AOS Classification Committee – North and Middle America

Proposal Set 2022-A

13 October 2021, revised 1 December 2021

Reinstate Northwestern Crow *Corvus caurinus* as a species

Background:

Slager et al.'s (2020a) proposal to the N&MA Committee in February 2020 resulted in the Northwestern Crow *Corvus caurinus* being classified as a conspecific with American Crow *C. brachyrhynchos*, and in *caurinus* being recognized as a geographical trend rather than as a species or subspecies. This was subsequently revised resulting in *C. caurinus* being recognized as subspecies *C. b. caurinus* (Chesser et al. 2021): "*Corvus caurinus* is treated as conspecific with *Corvus brachyrhynchos*, following Slager et al. (2020), and is now considered a subspecies of *brachyrhynchos*."

According to Chesser et al. (2021) the decision to treat *caurinus* as conspecific with *C. brachyrhynchos* was "based on 1) genomic data that indicate a lack of reproductive isolation with extensive introgression and backcrossing (Slager et al. 2020b), and 2) clinal variation, and a lack of consistent differences in size, ecology, and vocalizations where the two are in contact in southwestern British Columbia and northwestern Washington (Rhoads 1893, Johnston 1961, Slager et al. 2020)."

I applaud Slager et al.'s (2020a) overdue and valuable assessment of the degree of hybridization between the American Crow *Corvus brachyrhynchos* and the Northwestern Crow *C. caurinus*, a feature long suspected by ornithologists in Washington and British Columbia. Their findings verify hybridization between the two crows. However, the interpretation of widespread hybridization along 900 km of coastline between northern Washington and the BC north coast is less robust.

Butler's (2021) re-analysis of Slager's (2020b) data suggests a much narrower hybrid zone than what Slager et al. (2020a) proposed, and that has changed little in the past century.

New Information:

Slager et al.'s (2020b) valuable contribution shows that hybridization occurs – that point is unequivocal - clearly *caurinus* and *brachyrhynchos* interbreed extensively in Washington, and southern and a few coastal locations of British Columbia (but not Alaska; Slager et al. 2020b). Field ornithologists have long suspected hybridization occurred in a few locations in British Columbia, so Slager et al.'s (2020b) confirmation is no surprise.

Hybrid Zone

However, the contention that their evidence supports extensive hybridization "across >900 km of coastal Washington and coastal British Columbia" is not very robust. To support their claim of a wide hybridization zone, Slager et al. (2020a) analysed genomic data along the coast from Washington to southern Alaska, to compare to data from crows in the interior of BC and American states. They found widespread hybridization in Washington, on the southwestern mainland of British Columbia, southern Vancouver Island, and at a few central and north coast sites, but none in Alaska. Slager et al. (2020b) concluded there was a gradient of hybridization from south to north despite an unexplained and disproportionately high degree of *caurinus* present on Vancouver Island given the proximity to Washington. Slager et al. (2020b) used crow specimens from the heads of inlets with valleys close to the western edge of the breeding range of American Crows in the interior of British Columbia and that have long been suspected to be sites where both species occurred. His samples came from the edge of the range and did not include the outer coast of British Columbia or Haida Gwaii, which is the centre of the range of *Corvus caurinus* in British Columbia.

Slager et al (2020b) acknowledged that Vancouver Island crows stood out by not showing the degree of hybridization as crows on the adjacent mainland and being inconsistent with their interpretation of a latitudinal gradient. Moreover, the proportions of *caurinus* and *brachyrhynchos* types in Slager et al.'s (2020b) Figure 1 are nearly identical between Vancouver and the Central Coast of British Columbia, despite being 500 km apart. These inconsistencies suggest other factors are at play.

