wings and tail than nominate *dominicus*, but that bill length is comparable between the two taxa'. There is, however, some overlap in these measurements.

No genetic comparisons have been made between the two taxa, although given the plumage and morphometric differences, there are clearly some underlying genetic differences. McGuire *et al*. (2014) sampled *A. dominicus* but only Puerto Rican *A. d. aurulentus*; they did not include a sample of *A. d. dominicus*. That study found *A. dominicus* sister to *A. viridis* (Audebert & Vieillot, 1801) of Puerto Rico, and in turn sister to the *Eulampis* caribs of the eastern Caribbean (thus rendering *Anthracothorax* paraphyletic). This, unfortunately, provides no data on the species status of *A. d. dominicus* and *A. d. aurulentus*. However, mainland *Anthracothorax* of Central and South America (sister to the aforementioned clade) provide an interesting comparison. The four species in that group all differ with respect to the relative extent of green and black coloration on the underparts, comparable to the differences between males of *A. d. dominicus* and *A. d. aurulentus*. However, the taxonomy of those *Anthracothorax* is not clear-cut, with some taxa having been considered conspecific in the recent past (e.g., Green-breasted Mango *A. prevostii* and Veraguas Mango *A. veraguensis*).

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It appears that no other studies on the taxonomy of this group have been conducted, such as research on song or genetics. The two taxa, like others in the genus, appear to vocalise infrequently, if they vocalise at all (Kirwan *et al*. 2020). Thus, differences in plumage and average differences in morphometrics (described above) may be more relevant to species limits. WGAC recently considered this issue and voted to treat the two taxa as separate species. That decision was based on the differences in size and plumage described above.

Recommendation.—We recommend that *A. aurulentus* be considered a species separate from *A. dominicus*. Although more data would be desirable, the published plumage and morphometric data seem more consistent with species rank. Differences between the two taxa are consistent and diagnostic, and, more importantly, they are comparable to species-level differences in other taxa in the genus. The two taxa are clearly closely related and are (together) distinctive within the genus.

If considered as separate species, we recommend the following English names, used by del Hoyo & Collar (2014): Hispaniolan Mango for *dominicus* and Puerto Rican Mango for *aurulentus*. Ridgway (1911) and Cory (1918) used Haitian Mango and Porto Rican Mango, but the HBW names highlight the entire island on which *dominicus* is found and the Ridgway/Cory name for *aurulentus* is an outdated spelling variant.

Next steps.—This taxonomic change was enacted by NACC, in part because no data or explicit rationale were published to justify the prior change in their treatment as separate species. However, comparative genetic data are lacking for these taxa, and future work could focus on this topic. The differences in colour pattern between the two taxa are clear, but a study of relative genetic differences and quantification of plumage differences could provide additional data on species status. Although these taxa vocalise infrequently, any differences in displays or breeding behaviour could be quantified. Additionally, the variation in tail colour, especially in females, could be quantified to assess the degree of overlap in this trait.

GREENISH PUFFLEG *Haplophaedia aureliae*

Background.—Based on NACC proposal 2022-A-6 'Split *Haplophaedia assimilis* from Greenish Puffleg *H. aureliae*' and SACC proposal 923, both of which passed and reached the same conclusion regarding taxonomic treatment. Proposal authors: PCR, DFL & JVR.

Within the NACC region *Haplophaedia aureliae* (Bourcier & Mulsant, 1846) occurs only on a few mountains in eastern Panama (Cerros Pirre, Malí, and Tacarcuna) but is widely distributed on Andean slopes from Colombia south to northern Bolivia (e.g., Wolters 1975–82, Sibley & Monroe 1990, AOU 1998, Schulenberg *et al*. 2007). Numerous earlier sources (e.g., Simon 1921: 188, Peters 1945) treated *H. aureliae* as a single species, presumably leading to the current NACC treatment. However, since its inception, SACC has treated *H. aureliae sensu lato* as two species, Greenish Puffleg *H. aureliae* from eastern Panama at least through southern Ecuador, and Buff-thighed Puffleg *H. assimilis* (Elliot, 1876) of the eastern Andes of Peru and Bolivia. This was based largely on a comprehensive morphological analysis of the genus *Haplophaedia* by Schuchmann *et al*. (2000), which advocated reinstatement of species status for *H. assimilis* (including the subspecies *affinis*) in line with Cory (1919). In addition to treating *H. assimilis* as specifically distinct, Cory (1919) also regarded *H. floccus* (Nelson, 1912), *H. russata* (Gould, 1871) and *H. lugens* (Gould, 1852) as species; the first two of these have long been subsumed under *H. aureliae* by subsequent authors, whereas the latter is generally still considered specifically distinct. The two subspecies in the NACC region, *H. aureliae galindoi* Wetmore, 1967, of Cerro Pirre (in central Darién) and *H. aureliae floccus* of Cerro Tacarcuna and its spur Cerro Malí (eastern Darién) and adjacent Colombia, have been

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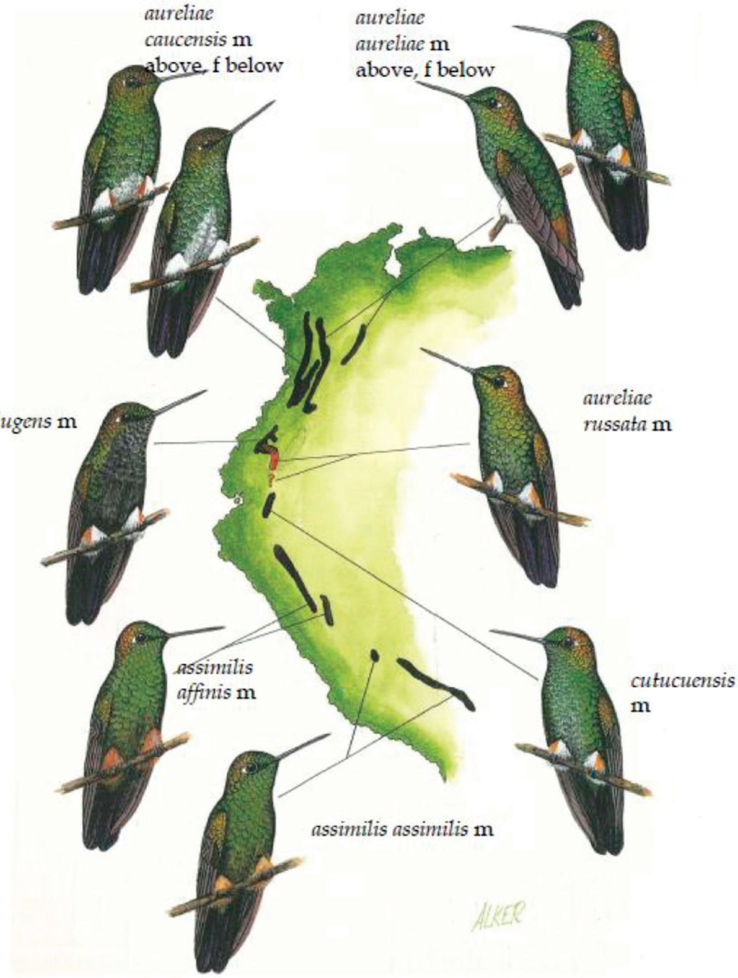

Figure 10. Plate 1 in Schuchmann *et al*. (2000), with labels added, showing the distribution of the South American taxa of *Haplophaedia*. Reproduced with permission from Karl-L. Schuchmann.

synonymised with *H. aureliae caucensis* (Simon, 1911) by some (including Heynen 1999a,b), but both were reinstated as subspecies in del Hoyo & Collar (2014).

Schuchmann *et al*. (2000) advocated specific status for both *H. assimilis* and *H. lugens*; their case for considering *H. assimilis* specifically distinct rested on its disjunct distribution, wholly buffy leg puffs vs. white or bicoloured puffs in *H. aureliae*, and the notably duller plumage of *H. aureliae* (the latter difference not being well shown in the illustrations accompanying the paper [reproduced here as Fig. 10], nor in del Hoyo & Collar 2014). Schulenberg *et al*. (2007), however, illustrated a white-puffed bird and did not mention *assimilis* or that (at least most; see below) Peruvian birds are buffy-puffed. *Haplophaedia assimilis* was treated as specifically distinct by Dickinson (2003), Gill & Wright (2006), Dickinson & Remsen (2013), Clements *et al*. (2021), Gill *et al*. (2021) and del Hoyo & Collar (2014), but not by NACC.

New information.—There does not appear to be significant new information bearing on the species status of *H. assimilis*, which has been universally accepted by the four major global checklists as well as by SACC. As far as we can determine, *H. assimilis* has not been

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sequenced (although *H. aureliae* and *H. lugens* have and are moderately diverged; McGuire *et al*. 2014). However, on the SACC list (Remsen *et al*. 2023), the need for a proposal to assess the validity of this split is mentioned. In the absence of any formal analysis, it appears that the two-species treatment is primarily based on two plumage characters, the buff puffs (differing in tone between the two groups) and overall duller plumage that distinguish *H. assimilis* from the various forms of *H. aureliae*.

However, a series of photos of specimens at LSUMZ (Figs. 11–12) does not support the major phenotypic break between *H. aureliae* and *H. assimilis* across the Marañón Valley mapped by Schuchmann *et al*. (2000; Fig. 10). Rather than supporting the distributions of morphological characters and thus taxon boundaries outlined by Schuchmann *et al*. (2000), the most striking difference among the series (other than the distinctive *H. lugens*, generally considered a separate species) is between two individuals identified as *H. assimilis* (Fig. 11; the left two, with the buffy puffs and lack of white scaling below; LSUMZ 98142, 190722) and the two birds from San Martín, Peru (LSUMZ 81858, 173888; from the north of the range illustrated in Schuchmann *et al*.'s plate 1 [Fig. 10], the outlying Alto Mayo of San Martín), with white puffs and strong scaling, not matching either the plate or description in Schuchmann *et al*. (2000), especially as *H. assimilis affinis* is illustrated there as having the most rufescent puffs. Also, as noted by OJ, the specimen of *H. aureliae cutucuensis* (LSUMZ 169636) from north of the Marañón Valley in Cajamarca (at the southern end of the range of any *H. aureliae* taxon and the next one to the north of *H. assimilis affinis*), seems indistinguishable from the two from San Martín. In response to this conundrum, OJ photographed the entire LSUMZ series (Fig. 12), which shows all the northern Peruvian series (upper row) to be white-puffed and heavily scaled, unlike all the southern Peruvian and Bolivian *H. assimilis* (lower row).

When assembling information in preparation for revising *Birds of Peru* (Schulenberg *et al*. 2007) in 2009, DFL discovered that the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), had three specimens of *H.* '*aureliae*', all from San Martín, Peru: two from the Alto Mayo (LSUMZ 24931, 24934; collected in 2002 on the same expedition as the LSUMZ specimens depicted in Figs. 11–12) and one from near 'Pataz' in the far south-west of San Martín (USNM 18565; *c*.225 km from Alto Mayo; Fig. 13). The former two, in agreement with the LSUMZ series, were white-tufted and had extensive white scaling below. The latter, however, was buff-tufted and lacked scaling. On discussing this with lead author Tom Schulenberg, it became clear that the two taxa must turn over somewhere between the Mayo and Huayabamba drainages (the latter containing the type locality for *H. assimilis affinis*), and that white-tufted birds occur south of the Marañón, without evidence of introgression. In their Acknowledgments, Schuchmann *et al*. (2000) listed the museums where they examined the 149 specimens used in their study. Although LSUMZ is not among them, they listed and mapped a specimen examined from Ray-Urmaña (06°28′12″S, 77°21′0″W; the type locality of *H. assimilis affinis*; Peters 1945) and another from nearby Chirimoto (06°31′1″S, 77°24′0″W) but did not mention specimen numbers. Both specimens were from Amazonas, so presumably were typical *H. assimilis affinis*.