Butler (2021) re-examined Slager et al.'s (2020b) supplemental data on the frequency of hybridization at coastal locations, comparing a latitudinal gradient explanation proposed by Slager with a nearest breeding explanation. He showed a better fit to the nearest known breeding *brachyrhynchos,* rather than a S-N gradient from Washington state to northern BC as proposed by Slager et al. (2020b). In other words, the source of the influx of *brachyrhynchos* genes is more likely from multiple locations, including via coastal valleys for the northern Vancouver Island, Central and North Coastal hybrids rather than from Washington State in the south as Slager et al. (2020b) proposed. There has been a long-held belief that American Crows (based on voice) spill out through the valleys on to the coast, as reviewed by Butler (2021), and which appears to be supported by Slager et al. (2020b).

Consistent with Butler's (2021) hypothesis of an easterly rather than southerly source are the data Slager et al. (2020b) presented from Alaska. North of Prince Rupert where the western boundary of the breeding range of the American Crow veers eastward away from the coast and where there can be no spillage down the valleys, the samples showed no introgression from *brachyrhynchos*. Slager et al. (2020b) said they were "98% pure" Northwestern.

Turning our attention to crows inhabiting the valleys in British Columbia, Slager et al. (2020b) found along the Skeena River only Northwestern Crows on the coast (N=6) and about 35 km upriver (N=1), and had 1 American and 1 Northwestern at the most easterly site (Kwinitsa River, Figure 3). Note that Slager et al. (2020b) only sampled 6 crows from the mouth of the Skeena River, where it flows into the Pacific Ocean, and he designated all as Northwestern Crows. This provides evidence, albeit with a small sample, of hybridization occurring away from the coast up a river valley. Note also that Munro and Cowan (1947) reported American Crows nearby in Hazelton over 70 years ago, and that Campbell et al. (1997) reported the species in the Skeena River over 20 years ago, which Slager et al. (2020b) simply confirmed.

Rather than the 900 km wide hybrid zone proposed by Slager et al (2020b), Butler's (2021) hybrid zone is closer to 200 km wide (Fig. 1) and much closer to the other species referenced by Slager et al (2020b).

Slager (2020a) refers to a Spencer F. Baird’s quote in his original description of *Corvus caurinus*.

"In all essential features it is like the [American Crow]; so much so, indeed, that but for the slight difference in size it would be difficult to tell skins of the two apart", and "it is so much like the [American Crow] as to be only distinguishable by its inferior size and habits. Indeed, it is almost a question whether it be more than a dwarfed race of the other species" (Baird 1858).”

This description is not too surprising now given that the type specimen for *Corvus caurinus* was from Fort Steilcoom near Seattle, Washington State, which Slager et al. (2020b) has nicely shown is near the southern edge of the hybrid zone of the two species. A new type specimen from within the known range of *C. caurinus* is warranted.

Isolation

The description by Slager (2020a) that crows “range north and south along the coast and occur along the immediate shoreline, inland, and everywhere in between” is an overstatement in my opinion. Both crows are low elevation species and rarely or never occur at high elevation in the Cascades, Coastal Range Mountains, and on Vancouver Island (Campbell et al. 1997, Davidson et al. 2015). Moreover, Campbell et al. (1997) stated equivocally that “at the northern end of its range [the Northwestern Crow] does not occur more than a few kilometers from tidewater” with exception that Northwesterns follow spawning salmon up rivers such as the Nass, Skeena, and Fraser rivers, and which not surprisingly matches where Slager et al. (2020b) found hybrids.

Instead, the question should be what has prevented the hybrid zone from becoming coast wide, as proposed by Slager et al (2020a)? The coast of British Columbia has been free of ice for over 10,000 years, which is plenty of time for hybridization to become widespread. I believe the answer lies in the topography and climate of British Columbia.

The steep walled uninhabited fjords of British Columbia appear to be a barrier to the movement of crows. Campbell et al. (1997) wrote that crows are “infrequent or absent from sheer rock margins of fjords” because of the steep rock faces and few invertebrates as food. All coastal areas where Slager et al (2020b) sampled crows were where low mountain passes with highways penetrated the mountains from the interior of British Columbia. Thus, the high mountains and fjords appear to be a barrier keeping most American Crows from the reaching the coast as well as most Northwestern Crows from the interior of British Columbia. Only where there are low mountain passes served by highways and human settlements at the heads of fjords do the two species ranges meet and hybridize.