We propose that the LSUMZ specimens from Alto Mayo are not *H. assimilis affinis* as originally identified but instead represent *H. aureliae cutucuensis*, adding another mid-elevation east slope Andean taxon that crosses the Marañón biogeographic barrier for a short distance before its distribution ends to the south. Hence, the turnover between *H. aureliae cutucuensis* and *H. assimilis affinis* is farther south than shown on the map in Schuchmann *et al*. (2000) and suggests a parapatric or possibly sympatric distribution in this region. The seemingly strong difference between white-puffed and white-scaled *H. aureliae cutucuensis* and rufous-puffed *H. assimilis affinis* shows no sign of being a cline (Fig. 12).

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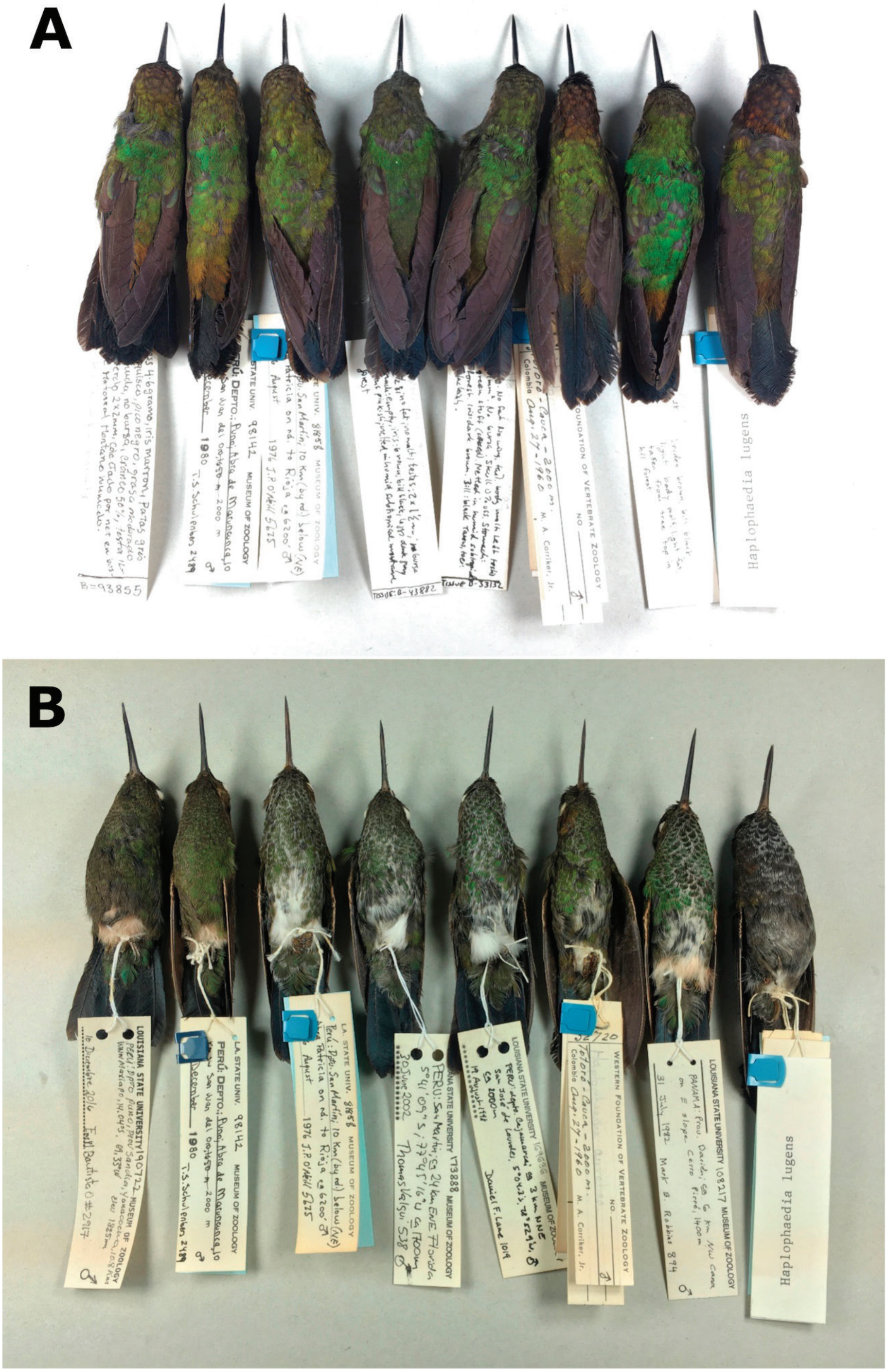

Figure 11. Photos of specimens of representative taxa in *Haplophaedia* housed at the Louisiana State University Museum of Natural Science, Baton Rouge in dorsal (A) and ventral (B) views. Taxa are arranged south (left) to north (right), except for *lugens* at the right end. From left to right are shown: two *affinis* (LSUMZ 190722, 98142), two also identified as *affinis* (LSUMZ 81858, 173888), one *cutucuensis* (LSUMZ 169636), *caucensis* (LSUMZ 32720), *floccus* (LSUMZ 108217) and *lugens* (LSUMZ 30510); we consider the two specimens from San Martín, Peru, to be *H. aureliae cutucuensis* (Oscar Johnson)

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Figure 12. All specimens of Greenish Puffleg *Haplophaedia aureliae cutucuensis* (upper row) and Buff-thighed Puffleg *H. assimilis* (lower row) housed at the Louisiana State University Museum of Natural Science, Baton Rouge. Specimen numbers listed left to right. The blue arrow in the upper row denotes the Marañón Valley, with specimens left of the arrow from north of the Marañón (LSUMZ 172057, 172058, 169635, 172059 and 16936) and specimens to the right of it from south of the Marañón in Colán and the Alto Mayo (LSUMZ 87525, 81857, 81852, 173887, 173888, 173866 and 81858). Specimens in the lower row from left to right are: LSUMZ 190722, 98138, 98139, 98140, 98142, 98141, 90603, 90604 and 90605. Samples of *cutucuensis* from south of the Marañón Valley were originally thought to represent *affinis* (Oscar Johnson)

Further study is clearly needed in this complex. Regardless, no data support the NACC single-species position (a holdover from pre-2000 treatments); instead, the data indicate that the two taxa are best considered separate species.

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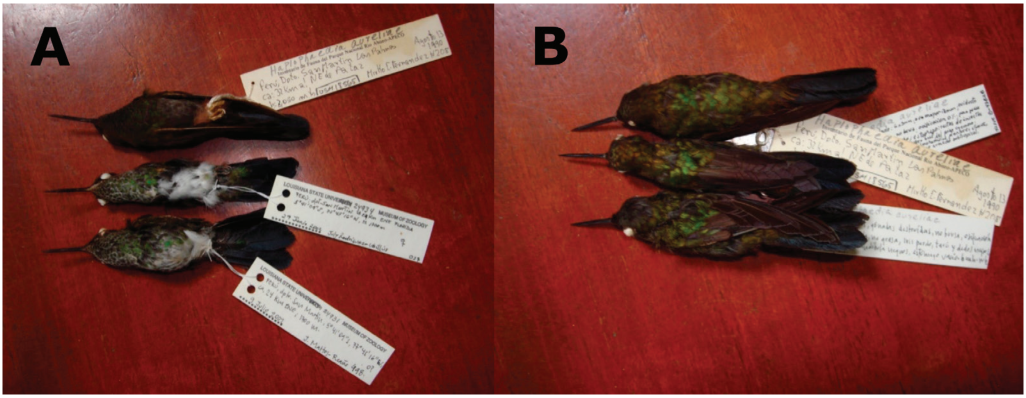

Figure 13. Peruvian specimens of *Haplophaedia* currently housed at the Museo de Historia Natural "Javier Prado" Universidad Nacional Mayor de San Marcos (MUSM) in ventral (A) and dorsal (B) views. In both photos the two lower individuals (LSUMZ 24934, 24931) are from the Alto Mayo, and the upper individual (MUSM 18565) is from 'Pataz' in San Martín, showing that these taxa turn over somewhere between the Mayo and Huayabamba drainages (Daniel F. Lane)

Recommendation.—Given that all major global lists and SACC have been following the Schuchmann *et al*. (2000) treatment for some two decades, and that there does not appear to be any published information that refutes it, we recommend following these sources. However, the published distributional ranges of *H. aureliae cutucuensis* and *H. assimilis affinis* (and thus the southern and northern limits of the two species, respectively) are incorrect.

Next steps.—Committee members generally agreed that the sharp break in phenotype over a short distance, with no sign of intergradation, indicates species rank for both taxa. Although the break between them is much further south than the species break proposed by Schuchmann *et al*. (2000), additional work is needed to determine the precise location of the turnover between *H. aureliae* and *H. assimilis*. Similar data where other taxa in *Haplophaedia* potentially come into contact would likewise be of interest. Quantification of any differences in songs, displays and genetics would elucidate the mechanics of reproductive isolation.

BLACK OYSTERCATCHER *Haematopus bachmani* and BLACKISH OYSTERCATCHER *H. ater*

Background.—Based on NACC proposal 2022-B-9 'Recognize *Haematopus bachmani* (Black Oystercatcher) as a subspecies of *H. ater* (Blackish Oystercatcher)' and SACC proposal 931, neither of which passed. Proposal author: KW.

Oystercatcher taxonomy has been an ongoing challenge due to morphological conservatism. The two general plumage types, black and pied, tend to correspond to rocky vs. soft shoreline specialisation, respectively (Jehl 1985, Hockey 1996). *Haematopus bachmani* Audubon, 1838, has been recognised as a species by the *Checklist* in every edition since the first. The ranges of *Haematopus bachmani* and *H. ater* Vieillot, 1825, are allopatric, so the most appropriate way to determine species limits is to infer them using the classic yardstick comparative method, which involves comparing phenotypic differences to those found between closely related species that are sympatric and therefore valid biological species (although it has been applied infrequently and not with the depth one might hope for; Murphy 1925, del Hoyo & Collar 2014). *Haematopus bachmani* occurs in parapatry with the more widespread American Oystercatcher *H. palliatus* Temminck, 1820, whereas *H. ater* and *H. palliatus* are broadly sympatric on the Pacific coast of South America, and both *H. ater* and *H. bachmani* hybridise with the pied species (Jehl 1978, 1985, Hockey 1996).

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The taxonomic notes provided in the sixth and seventh editions of the AOU Check-list (AOU 1983, 1998) mentioned that some authors had considered *H. bachmani* and *H. palliatus* to be conspecific; there is a hybrid zone *c.*480 km wide in Baja California (Jehl 1985, CBRC 2007). Species status of *H. bachmani* and *H. ater* has not been evaluated by NACC in the past 40 years, and we have no evidence that it was before then, either.

Murphy (1925: 13–15) elaborated the differences and similarities between *H. ater* and *H. bachmani* thus: For *H. bachmani*: 'Juvenal birds closely resemble the young of *H. ater*, the feathers of the upper surface, breast, and flanks being edged with pale tawny brown. It is interesting that the down of chicks of this species is much darker than that of *H. ater* or of any other American form.' And for *H. ater*: 'Superficially resembling *H. bachmani*, *H. ater* is widely separated from all other oyster-catchers in the form of the bill, the excessive compression of which approaches that of *Rynchops*. The distinctive character of the bill is apparent even in chicks taken from the egg. Colour differences between *H. ater* and *H. bachmani* are much greater among downy young than among adults. The young of *ater* are relatively pale, only slightly darker, indeed, than those of *H. palliatus*, which they much resemble. The white area is confined to the breast, instead of covering the belly and flanks as in *palliatus*, but it is far more extensive than in *bachmani*.'

As Jehl (1985) remarked, although AOU (1983) and Murphy (1925) recognised *H. bachmani* and *H. palliatus* as separate species, most other authors at that time did not. For example, *bachmani* and *palliatus* were considered conspecific by Peters (1934), Friedmann *et al*. (1950) and Mayr & Short (1970)—all of these treated *bachmani* and *palliatus* as subspecies of Eurasian Oystercatcher *H. ostralegus* Linnaeus, 1758. This situation has changed, however, and most authorities now recognise *H. palliatus* and *H. bachmani* as separate species (see Avibase; https://avibase.bsc-eoc.org). Thus, Jehl's (1985) work appears to have influenced this issue.

Although Peters (1934) considered *H. palliatus* and *H. bachmani* as subspecies of *H. ostralegus*, he maintained *H. ater* as a separate species. This work did not provide any rationale behind its taxonomic decisions, but taxonomy could have been based on Murphy (1925) or been simply inertia. As Hockey (1996) related, allopatric black forms of *Haematopus* have been considered separate species, whereas pied forms are often considered subspecies.

In his study of the hybrid zone between *H. bachmani* and *H. palliatus*, Jehl (1985) found assortative mating, a stable (though 480 km-wide) hybrid zone (after late-19th and early-20th century disruption), and inferred selection against hybrids, leading him to conclude that the two are valid species. He surmised that the primary mechanism of reproductive isolation was likely postzygotic, focusing especially on predation on chicks of mixed pairs in which some would have plumage coloration inappropriate for their beach colour, i.e., through loss of crypsis. Given the high rates of chick predation in some oystercatcher species (60–85%; Hockey 1996), this selective mechanism seems plausible.

Haematopus ater also hybridises with *H. palliatus* in Argentina; Jehl (1978) described a single hybrid specimen between *ater* and Magellanic Oystercatcher *H. leucopodus* Garnot, 1826 (also a pied form) from Santa Cruz province. This *H. ater* × *H. leucopodus* hybrid is uncommon compared to *H. ater* × *H. palliatus* crossings, which he noted occur in this area of overlap 'with appreciable frequency' (Jehl 1978: 346). Both the *bachmani* × *palliatus* and *ater* × *palliatus* hybrid zones should be revisited with population genetics studies to determine the degrees of introgression (given clearly incomplete reproductive isolating mechanisms).

New information.—Remarkably little modern work is available on *Haematopus* systematics or species limits. Using mtDNA (COI) barcoding, Hebert *et al*. (2004) found that the difference between *H. palliatus* and *H. bachmani* was remarkably low compared to other North American bird species-level differences, and they considered that this was

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consistent with treating them as a single species. Senfeld *et al*. (2020) also examined mtDNA (2,835 bp) and found *H. palliatus*, *H. ater* and *H. bachmani* to be very closely related, with *H. bachmani* perhaps sister to the other two. This clade as a whole is distinct from the pied *H. leucopodus*. Del Hoyo & Collar (2014: 420) considered *H. bachmani* and *H. ater* as conspecific, stating that 'Race *bachmani* has normally been considered a separate species, but the two are almost identical in plumage and voice, apparently differing only in greater depth of bill of nominate *ater*. Two subspecies recognised.' It is worth contrasting this brief emphasis of similarities with Murphy's (1925) emphasis on differences quoted above.

Careful analysis of vocalisations is needed. Subjectively, listening to some of the recordings on Xeno-canto mirrors the mtDNA relationships: *H. bachmani*, *H. ater* and *H. palliatus* are similar, whereas *H. leucopodus* is different. It is perhaps no accident that these similarities and differences are reflected in the rates of hybridisation where the taxa overlap. Future work is also needed to rigorously quantify morphological similarities and differences. Murphy's (1925) evaluations disagree somewhat with del Hoyo & Collar's (2014) conclusions.

With neither appreciable song nor plumage differences between *H. ater* and *H. bachmani*, we suspect that neither assortative mating nor the putative postzygotic isolating mechanism of strong plumage colour selection favoured by Jehl (1985) would be very effective in preventing substantial hybridisation (especially given hybridisation of both with *H. palliatus*). There are, however, differences in bill morphology and downy plumage colour that might be targets of postzygotic selection in hybrids (Murphy 1925). We realise that such conjectures are rather unsatisfactory, but that is one of the acknowledged weaknesses of the Biological Species Concept when asking whether allopatric forms are 'different enough' to warrant recognition as species.

Taxonomy and nomenclature.—*H. ater* Vieillot, 1825, has priority over *H. bachmani* Audubon, 1838. See Murphy (1925) for discussion of the taxonomic history of *H. ater* and its priority for that taxon. Thus, if these two taxa are considered the same species, *H. bachmani* would become *H. ater bachmani*. Murphy's (1925) study of the two supports considering *bachmani* a valid subspecies if lumped with *H. ater*.

Recommendation.—Based on current evidence, especially the strikingly different phenotypes of both *H. bachmani* and *H. ater* vs. *H. palliatus* and the noteworthy levels of hybridisation with the latter pied form, these taxa should be considered a single biological species with two allopatric subspecies-level populations. It is especially compelling that the strikingly different phenotypes of *H. bachmani* and *H. palliatus* appear to be barely limiting hybridisation in a region of overlap to a level that only some authorities (us included) consider to be 'low enough' to be separate biological species. Given the remarkably close mtDNA relationships among *H. palliatus*, *H. bachmani* and *H. ater*, it seems likely that the phenotypic similarities between the latter pair (including vocalisations) would be insufficient to preclude more extensive hybridisation if the two were to come into contact.

Next steps.—Recent research is scant on relationships among *Haematopus* taxa, making this an area ripe for study. Committee members from NACC and SACC were opposed to the taxonomic treatment recommended in this proposal and raised concerns in particular regarding differences in vocalisations. Although data on vocalisations are unpublished, some SACC committee members and commentators noted diagnostic differences in vocalisations between *H. ater* and *H. bachmani* (DFL unpubl. obs.; P. Boesman and A. Jaramillo *in litt*. 2022), including differences in note shape, whether the introductory notes rise or fall in pitch, and in the length of the flight call notes. These potential differences could be the focus of a formal vocal analysis and playback experiments. Thorough quantification of how oystercatcher species limits are shaped by vocalisations, pied vs. all-black plumage, habitat

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(sandy vs. rocky shorelines), and bill shape and size is needed to improve our taxonomic treatments. These studies would benefit from a global analysis, given the apparent repeated evolution of pied vs. all-black plumage in oystercatchers. For *H. ater*, quantification of the degree of hybridisation with *H. palliatus* is of particular interest, as hybrids are thus far known only from Argentina (Jehl 1978), despite widespread sympatry. The bill structure differences and plumage differences in chicks noted by Murphy (1925) provide further support for maintaining *H. ater* and *H. bachmani* as separate species.

HOOK-BILLED KITE *Chondrohierax uncinatus*

Background.—Based on NACC proposal 2022-B-4 'Treat *Chondrohierax wilsonii* (Cuban Kite) as a species separate from *C. uncinatus* (Hook-billed Kite)' which passed. Proposal author: OJ.

Chondrohierax uncinatus (Temminck, 1822) is a widespread polytypic raptor that occurs from central Mexico to Argentina, with three subspecies currently recognised (Clements *et al*. 2021). The nominate is widespread throughout continental parts of its range. The two other widely recognised subspecies are *C. u. mirus* Friedmann, 1934, on Grenada and *C. u.*

Figure 14. Specimens of male *Chondrohierax* (USNM 453087, 383326) in ventral (A) and lateral (B) views, and of females (USNM 453097, 368480) in ventral (C), lateral (D) and dorsal (G) views, housed at the National Museum of Natural History, Washington, DC. Specimens of *Chondrohierax* in ventral (E) and lateral (F) views housed at Louisiana State University Museum of Natural Science, Baton Rouge. Although the bird on the left in E and F is labelled a male, it is possibly a female or subadult male based on plumage. In each photo, *C. wilsonii* is on the left, *uncinatus* is on the right (© Jacob Saucier: A–D and G, Marco Rêgo: E–F)

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Figure 15. Hook-billed Kite *Chondrohierax uncinatus uncinatus* showing geographic variation in continental populations, in ventral (A), lateral (B) and dorsal (C) views. Two male *uncinatus* (darker bird from Mexico [USNM 144167], typical male from Colombia [USNM 383326]) on left, typical female *uncinatus* (USNM 368480) on right (© Jacob Saucier)

wilsonii (Cassin, 1847) in Cuba. Friedmann (1934) described, as subspecies, the populations from northern and central Mexico (somewhat darker; '*aquilonis*') and western Amazonia (larger bill and broader rectrices; '*immanis*'), but neither is generally recognised. The array of plumage variation within all taxa is confusing and includes strong sexual dimorphism, distinct juvenile plumages, and a dark/melanistic morph in both adults and juveniles. A white-bellied morph bears a strong resemblance to comparable plumages of some forest falcons (*Micrastur*), at least in juveniles. Additionally, individual variation is considerable, especially in bill size, with especially large-billed birds originally described as a separate species ('*megarhynchus*'; now considered a synonym of *uncinatus*; see Friedmann 1934, Hellmayr & Conover 1949).

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TABLE 2

Mensural data for three taxa of *Chondrohierax*. Data from Friedmann (1950). Means in parentheses, where available. Bill length is the length of the culmen from the cere. Toe length is the length of the middle toe without the claw. All measurements in mm.

Taxon	**Sex**	**Wing length**	**Tail length**	**Bill length**	**Tarsus length**	**Toe length**
C. u. uncinatus	Males (*n* = 26)	265–301 (285.8)	173–210 (191.1)	27.0–35.5 (31.3), one 42.0	32.0–37.0 (35.1)	28.0–35.0 (31.1)
	Females (*n* = 31)	268–321 (284.9)	191–228 (202.8)	28.0–37.0 (31.6), one 43.5	31.0–37.0 (33.8)	28.0–34.0 (30.9)
C. u. mirus	Males (*n* = 3)	250–265 (257)	165–182 (172.7)	28–32 (30)	30–38 (34.5)	25
	Females (*n* = 2)	269–270	180–183	30	41	31
C. wilsonii	Males (*n* = 2)	240–244	177–178	35.5–37.5	29–30	26–27
	Females (*n* = 2, including the lectotype)	251–262	181–188	35.0–38.5	28–30	28–29

Morphological differences among the three taxa were well described by Friedmann (1934, 1950) and are summarised here. In his key to *Chondrohierax*, Friedmann (1950) considered the main difference between *C. u. wilsonii* and the other taxa to be: 'upper mandible [*sic*] pale yellowish white, inclining to bluish horn at base; feathers of upperparts with concealed white bars on their bases'. Friedmann (1950) also mentioned the solidly tawny nuchal collar of female *uncinatus* in contrast to the 'white or pale buff [nuchal collar], barred with russet or chestnut' of female *wilsonii* (males have no nuchal collar), as well as the narrower barring below on *wilsonii*. Friedmann's other mainland subspecies ('*aquilonis*' and '*immanis*') were separated based largely on the saturation of the overall coloration (i.e., minor differences), so although individual variation is considerable, differences among continental populations are few. The mostly yellow bill and barred vs. unmarked nuchal collar seem to be the most consistent characters separating *C. u. wilsonii*. The rationale used by del Hoyo & Collar (2014) for considering *C. u. wilsonii* a separate species included the smaller size and larger bill, so we have included measurements from Friedmann (1950) for *C. u. uncinatus*, *C. u. mirus* and *C. u. wilsonii* in Table 2. These size differences seem minor and given that bill size especially is known to vary drastically among individuals within *C. u. uncinatus*, these differences are unlikely to be useful as species-level characters. Wing length does appear substantially shorter in *C. u. wilsonii* than in *C. u. uncinatus*, however.

Taxon *wilsonii* was described as a species by Cassin (1847) and considered as such by most authors (e.g., Peters 1931, Friedmann 1934, 1950, Bond 1940) until Amadon (1960) treated it as a subspecies of *C. uncinatus*. He cited considerable individual variation in bill size in *C. uncinatus* (i.e., Hellmayr & Conover's justification for treating *megarhynchus* as a synonym of *uncinatus*) to suggest that the difference in bill size between *C. u. wilsonii* and *C. u. uncinatus* was insufficient for species status. Friedmann (1934) also listed the concealed white barring on the back as a character for separating *C. u. wilsonii*, but Amadon (1960) noted that this can be present in immatures of *C. u. uncinatus*. Amadon (1960) also suggested that the mostly pale maxilla of *C. u. wilsonii* may not be a species-level character, because the pale colour of the mandible can extend onto the maxilla in some *C. u. uncinatus*. However, based on photographs of live birds, the pale coloration on the bill of *C. u. uncinatus* is largely restricted to the lower part of the cere, rather than the maxilla. Therefore, Amadon's (1960) primary justification for considering *wilsonii* a subspecies of *C. uncinatus* was that

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Figure 16. Specimens of Hook-billed Kite *Chondrohierax uncinatus mirus* of Grenada in ventral (A), lateral (B) and dorsal (C) views. In each photo male (USNM 353659) on left, female (USNM 353658) on right (© Jacob Saucier)

differences in bill size and in the hidden white bases to the dorsal feathers were shown by other taxa of *Chondrohierax*, and that bill colour alone was insufficient to treat *C. u. wilsonii* as a separate species.

Later authors (e.g., AOU 1983, Howard & Moore 1991, Clements 2007, Clements *et al*. 2021) consistently treated *wilsonii* as a subspecies of *C. uncinatus* (following Amadon 1960),

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until del Hoyo & Collar (2014), using the Tobias point system (Tobias *et al.* 2010), elevated *C. wilsonii* to species status with the following rationale: 'Until recently was considered conspecific with *C. uncinatus*, but trend now widespread to accept species status: differs on account of all-yellow bill (3); larger bill (at least 1); barred collar (2); smaller overall size (at least 1). Molecular evidence has been interpreted as supporting this split (Johnson *et al*. 2007).' Note, however, that the bill lengths of *wilsonii* and *uncinatus* overlap slightly (Table 2). The IOC list split *wilsonii* based on morphological differences and modest mtDNA divergence (Gill *et al*. 2022). See Kirwan & Kirkconnell (2022) for details of the taxonomic history of *wilsonii*.

New information.—Very little. Results from a genetic study (Johnson *et al*. 2007) were the basis for NACC proposal 2007-B-4 to split *wilsonii* from *C. uncinatus*, which did not pass (the vote was 5-5). To our knowledge, there has been no additional work on the genus relevant to taxonomy. No recordings of *wilsonii* are known, but the voice is described as 'whistles similar to Hook-billed Kite' (Kirwan *et al*. 2019). A single in-life photo has been published but is of too poor quality to assess the characters that distinguish these taxa (see p. 23: https://www.aba.org/birding_archive_files/v42n1p22.pdf), and at least one NACC member doubted whether this photo is correctly identified, suggesting it may instead represent a species of *Accipiter*.

Taxon *wilsonii* is Critically Endangered, or possibly extinct, with very few sightings in recent years, despite several focused surveys (Gallardo & Thorstrom 2019, BirdLife International 2021). It may now be restricted to a remnant population in the mountains of the far east of the island (Gallardo & Thorstrom 2019, Kirkconnell *et al*. 2020). Its declines are attributed to loss of habitat, loss of its main prey item (snails) and persecution due to the mistaken belief that it hunts gamebirds. Conservation status does not have any bearing on taxonomic decisions, but the lack of new data makes a decision on species status difficult. There are almost 40 specimens in collections worldwide (Kirkconnell *et al*. 2020), of which we have access to a small series, which combined with the detailed descriptions of Friedmann (1934, 1950; see above) can help with the analysis. Additional information can be found in the 2007 NACC proposal.

Jacob Saucier and Marco Rêgo graciously photographed some of the series of *Chondrohierax* housed at USNM and LSUMZ (Figs. 14–16). These include photos of *wilsonii*, *uncinatus* and *mirus*, although the USNM specimen of female *wilsonii* (USNM 453097) is unfortunately rather faded. In all photos, note the pale bill and narrower but more extensive barring below of *wilsonii* compared to *uncinatus*/*mirus*. The LSUMZ *wilsonii* specimen (LSUMZ 141440) is labelled as a male, but the brown dorsum, narrow tail bars and barred nuchal collar all suggest it is a female (or perhaps a subadult male). The USNM male *wilsonii* (USNM 453087) has an unbarred nuchal collar and is greyer above. From these photos, it appears that both sexes of *mirus* show an unbarred tawny nuchal collar, whereas this character is found only in females of *uncinatus*. The specimens of *wilsonii* that possess a nuchal collar have this area barred rather than unbarred tawny, although in the female USNM specimen this region is too faded to assess the original colour.

Johnson *et al*. (2007) sequenced just two mitochondrial genes, cyt-b and ND2 (so all the standard gene tree/species tree caveats apply) but found that *C. u. wilsonii* was sister to the remainder of *Chondrohierax* and 1.8–2.0% divergent, with a divergence time estimate of 400,000–1.25 million years. Both the phylogeny and haplotype network of Johnson *et al*. (2007) showed that the Grenada taxon *mirus* was largely undifferentiated at those loci from continental populations (*C. u. uncinatus*). Johnson *et al*. (2007) estimated migration rates between North and South American populations of *C. u. uncinatus*, but not between *C. u. uncinatus* and either of the insular taxa. However, within *C. u. uncinatus* they were

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close to zero (albeit with broad confidence intervals), perhaps suggesting that there is low connectivity even within continental populations.

Recommendation.—The comparative genetic distances between *C. u. wilsonii* and *C. u. uncinatus*/*mirus* are borderline regarding species status, especially given that it is based on only two mitochondrial genes, so are not as informative as one would like. The morphological differences do seem quite pronounced for a raptor, however. The combination of the solid yellow bill of *C. u. wilsonii* and differences in the pattern of the nuchal collar and width and extent of the barring below, all afford *C. u. wilsonii* quite a different appearance. Furthermore, geographic variation within the remainder of the widely distributed *Chondrohierax* is minor; thus, *C. u. wilsonii* is the morphological outlier within the genus. We recommend that *wilsonii* be treated as a separate species from *C. uncinatus*. The English name of Hook-billed Kite could stay with *C. uncinatus*, given that *wilsonii* is a peripheral isolate. The name Cuban Kite, already used by BirdLife International and the IOC checklist, is appropriate for *C. wilsonii*.

Next steps.—Little is known of the natural history or vocalisations of *C. wilsonii*, which is unsurprising given its rarity. Future research could focus on locating remaining individuals and documenting as much of the species' natural history as possible to aid its conservation.

SHARP-SHINNED HAWK *Accipiter striatus*

Background.—Based on NACC proposal 2022-B-5 'Treat *Accipiter chionogaster* (White-breasted Hawk) as a separate species from *A. striatus* (Sharp-shinned Hawk)', which did not pass. Proposal author: SMB.

Accipiter striatus Vieillot, 1808, is a small raptor widespread throughout North America, Middle America, the Caribbean, and parts of South America. Most authorities recognise ten subspecies, which are usually divided into three main subspecies groups. Across this broad distribution and these taxa, variation in plumage, differences in ecology and possible differences in behaviour are extensive (Bildstein *et al*. 2020). Given this, Sharp-shinned Hawk as currently recognised on the *Checklist* has at times been treated as up to four species, although it is more typically regarded as comprising three or four groups: northern migratory *striatus* (which itself is sometimes divided into a northern migratory *velox* (A. Wilson, 1812) group and a Caribbean resident *striatus* group), white-breasted *chionogaster* (Kaup, 1852) of southern Middle America, and rufous-thighed *erythronemius* (Kaup, 1850) of South America. Of the four main global checklists, only Gill *et al*. (2022) recognises four species in the complex, including *A. striatus* (including the *velox* group), *A. chionogaster*, *A. ventralis* P. L. Sclater, 1866, of northern South America, and *A. erythronemius*, following the treatment of Ferguson-Lees & Christie (2005). The other major world checklists treat the complex as a single species.

New information.—Little new information sheds light on this complex. In comparing *A. s. chionogaster* to the 'northern' group, the main difference is in plumage of adults, with the *chionogaster* group having clean white underparts with some pale buff on the tibial feathers, compared to the rich rufous to orange barring on the underparts of northern birds. *A. s. chionogaster* tends also to be darker above, being described as 'sooty to fuscous black' vs. 'gray to grayish blue' (Bildstein *et al*. 2020). The juvenile plumage of *A. s. chionogaster* has similarly pale underparts and is very lightly streaked below compared to northern subspecies (Storer 1952).

Although *A. s. chionogaster* differs significantly in plumage from the widespread and migratory *A. s. velox* of North America, *A. s. suttoni* and *A. s. madrensis* of Mexico (mountains of Chihuahua, Sonora, south to Veracruz; and Sierra Madre del Sur in Guerrero and Oaxaca, respectively) are intermediate between *A. s. velox* and *A. s. chionogaster*. The underparts of

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A. s. suttoni are paler than those of *A. s. velox*, and *A. s. madrensis* is paler than *A. s. suttoni*. This pattern suggests that *A. s. chionogaster* is just the pale extreme of a step cline (Storer 1952, Bildstein *et al*. 2020). Although the distribution of *A. s. chionogaster* is separated from *A. s. madrensis* by the Isthmus of Tehuantepec, an important biogeographic barrier, Storer (1952) suggested that the paleness of *A. s. madrensis* could be the result of introgression from *A. s. chionogaster*, which influenced his decision to consider *chionogaster* conspecific with *A. striatus*.

Subspecies *chionogaster* is similar in size to northern birds. Dickey & van Rossem (1938) reported that the only difference between *A. s. chionogaster* and northern *A. s. velox*, which is sympatric with *A. s. chionogaster* in winter, was the slightly longer bill and longer middle toe of *A. s. chionogaster* (Jenner 2010); northern *A. s. velox* and *A. s. chionogaster* overlap in wing and tail length (Storer 1952). In a supertree generated by Mindell *et al*. (2018), *A. s. chionogaster* was sister to the *striatus* group, with very short branch lengths. However, only three subspecies of *A. striatus* were sampled. In a recent study by Catanach *et al*. (2021), ultraconserved elements (UCEs) were used to study the systematics of Sharp-shinned Hawks, with a focus on Caribbean taxa. In addition to the island subspecies, this study included samples of some mainland taxa, including *chionogaster*, *velox*, *ventralis* (mountains from Venezuela to Bolivia) and *erythronemius*. They found that *A. s. chionogaster* was sister with strong support to *A. s. velox*, with these two sister to *A. s. ventralis*. These three were in turn sister to the clade of Caribbean taxa (Catanach *et al*. 2021). However, because Caribbean taxa were the focus, additional work is needed to further clarify relationships among the taxa from North, Middle and South America, especially to address the potential for gene flow among these phenotypically variable and geographically widespread groups.

Jenner (2010) described the vocalisations and various aspects of the life history of *A. s. chionogaster*, including its breeding biology and moult patterns. The post-juvenile moult (preformative moult of Howell *et al*. 2003) of *A. s. chionogaster* in Honduras and El Salvador was completed in most individuals before the breeding season in their second calendar year, meaning that birds acquired adult-like plumage prior to their first breeding season; the same moult in *A. s. velox* begins near the start of the breeding season in their second calendar year (Bildstein *et al*. 2020). The early progression of moult in *A. s. chionogaster* perhaps contributed to the higher proportion of first-year birds breeding compared to other taxa (Jenner 2010). The courtship display of *A. s. chionogaster* was described as similar to that of other *Accipiter*, although some birds rock back and forth in the air so that the white underparts seemed to be prominently displayed. If display of the white underparts is an important aspect of courtship, it could represent a potential pre-mating barrier (Jenner 2010). Courtship began in October, and the breeding season lasted for *c*.9 months in Honduras and El Salvador; importantly, courtship and pair formation at these two locations occur before most northern migrant Sharp-shinned Hawks (*velox* group) arrive in the area, suggesting temporal reproductive isolation between them (Jenner 2010).

Recommendation.—The Sharp-shinned Hawk complex is extremely variable in plumage and is widely distributed in North and South America. As others have recognised, the three to four groups may each represent distinct species (e.g., Sibley & Monroe 1990, Bierregaard 1994, Ferguson-Lees & Christie 2005, Gill *et al*. 2021). Differences in moult timing, potential differences in courtship displays, and the timing of breeding of *A. s. chionogaster* relative to the northern migrant *velox* group could all represent important species-level differences, although they are expected within a species with such a broad latitudinal distribution. However, to date, there are no phylogeographic, population-level studies of genetic diversity within mainland taxa that could shed important light on the status of not only *A. s. chionogaster*, but also the South American taxa.

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Although we predict that additional data will show that *A. s. chionogaster* represents a separate biological species, we recommend it be maintained as a subspecies of Sharp-shinned Hawk for the time being, until additional data become available.

Next steps.—Genetic work with greater geographic sampling is needed to quantify genetic differences and degree of gene flow among continental taxa. Work is needed especially on describing variation in vocalisations (particularly the 'long call') and displays. Analyses of plumage variation are needed but should also be compared to the degree of intraspecific plumage variation in other *Accipiter*. There is a need for an analysis of the putative step clines in plumage, with adequate geographic sampling across the entirety of the cline.

ELEGANT TROGON *Trogon elegans*

Background.—Based on NACC proposal 2022-A-7 'Recognize *Trogon ambiguus* (Coppery-tailed Trogon) as a separate species from *T. elegans* (Elegant Trogon)', which did not pass. Proposal author: JVR.

Trogon elegans Gould, 1834, currently consists of two groups separated by a range gap in the Isthmus of Tehuantepec: the *ambiguus* Gould, 1835, group (Coppery-tailed) north of the Isthmus (south-east Arizona to south-west Mexico) and the *elegans* group (Guatemala to north-west Costa Rica). The two groups have long been known to differ in some key plumage features. Each group comprises two subspecies.

Ridgway (1911) treated the two groups as separate species. His key separated them by tail colour (coppery to golden in *T. e. ambiguus* and *T. e. goldmani*; greenish bronzy in *T. e. elegans*) and pattern of the lateral rectrices (vermiculated in *T. e. ambiguus* plus *goldmani*; barred in *T. e. elegans*). Cory (1919) followed Ridgway (1911). Peters (1945) lumped them into a single species without providing rationale (and we could not find anything published to support Peters' treatment). Eisenmann (1955) also treated them as conspecific. The AOU (1957) treated them as conspecific and called the combined species 'Coppery-tailed Trogon'. Mayr & Short (1970) treated it as an uncomplicated polytypic species (i.e., no concerns on species limits). On the other hand, Oberholser (1974) continued to treat *T. ambiguus* as a separate species, writing:

> This species is generally considered a subspecies of *Trogon elegans*. This treatment appears to have developed from the seeming intergradation evident when comparing female and immature birds, or those in transition plumage. Fully adult males of *Trogon ambiguus ambiguus* are entirely distinct in lacking the regular narrow black barring of the three outer tail feathers, which is so conspicuous and characteristic a feature of *T. elegans*, and which is very different from the mottled appearance of the same feathers in *T. ambiguus*. Examination of a large number of specimens shows no indication of intergradation in this respect. Even in the female of *T. elegans* the outer tail feathers are more numerously and regularly barred with black than are the same feathers in the adult female of *T. ambiguus*. Thus, it would seem to be more representative of the true relationships of these two birds to consider *T. ambiguus* a distinct species. Van Rossem has described the bird from n.w. Mexico as *Trogon elegans canescens*,[1] but the bird from e. Mexico, which race has occurred in extreme s. Texas, is the "Typical," or nominate form, *T. a. ambiguus*.

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[1] *Bull. Mus. Comp. Zool.* 77 (Dec. 1934): 441 (San Javier, Sonora, Mexico).

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The AOU (1983) treated them as conspecific, with only the statement: 'sometimes regarded as a separate species, *T. ambiguus*'. Howell & Webb (1995) also treated them as conspecific. The AOU (1998) treated them as conspecific but recognised the two groups: 'Notes.—Groups: *T. ambiguus* Gould, 1835 [Coppery-tailed Trogon] and *T. elegans* [Elegant Trogon].' Collar (2001) treated them as conspecific but mentioned the two groups. Dickinson & Remsen (2013) treated them as separate groups but also cited Oberholser (1974) as evidence for a possible return of species rank to the *ambiguus* group. Knowing that this was a data-free Peters (1945) lump followed uncritically by subsequent authorities, Dickinson & Remsen (2013) were tempted to reinstate *ambiguus* as a species but did not want to conflict with the current AOS treatment (*fide* JVR); also, with a substantial lowland gap between the two, Oberholser's (1974) point on lack of intermediates is nearly irrelevant.

New information.—Nothing really new. Del Hoyo & Collar (2014) treated them as separate species and outlined the well-known plumage differences between the two (see Fig. 17). These authors argued that *ambiguus* is:

> Usually considered conspecific with *T. elegans*, although for long recognised as distinctive: differs in its finer-grained vermiculations on wing panel (1); overall golden tone to green of breast, hindcrown and upperparts, the same gene presumably responsible also for uppertail being bronzy-coppery rather than yellowish blue-green (3); undertail pattern without close bold barring but instead with vague, incomplete vermiculations and with outer vane of outer rectrix all white, so that undertail looks almost entirely white (3).

Genetic data.—Monteros (1998) treated *T. e. elegans* and *T. e. ambiguus* as conspecific; although his GenBank accession suggests two individuals, they were not separated in the

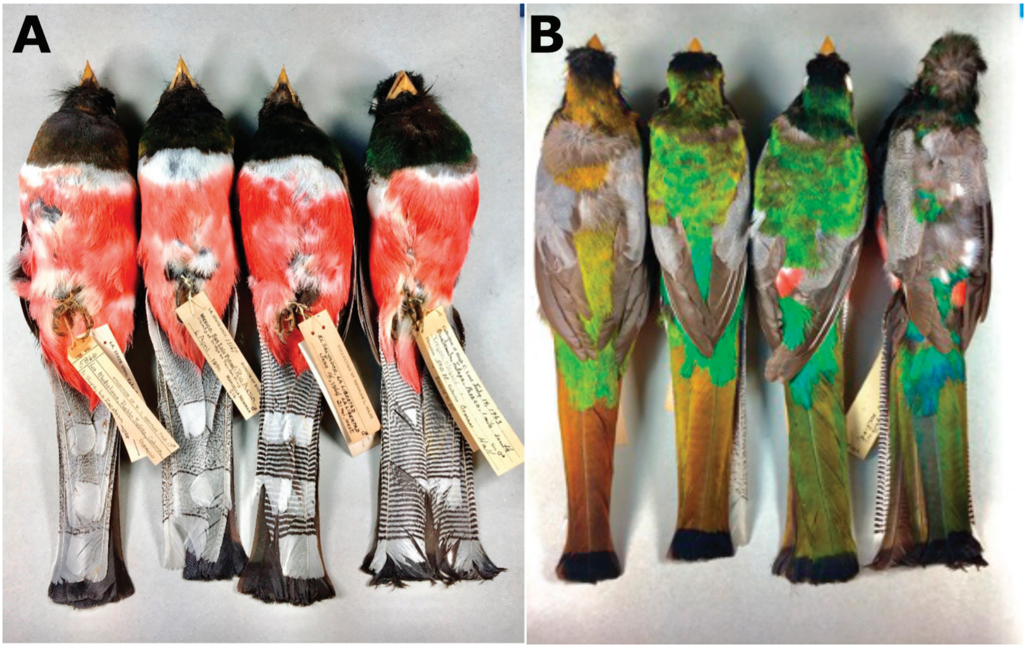

Figure 17. Male specimens of Elegant Trogon *Trogon elegans* in ventral (A) and dorsal (B) views. In each photo, the left two specimens are of *ambiguus*, and the right two are *elegans*; left to right: LSUMZ 40305, 15167, 50543 and 65719 (Oscar Johnson)

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analysis and their origin was not given. Moyle (2005) included only one representative, a sample of *T. e. elegans* from El Salvador. DaCosta & Klicka (2008) included single samples from El Salvador and Mexico; unsurprisingly, they were sister taxa, and the genetic distance was small.

Voice.—No analysis has been published, but Xeno-canto has many recordings of the songs of both groups. Both share an unusually hoarse, somewhat frog-like repeated syllable that is much raspier and less mellow than those of other *Trogon* songs. However, they do suggest that a formal analysis would reveal that *T. e. ambiguus* has a faster delivery with more syllables than does *T. e. elegans*. A recording of *T. e. ambiguus* from Sonora (XC 450735), and one of *T. e. elegans* from Costa Rica (XC 6773) illustrate the potential differences that require quantification.

Discussion and Recommendation.—Trogon species limits are associated with vocal differences, not plumage differences. In fact, Dickens *et al*. (2021) showed specifically that the same set of plumage differences noted by del Hoyo & Collar (2014) above differ among the three Amazonian subspecies of *T. rufus* J. F. Gmelin, 1788, yet each of them intergrades wherever in contact. *T. rufus* being the sister lineage to *T. elegans*, inference based on the biology of closely related taxa (the 'yardstick method') indicates that these plumage characters are not meaningful in terms of barriers to free gene flow yet are considered positive evidence for treating two taxa as species by Tobias *et al*. (2010).

This is yet another case of an old decision to treat two distinctive taxa as conspecifics based solely on plumage similarities and virtually no explicit rationale. Further, an analysis of plumage characters in the sister lineage shows that these are not barriers to gene flow, whereas a perusal of online recordings of voices further hints that the decision to treat the two groups as conspecific was unjustified. Nevertheless, our recommendation is to maintain *ambiguus* as a subspecies of *T. elegans*, pending a formal analysis of voice.

Note on English names.—If *T. e. ambiguus* were to be elevated to species status, then the sensible names, consistent with NACC guidelines, would be to restrict Elegant Trogon to *T. elegans* and resuscitate Coppery-tailed Trogon for *T. ambiguus*, i.e., returning to the historical names for the species prior to their treatment as conspecific.

Next steps.—Most committee members considered a formal analysis of vocal differences to be critical to determining species limits in this group, especially to assess potential overlap in vocal characters between the two subspecies groups. An analysis of genetic variation within and between the two groups might be instructive, particularly if samples were obtained close to the Isthmus of Tehuantepec.

AMERICAN THREE-TOED WOODPECKER *Picoides dorsalis* and EURASIAN THREE-TOED WOODPECKER *P. tridactylus*

Background.—Based on NACC proposal 2023-C-3 'Treat American Three-toed Woodpecker *Picoides dorsalis* as a subspecies group of *P. tridactylus*', which did not pass. Proposal author: KW.

Adoption of the species limits advocated here would change *Picoides dorsalis* Baird, 1858 (American Three-toed Woodpecker) to a subspecies group of *Picoides tridactylus* (Linnaeus, 1758) (the English name for which is presently Eurasian Three-toed Woodpecker but which would thus be best rendered as Three-toed Woodpecker). This is how NACC treated this complex in the last four print editions of the *Checklist* (1931–98), only changing the English name after the fifth edition (deleting 'Northern' from Three-toed Woodpecker), then later treating *P. dorsalis* as a species (Banks *et al*. 2003). There are three North American subspecies: *dorsalis*, *fasciatus* and *bacatus*; all three would revert to being subspecies of *P.*

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tridactylus sensu lato (e.g., AOU 1931–98, Peters 1948, Short 1982, Winkler *et al*. 1995, Winkler & Christie 2002).

In brief, prior to adoption of the Biological Species Concept (BSC), *dorsalis* (under the name *americanus*, which was subsequently synonymised with *dorsalis*, though see discussion in Tremblay *et al*. 2018) was often considered a species, and then it was generally treated as a subspecies of *P. tridactylus*. After AOU (1931), NACC treated it this way until Banks *et al*. (2003), who wrote:

> New World and Old World populations of Three-toed Woodpeckers are split on the basis of differences in mitochondrial DNA (Zink *et al*. 1995, 2002) and voice (Winkler & Short 1978, Short 1982). Ridgway (1914) considered New World and Old World populations to be separate species, and the merger of New World *dorsalis* into Old World *tridactylus* (e.g., AOU 1931, Peters 1948) was never explained.

The editorial style constraints of AOU (1931) and the 'Peters' *et al*. volumes generally (if not completely) precluded authors from explaining their treatments in detail. The implicit explanation, of course, was their recognition that phenotypic differences were, relatively speaking, more in line with subspecies treatment under the BSC. Concordance in this treatment was broad, and, basically, it is this phenotypic similarity, now quantified (del Hoyo & Collar 2014; see below) that brings us back to this issue today.

In contrast to Banks *et al*. (2003), Winkler & Short (1978) and Short (1982) noted vocal differences between North American and Eurasian birds but did not consider them sufficiently different to suggest these groups should be considered biological species. As Winkler & Short (1978: 16) wrote:

> The Call Note of Central European birds (Germany, Austria) is shaped like a broad arrowpoint, with the fundamental tone emphasised and possesses significant introductory and ending elements (fig. 3L, M, table 2; see Ruge 1975). Swedish birds have essentially the same calls. North American birds (New York) are different in all their measurable characters. Unfortunately, our recordings are insufficient for comparison of these geographical groups. This species, the only Holarctic woodpecker, would be an ideal subject for the study of geographical variation ...

In general, authors of monographs on woodpeckers operating without the editorial constraints of the AOU *Checklists* or the Peters volumes (e.g., Winkler & Short 1978, Short 1982, Winkler *et al*. 1995) considered the evidence to treat these taxa as one biological species sufficiently strong that they did not mention the possibility of a species-level split, despite repeated opportunities to do so.

Enter mtDNA. Analyses of and inference from three mtDNA datasets for these taxa have been published, and all three sets of authors recommended a species-level split. The first study (Zink *et al*. 1995) was a small sample (n = 9) using restriction fragment length polymorphisms (RFLPs) to compare Eurasian and North American populations, which found *c*.5.5% divergence. The second study (Zink *et al*. 2002) used more birds (n = 29), broader geographic sampling and 1,234 bp (from ND2, ND3, and cyt-*b*) and found 3.8% divergence. The third mtDNA dataset is that of Johnsen *et al*. (2010), who used mitochondrial COI barcode data (sampling details not published) to report a 3.7% COI divergence. (In addition, KW has access to a small as-yet unpublished mtDNA dataset indicating that between continents the birds are *c*.2.5% divergent in ND2 using Jukes-Cantor corrected *p*-distance (KW, Univ. of Alaska Museum, unpubl. data, 2023).

The mtDNA data are intriguing, and they played a prominent role in splitting these taxa. With genetic data available, Winkler & Christie (2002) also split the two groups into separate species. But that was a time when we were still relying on the powers of mtDNA to diagnose species limits, which most now know can be incorrect.

Plumage variation of the entire complex is rather pronounced, showing that there is quite a bit of variation occurring without much mtDNA variation to correspond with it; the continental clades show little if any structure (see Zink *et al*. 2022). Finally, as Winkler & Short (1978) noted, when *P. tridactylus* is treated as a single species, it is the only Holarctic woodpecker.

New information.—Currently, the world lists treat *P. dorsalis* either as a species (Dickinson & Remsen 2013, Clements *et al*. 2022) or as a subspecies group of *P. tridactylus* (del Hoyo & Collar 2014, Gill *et al*. 2022).

Between Winkler & Christie (2002) and del Hoyo & Collar (2014), the Tobias *et al*. (2010) method was applied to this taxonomic question and the two groups scored so low (*c*.2) that they were again considered conspecific. Del Hoyo and Collar (2014) discussed the situation thus:

> In recent decades North American subspecies commonly treated as forming a separate species (*P. dorsalis*) on basis of genetic evidence (Johnsen *et al*. 2010), but morphological differences involve merely narrower postocular stripe (1) and smaller size (according to published measurements, no more than 1); all-white outer tail feathers shared by East Asian subspecies *albidior* and *crissoleucus*, and notion of less white in forecrown not supported by specimen evidence. Distinctive form *funebris*, however, here allowed species status (see related note/s). Currently accepted subspecies designated according to coloration, but variation is clinal, birds becoming darker and larger from N to S; comprehensive revision based on genetic and biogeographical grounds required.

Note, however, that the del Hoyo & Collar (2014) treatment effectively ignores genetic differences: genetic data do not form part of the Tobias *et al*. (2010) scoring methodology. Although the mtDNA data are equivocal, they are intriguing. Study of the nuclear genome is warranted (and likely forthcoming).

Recommendation.—Although it is likely that a proposal to split these taxa today based on current information would not pass and that single-species status is probably warranted, we recommend maintaining the two-species treatment for now. The phenotypic evidence alone suggests single-species treatment, but the mtDNA data indicate that substantial divergence has occurred. However, until we possess nuclear data, it would be premature to make another change based essentially on different opinions about a body of evidence that has not really changed much. In other words, it would be better to eventually make one change if clearly needed and not risk having to reverse a change if the future nuclear data (and perhaps that much-needed comparative work on voice across the range) do end up supporting the current taxonomic treatment.

Next steps.—As noted in the proposal, more comprehensive genomic work on the complex is needed, as well as a quantitative analysis of vocal differences. Committee members noted possible vocal differences, including the drumming of *dorsalis* diminishing near the end instead of ending abruptly and the *pik* notes sounding higher-pitched, and European birds having a lower-pitched, richer call. This is supported by the vocal differences between the two groups noted by Winkler & Short (1978), although they had recordings from only a few localities. Unfortunately, vocal data appear to be lacking for most of the eastern Palearctic taxa.

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GOLDEN-OLIVE WOODPECKER *Colaptes rubiginosus*

Background.—Based on NACC proposal 2023-C-4 'Treat *Colaptes aeruginosus* as a separate species from Golden-olive Woodpecker *C. rubiginosus*', which did not pass. Proposal author: RTC. Additional information added post-proposal by DFL & OJ.

Colaptes rubiginosus (Swainson, 1820) is currently treated by NACC and SACC as a highly polytypic species ranging from north-east Mexico south to north-west Argentina. Under this classification, *C. r. aeruginosus* (Malherbe, 1862) is the northernmost subspecies, distributed from Nuevo León and Tamaulipas south to central Veracruz. The main plumage differences between *C. r. aeruginosus* and the geographically closest subspecies of *C. rubiginosus* (*C. r. yucatanensis* S. Cabot, 1844, which is found from southern Mexico to Panama) are the extent of the red supercilium on the male, which extends only from the nape to behind or above the eye in *C. r. aeruginosus* but from the nape to the bill in *C. r. rubiginosus*; the rear ear-coverts, which are plain in *C. r. aeruginosus* but barred in *C. r. rubiginosus*; the shape of the barring on the underparts, which is wavy or scale-shaped in *C. r. aeruginosus* but straight in *C. r. rubiginosus*; and the proportionately longer tail of *C. r. aeruginosus*.

Standard taxonomic references from the first half of the 20th century, e.g., Ridgway (1914), Cory (1919) and Peters (1948), considered the current NACC species *C. rubiginosus* to consist of more than one species but had different views of species limits. Ridgway (1914) considered *C. rubiginosus sensu lato* to consist of four species: *C. aeruginosus*, *C. rubiginosus*, *C. chrysogaster* (von Berlepsch & Sztolcman, 1902) of Peru, and *C. gularis* (Hargitt, 1889) of Colombia. Cory (1919) merged *gularis* into *C. rubiginosus* and thus recognised only three species: *C. aeruginosus*, *C. rubiginosus* and *C. chrysogaster*. Peters (1948) further merged *chrysogaster* into *C. rubiginosus* and thus recognised only two species: *C. aeruginosus* and *C. rubiginosus*. The latter two were first considered conspecific by Baptista (1978), who identified intermediates in the vicinity of Xalapa and Córdoba in central Veracruz. Short (1982) followed Baptista (1978) in treating *aeruginosus* as a subspecies of *C. rubiginosus*, noting that the differences between the two fall within the scope of variation shown by the other 17 subspecies of *C. rubiginosus*. Short (1982) specifically mentioned subspecies *tucumanus* (Cabanis, 1883) of the southern Andes, as follows: '[*aeruginosus*] is judged to be no more distinct than other ones such as *tucumanus*, and it shares the sexual dimorphic pattern of other races of *rubiginosus*'. The latter statement is a reference to the closely related *C. auricularis* (Salvin & Godman, 1889), which is less sexually dimorphic in crown coloration. We note, however, that despite some plumage similarities, vocalisations between *C. auricularis* and *C. rubiginosus* are distinct.

Indeed, the plumage differences shown by *C. r. aeruginosus* represent only a small part of the variation within *C. rubiginosus*, and some of the characters that purportedly distinguish *C. r. aeruginosus* from the rest of *C. rubiginosus* are highly variable within *C. rubiginosus*. For example, the extent of the red on the head varies from a rather short supercilium in *C. r. paraquensis* (Phelps & Phelps Jr., 1948) and *C. r. guianae* (Hellmayr, 1918), in addition to *C. r. aeruginosus*, to covering most or all of the head in subspecies such as *C. r. gularis*; the rear ear-coverts are also variable. Other characters that differ among subspecies of *C. rubiginosus* include ventral coloration and the extent and colour of the ventral barring. The shape of the barring, however, does appear to distinguish *aeruginosus* from other subspecies of *C. rubiginosus*, and is the only qualitative feature mentioned by Ridgway (1914) in his key to the complex. Ridgway (1914) distinguished *C. aeruginosus* by the 'Chest and breast irregularly barred or squamate; larger (wing averaging more than 130; tail more than 85)' whereas *C. rubiginosus* was characterised by the 'Chest and breast regularly barred; smaller

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(wing averaging less than 130; tail less than 80).' Many of these differences are shown in Fig. 18.

AOU (1983, 1998) treated *aeruginosus* as conspecific with *C. rubiginosus*, presumably following Short (1982), but the two taxa were tentatively considered species by Howell & Webb (1995) based on differences in plumage and voice, the latter characterised as:

> *rubiginosus*—'A sharp, slightly explosive *kee'ah* or *k'yaah*, recalling a flicker, and a rapid, shrill, churring rattle'.
>
> *aeruginosus*—'A sharp, nasal, squirrel-like *kyow'n* or *chey-ey*, at times repeated in short series, and a steady series of sharp *weeyk!* or *wheeir* notes, 10/4–6 s, suggesting Squirrel Cuckoo [*Piaya cayana*] song; also a low, short, guttural chatter, audible at close range. Voice thus quite different from Golden-olive Woodpecker [*rubiginosus*].'

Howell & Webb's (1995) taxonomic note on a potential split read as follows: 'Distinct vocalizations and plumage differences suggest specific status for Bronze-winged [*aeruginosus*] and Golden-olive [*rubiginosus*] woodpeckers. Field studies are needed to investigate the extent of intergradation (if any?) in cen Ver.', apparently overlooking the findings of Baptista (1978). Accordingly, their text and distribution maps indicated that the range of *C. r. aeruginosus* extends south to central Veracruz and that the range of the adjacent subspecies of *C. rubiginosus* extends north to central Veracruz.

New information.—As part of a study of the genera *Piculus* and *Colaptes*, Moore *et al*. (2011) sequenced four individuals of *C. r. rubiginosus sensu lato*, two from Mexico and two from Peru, for three mitochondrial genes (cyt b, COI, 12S rRNA), and found with high support that the Mexican and Peruvian individuals were not sisters: the Peruvian birds were sister to Black-necked Woodpecker *C. atricollis* (Malherbe, 1850) whereas the Mexican birds were sister to *C. auricularis*.

Moore *et al*. (2011) did not identify their samples to subspecies and described their samples from Mexico simply as belonging 'to a Mexican subspecies of *rubiginosus*'. However, based on collecting localities, their Mexican samples (from the Sierra de Santa Marta in southern Veracruz) would be *C. r. yucatanensis* and their Peruvian samples (from Lambayeque) would be *C. r. rubripileus* (Salvadori & Festa, 1900). They concluded their paper by stating the following: 'Genetic analyses based on extensive taxon sampling of *C. rubiginosus*, *C. auricularis* and *C. atricollis* that includes the many subspecies of *C. rubiginosus* and the two disjunct subspecies of *C. atricollis* are required to clarify these relationships.'

Gill & Wright (2006) split *C. r. aeruginosus*, as suggested by both Monroe & Sibley (1997) and Howell & Webb (1995), and this split was maintained in subsequent versions of the IOC world bird list. In a later edition of the IOC list, Gill & Donsker evidently assumed that Moore *et al*.'s (2011) Mexican samples were referable to *C. r. aeruginosus* and consequently that their study bolstered the case for treating *aeruginosus* as a species separate from *C. rubiginosus* (e.g., as in Gill *et al*. 2021), retaining all other subspecies, including *C. r. yucatanensis*, in *C. rubiginosus*. The note on the IOC list is as follows: '*C. aeruginosus*, previously treated as a ssp. of *C. rubiginosus*, is sister to *C. auricularis*; *C. rubiginosus* is sister to *C. atricollis* (Moore *et al*. 2011).'

Although both Mexican samples used by Moore *et al*. (2011) are Field Museum tissues, only one of them is vouchered there (FMNH 343228); the other (FMNH 395799) is at UNAM (as UNAM 7788). Ben Marks kindly provided photos of the vouchers and the identifications have now been confirmed as *C. r. yucatanensis* rather than *C. r. aeruginosus*, meaning that the IOC's note suggesting treatment of *C. r. aeruginosus* as a separate species was based on

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Figure 18. Males of eight subspecies of Golden-olive Woodpecker *Colaptes rubiginosus* in ventral (A), dorsal (B) and lateral (C) views. From left to right are specimens of the following subspecies: *aeruginosus* from north-east Mexico (USNM 158576), *yucatanensis* from southern Mexico (USNM 371719), *guianae* from Guyana (USNM 626803), *gularis* = '*pacificus*' from western Colombia (USNM 436350), *buenavistae* from eastern Colombia (USNM 368967), *chrysogaster* from central Peru (USNM 159795), *canipileus* from Bolivia (USNM 264920) and *tucumanus* from north-west Argentina (USNM 645718). Unfortunately, USNM lacks several distinctive subspecies, such as *paraquensis* and *viridissimus*, so photos of these taxa are not included here (R. Terry Chesser)

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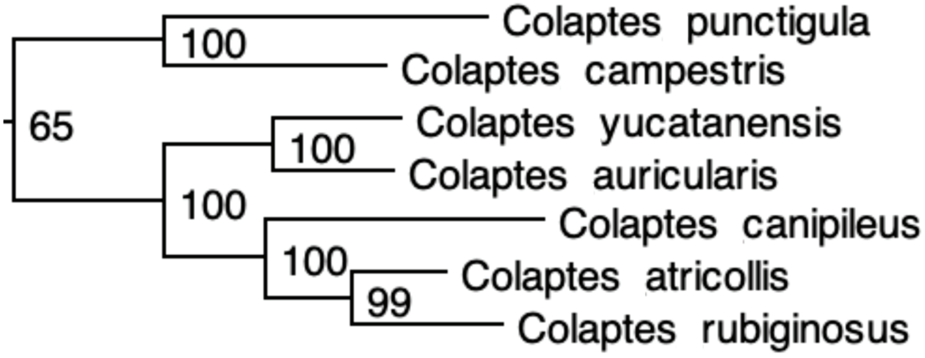

Figure 19. Excerpt of a woodpecker supertree showing relationships among taxa in *Colaptes*. Phylogeny based on data from Dufort (2016) and visualised in Dendroscope 3.8.3 (Huson & Scornavacca 2012). Numbers to the right of the nodes are bootstrap values.

inaccurate assumptions, as the genetic data were from *C. r. yucatanensis* and *C. r. rubripileus*; data from *C. r. aeruginosus* are lacking.

Dufort (2016) published a woodpecker supertree, using sequences from GenBank, that apparently (we could not find a list of samples used in this paper) included Moore *et al*.'s samples and identified them as *C. yucatanensis*, because there is a terminal taxon labelled with this name in the same position as in the Moore tree (as sister to Grey-crowned Woodpecker *C. auricularis*; Fig. 19). Two other terminal taxa in the Dufort tree are also part of *C. rubiginosus*, i.e., '*Colaptes canipileus*' and '*Colaptes rubiginosus*.' These two taxa are not sister to *yucatanensis*, nor do they form a monophyletic group themselves; instead, they are successive sisters to *C. atricollis* (Fig. 19).

We searched GenBank for sequences of *C. rubiginosus* and found that the only records for this species, other than the Moore *et al*. (2011) sequences from Mexico and Peru, are from Guyana, suggesting that the taxon labelled '*Colaptes canipileus*' in the Dufort tree actually represents Moore *et al*.'s samples of subspecies *C. r. rubripileus* (*C. r. canipileus* [d'Orbigny, 1840] occurs in southern Peru and Bolivia rather than north-western Peru) and that the taxon labelled '*Colaptes rubiginosus*' represents samples from Guyana, which would be either subspecies *C. r. guianae* (Hellmayr, 1918) or *C. r. nigriceps* (Blake, 1941).

Of note is the fact that none of the subspecies that form separate lineages in the Moore *et al*. (2011) or Dufort (2016) studies (*yucatanensis*, *rubripileus* and *guianae*/*nigriceps*) correspond to the subspecies formerly considered species by Ridgway, Cory or Peters, namely *aeruginosus*, *chrysogaster* and *gularis*. Instead, all taxa sampled for mtDNA were considered conspecific with *C. rubiginosus* by these references, and their distinctive mtDNA lineages provide an indication of the complexity of variation in this species.

More recently, Shakya *et al*. (2017) published a phylogeny of most species of woodpeckers based on both mtDNA and nuclear introns. Unfortunately, they only included a single tissue of *C. rubiginosus*, a sample from Guyana.

Del Hoyo & Collar (2014) also considered *C. r. aeruginosus* as a separate species from *C. rubiginosus*, using the same division as Gill *et al.* (2021), but based their decision on plumage and the vocal descriptions in Howell & Webb (1995):

> Until recently treated as subspecies of *C. rubiginosus*, but differs in male's red supercilium extending from nape to above eye *vs* extending from nape to bill (2); rear ear-coverts clear *vs* barred (1); bars on underparts more scale-shaped (1); wings and tail longer (effect size for tail *vs C. r. yucatanensis* 3.63; score 2); wholly different

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> song (deliberate slow-paced series of c. 6 typical picoid high-pitched calls, "kwi, kwi, kwi, kwi, kwi, kwi" *vs* protracted rising rattling trill), extensive playback experiments yielding frenzied response from own taxon, no response from other taxon (Howell & Webb 1995, Howell *in litt*. 2013b) (4).

As noted above, the extent of the red supercilium and the barring on the ear-coverts are variable within *C. rubiginosus* and should not be considered diagnostic differences vs. *C. r. aeruginosus*.

The vocal data are much more convincing than the genetics or morphology, at least based on current sampling. The difference in what some authors call 'songs' and others term 'long calls' seems clear, although the sample size for *C. r. aeruginosus* is not large (we found eight independent recordings on Xeno-canto and Macaulay). There are no recordings of some subspecies of *C. rubiginosus*, but variations of the 'rattle' call can be heard in many parts of its range (based on a spot-check of Xeno-canto and Macaulay), including from *C. r. yucatanensis*. We suspect that the slow rising series of notes in a recording of *C. r. aeruginosus* from Tamaulipas (XC 227966) is homologous to the 'rattle' call in *C. r. rubiginosus*, which if confirmed would be a large vocal difference from the rest of the *C. rubiginosus* complex. There are also several vocal samples labelled *C. r. aeruginosus* from Veracruz (mostly from around Xalapa), but there is only one recording from the southern half of the state where *C. r. yucatanensis* occurs. That is of an individual not seen when recorded but later identified as *C. rubiginosus*. The call of this individual, from Orizaba, *c.*80 km south of Xalapa, included the rattle (see XC 305868). Nevertheless, conclusions drawn from such low sample sizes are perilous, and the degree of intergradation where the two forms meet (as in Baptista 1978) remains to be investigated. That Moore *et al.*'s (2011) samples from southern Veracruz might contain mtDNA from *C. r. aeruginosus* (mitochondrial introgression being one possible explanation of their genetic results) suggests that the degree of intergradation may be a significant question.

The vocal differences alluded to above are just one of several cases of vocal divergence in the *C. rubiginosus* complex. Based on our observations (DFL), there may be as many as four vocal groups that might represent distinct species, but how these align with genetic differences is unclear. These other groups are based on the common vocalisations besides the rattle song: *aeruginosus* (see descriptions above), a clear-voiced group in Middle America that gives a descending *keer!*, a grating-voiced group in the north-west Andes south to the Pacific coast of Peru, and a group from the eastern slope of the Andes, the Guiana Shield, and Trinidad & Tobago that gives a rising *kree?*

Summary and Recommendation.—When we first looked into this potential species split, we expected to recommend that it be adopted due to the aggregate weight of the vocal and genetic differences, added to the earlier species recognition of *aeruginosus* by Ridgway, Cory, and Peters. This was in spite of drawbacks to each individual dataset: the relative lack of vocal sampling in the northern part of the range of *C. r. yucatanensis*, the lack of nuclear genetic data and the limited sampling within *C. rubiginosus*, and the morphological variation within *C. rubiginosus*.

Now that we know that there are no genetic data for *C. r. aeruginosus*, that the three subspecies of *C. rubiginosus* sampled to date form different mitochondrial lineages, and that none of the other species recognised by Ridgway or Cory have been sampled, the situation is more complex than it first appeared. It is likely that *C. rubiginosus* consists of more than one species, but how many and how the various subspecies should be apportioned is unclear. Moreover, a simple separation of *C. aeruginosus* from all other subspecies of *C. rubiginosus* would still leave a paraphyletic *C. rubiginosus*.

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This is a vexing issue. An argument can be made for recognising *C. aeruginosus* based on the vocal differences and the prior recognition by Ridgway, Cory, and Peters, irrespective of the complications inherent in the genetic data and the complex situation in the rest of the distribution. That is to say that Short (1982), based on consistent differences in the characters identified by Ridgway (shape of the ventral barring and size) and despite the phenotypic variability in many other characters, should not have lumped *C. aeruginosus*, and that the vocal differences provide sufficient rationale to return it to species status. This is tempting but we are reminded of recent cases in which intermediacy in vocalisations (or other phenotypic characters) has been found upon deeper investigation of what seemed to be consistently different characters in proposed species splits (e.g., *Patagioenas fasciata*; see above). In this respect, the extent of intergradation between the *rubiginosus* group and *C. r. aeruginosus* in central Veracruz (Baptista 1978) needs to be investigated: are additional recordings or specimens now available from this area? Or have details of the playback trials noted in del Hoyo & Collar (2014) been published or otherwise made available? Such information might be sufficient to recommend recognising *C. aeruginosus* as a species.

Ultimately, there are too many uncertainties for us to recommend that we treat *C. aeruginosus* as a separate species from *C. rubiginosus* without further information of the type mentioned above or pending a more complete study of genetic and phenotypic variation within *C. rubiginosus* (involving, at a minimum, genetic data for *aeruginosus*).

If this taxonomic treatment is adopted, then we suggest the English name Bronze-winged Woodpecker for *C. aeruginosus*. It was the name used by the AOU (1983, 1998) for the *aeruginosus* group and is also in use for *C. aeruginosus* (e.g., IOC list). If *C. aeruginosus* is split, Golden-olive Woodpecker would be retained for the much more widespread *C. rubiginosus*, pending further splits within that species.

Next steps.—Because multiple species are likely involved, this complex requires a thorough study of geographic variation in vocalisations and plumage, better sampling for genetic data, and assessment of putative contact zones and levels of intergradation between subspecies. Data from Baptista (1978) suggest intergradation in central Veracruz, but the extent of this zone of introgression has not been quantified. In particular, quantification of vocal differences between *C. r. aeruginosus* and *C. r. yucatanensis* would be informative regarding species limits. Genetic data are also suggestive of multiple species in the group, as indicated by the paraphyly found by Moore *et al*. (2011) and Dufort (2016), but these studies were confounded by problems with the identification of samples (an issue clarified here) and, presumably, lack of nuclear data for most samples of *C. rubiginosus*. Moreover, many taxa were unsampled in those studies, and future work could focus on broader genetic sampling of more taxa.

OLIVE-THROATED PARAKEET *Eupsittula nana*

Background.—Based on NACC proposal 2023-A-15 'Treat *Eupsittula astec* as a separate species from Olive-throated Parakeet *E. nana*', which did not pass. Proposal author: SMB.

The genus *Eupsittula*, as currently recognised, comprises five species of medium-sized green parakeets that vary primarily in the amounts of brownish olive on the underparts and red/orange on the face. They are distributed from Mexico south through Central America and South America to Bolivia and extreme northern Argentina, with *Eupsittula nana* (Vigors, 1830) also occurring on Jamaica. Although currently treated as a single species by most global checklists, *E. nana* historically was often considered two separate species, with *E. nana sensu stricto* restricted to Jamaica, and *E. astec* (Souancé, 1857) in eastern Mexico and Central America from central Tamaulipas to western Panama.

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E. nana was described as *Psittacara nana*, and *E. astec* was described as a separate species, *Conurus astec*, albeit prior to the adoption of the BSC. In distinguishing *E. astec* from *E. nana*, Souancé (1857) noted the latter's longer tail, darker coloration, larger and entirely pale bill, and the entirely bare cere. The two taxa were considered distinct species by most subsequent authors, including Ridgway (1916), who noted that *E. nana* had a much larger and relatively deeper bill than all other *Eupsittula*, although he also noted that its plumage was very similar in coloration to that of *E. astec*. Cory (1918) considered the two separate species, as did Peters (1937) and Friedmann *et al*. (1950).

Bond (1945) was the first to mention that the two might better be considered as conspecific (although he still maintained them as separate species). Following Bond (1945), Marien & Koopman (1951) also believed that the two were probably better treated as conspecific using a yardstick assessment and comparing them to other parakeets (although they did not explicitly make a taxonomic recommendation). They noted that *E. n. nana* and *E. n. astec* are more like each other than sympatric members of what they called the subgenus *Eupsittula*, and that there is more variation within some species, e.g., Golden-capped Parakeet *Aratinga auricapillus* (Kuhl, 1820), than there is between *E. n. nana* and *E. n. astec*. It is worth noting, however, that most of their comparisons were between members of what is now recognised as *Aratinga*, or even between a member of *Eupsittula* and *Aratinga*, e.g., comparisons between Brown-throated Parakeet *E. pertinax* (Linnaeus, 1758) and Sun Parakeet *A. solstitialis* (Linnaeus, 1758), or within *A. auricapillus*, so these comparisons may not be as relevant given what we now know about relationships (Remsen *et al*. 2013, Provost *et al*. 2018). Marien & Koopman (1951) mentioned that *E. n. nana* is larger than *E. n. astec*, and that *E. n. nana* usually lacks the yellow feathering around the cere that is present in *E. n. astec*, although some birds can show some yellow feathering. Forshaw (1973) was the first author to definitively consider the two as conspecific, although Parkes (1976) continued to treat *E. astec* as a species in his discussion of the taxon *E. astec melloni* (Twomey, 1950). The sixth edition of the AOU *Check-list* listed the two taxa as conspecific (AOU 1983) and most global checklists have followed this approach, including Clements (Clements *et al*. 2021), Howard & Moore (Dickinson & Remsen 2013) and IOC (Gill *et al*. 2022). Del Hoyo & Collar (2014), using the scoring methodology for species delimitation of Tobias *et al*. (2010), considered the two taxa to be species: '[*nana*] differs in its darker, browner breast and lower underparts (2); darker (royal- *vs* turquoise- = 1) and much more extensive (= 1) blue with broader black fringes (= 1) in flight-feathers (total = 3); larger size, with effect size on bill 6.91 and on tail 3.97 (score 3)' (del Hoyo & Collar 2014). Howell & Webb (1995) also treated the two taxa as separate species, although they did not provide their rationale.

Vocally, the two taxa seem very similar. Collar *et al*. (2020) mentioned that there are no described vocal differences between *nana* and *astec*. There appear to be no other mentions of vocal differences (or lack thereof) in other publications. In listening to a small selection of recordings in Macaulay Library, the two do possibly seem different, with *astec* seemingly sounding slightly higher-pitched and faster than *nana*. Some example recordings of the two are: *nana* (ML 358958021, ML 164604) and *astec* (ML 82419181, ML 10334).

New information.—The only relatively new information is a study of the phylogeography of *E. nana* to understand the nature of a population on Hispaniola (Latta *et al*. 2010). Using mtDNA sequence data, Latta *et al*. (2010) found that *E. n. nana* and *E. n. astec* had 1.73–1.88% sequence divergence and were reciprocally monophyletic based on a sample of 16 individuals (Fig. 20). Birds from Hispaniola were included in the *E. n. nana* clade, and did not differ from those on Jamaica, and the authors suggested they represent an introduced population (Latta *et al*. 2010). Based on the degree of genetic divergence and reciprocal monophyly shown in the mtDNA sequences, together with morphological differences,

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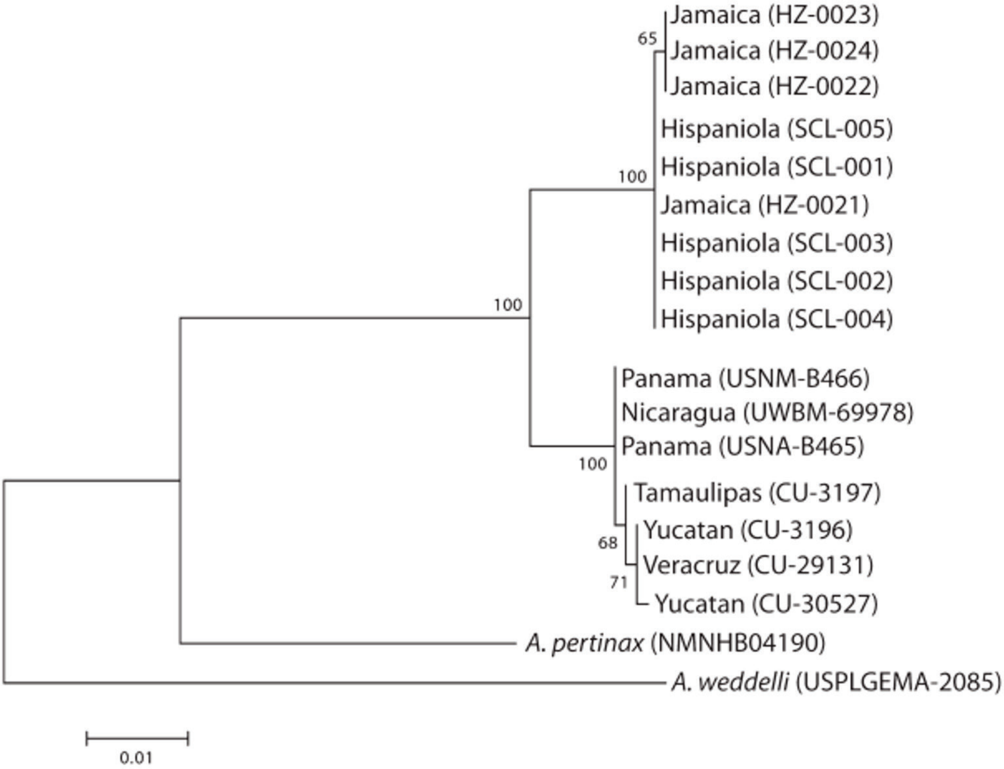

Figure 20. Neighbour-joining tree (constructed in MEGA 4.1; Kumar *et al*. 2008) showing relationships between the island and mainland populations of Olive-throated Parakeet *Eupsittula nana*. Values at nodes denote relative percent support from 2000 bootstrap iterations. Adapted from Latta *et al*. (2010); reproduced with permission from the *Caribbean Journal of Science*.

Latta *et al*. (2010) considered that *nana* and *astec* represent phylogenetic species but did not comment on the potential for reproductive isolation. However, Latta *et al*. (2010) noted that the genetic divergence was similar to that between some currently recognised species of *Aratinga*. Ferraroni (2015) analysed plumage and osteological characters in these taxa and found that the orange feathers on the nares and the brown-olive versus dark brown-olive underparts were diagnostic of the two taxa, and recommended raising both to species rank under the Phylogenetic Species Concept.

Recommendation.–Assessing the species status of insular taxa is a perpetual problem in systematics, and the case of these two *Eupsittula* parakeets, *nana* and *astec*, is no exception. The two were described as separate species and maintained as such by many authorities until the 1970s. In its first treatment of the group, the AOU (1983) treated them as a single species, and most global authorities have followed this. However, the two have diverged in plumage, morphometrics (especially the 'much larger and relatively deeper' bill of *E. n. nana*; Ridgway 1916) and genetics (Latta *et al.* 2010), albeit not very strongly. Based on these differences, del Hoyo & Collar (2014) considered the two taxa to be separate species. The two appear to be sister (Latta *et al*. 2010), although no phylogeny has included all *Eupsittula* taxa together, so technically there is still a remote possibility that *E. n. astec* or *E. n. nana* could each be more closely related to another species. Given the morphological differences and genetic divergence (although studied using only one gene of mtDNA), the recommendation is to treat *astec* as a separate species from *E. nana*, as the original merger

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of the taxa was not entirely well justified and seems to be based partly on comparisons of differences between species in different genera. If two species are recognised, then the names previously used for these taxa are recommended: Aztec Parakeet for *Eupsittula astec* and Jamaican Parakeet for *Eupsittula nana*.

***Next steps*.**–Although some committee members thought that these likely represent separate species, others believed that a comprehensive study of vocal, structural and genetic data is needed. Others felt that, even with the known variation within each taxon and the degree of divergence in song, morphology and genetics, these represent differences more typical of parrot taxa treated as subspecies. Based on phenotype, it is possible albeit unlikely that these taxa are more closely related to other species of *Eupsittula* than to each other; a genetic study that includes both taxa, along with other species in the genus, is needed. Analyses of morphological differences—especially bill and body size, extent of yellow on the head, and extent of streaking on the throat—would be informative, in particular assessing the extent of intra- versus inter-taxon variation and placing this in the context of interspecific morphological differences between other species pairs of parakeets in the Arini. Therefore, NACC continues to treat the two taxa as subspecies of the same species at this time.

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