A second isolating feature might have been the migratory nature of the American Crow in the interior of British Columbia and the sedentary nature of the Northwestern Crow on the coast. Campbell et al. (1997) showed that most American Crows migrated south in the autumn with a few remaining behind near human habitation, especially in the southern interior. In south coastal British Columbia and Puget Sound, Washington, the two species reside year-round providing opportunity to hybridize, but along the central and north coast there would be fewer opportunities to find a mate before the nesting season began.

To summarize, I concur with Slager et al. (2020b) that hybridization occurs between the two species. I also agree with Slager et al (2020b) of the existence of a hybrid zone in Puget Sound, the Lower Mainland of BC, and southern Vancouver Island. However, I disagree that the BC coast is a gradient of hybridization. The data better support a 200 km zone along the southern edge rather than a 900 km gradient as proposed by Slager (2020b). The pockets of hybridization in a few central coast locations are not part of a continuum as Slager et al. (2020b) proposed, but more likely the result of American Crows from the interior of British Columbia spilling through the Coast Range Mountains via valleys and rivers. American Crows are confined to the heads of valleys along the BC coast.

With all due respect, Slager et al. (2020b) had small sample sizes to work with along the BC coast and vast areas went unsampled. They had very few from the west coast of Vancouver Island and north coast, and none from either the central coast or Haida Gwaii, which is the centre of the range for *C. caurinus*.

Recommendation:

Butler (2021) proposed that the hybrid zone between *brachyrhynchos* and *caurinus*, as described by the data, extends from Puget Sound to central Vancouver Island, and in pockets at the heads of a few coastal inlets south of Prince Rupert (Figure 3). It is recommended that *C. caurinus* be reinstated as a species occurring in Alaska and along the outer coast of British Columbia including north and western Vancouver Island pending further sampling.

Literature Cited:

Butler, R.W. 2021. Taxonomy of the Northwestern Crow *Corvus caurinus*. British Columbia Birds 31: 41-46.

Campbell, RW, NK Dawe, I. McTaggart Cowan, JA Cooper, MCE McNall and GEJ Smith. 1997. The birds of British Columbia, Vol. 3., UBC Press, Vancouver.

Chesser, T. et al. 2021. Addendum to the Sixty-first Supplement to the American Ornithological Society's *Check-list of North American Birds*. Ornithology 138 (**online**).

Davidson, P.J.A., R.J. Cannings, A.R. Couturier, D. Lepage, and C.M. Di Corrado (eds.). 2015. The Atlas of the Breeding Birds of British Columbia, 2008-2012. Bird Studies Canada, Delta, B.C.

Marzluff, J. M., et al. 2001. Pp 332-363 *in* Avian ecology and conservation in an urbanizing world (J. M. Marzluff, R. Bowman, and R. Donelly, eds.). Kluwer Academic Press, Norwell, MA.

Munro JA and I McTaggart Cowan. 1947. A review of the bird fauna of British Columbia. BC Prov. Mus. Spec. Publ. No. 2, Victoria.

Slager, D. L. 2020a. Treat Northwestern Crow *Corvus caurinus* as conspecific with American Crow *C. brachyrhynchos* 2020-C-15 N&MA Classification Committee 25 February 2020.

Slager, D. L., K. L. Epperly, R. R. Ha, S. Rohwer, C. Van Hemert, and J. Klicka. 2020b. Cryptic and extensive hybridization between ancient lineages of American crows. Molecular Ecology. http://dx.doi.org/10.1111/mec.15377

Submitted by: Robert Butler, PhD, Pacific WildLife Foundation, Port Moody, BC, Canada, and Professor (adjunct), Center for Wildlife Ecology, Department of Biological Sciences, Simon

Fraser University, Burnaby BC, Canada. I am a Fellow of the AOS who has published original research on crows in British Columbia beginning in 1973 including the *Birds of the World* account for the Northwestern Crow (Verbeek and Butler 1999).

Date of Proposal: 25 August 2021

External comment on Proposal 2022-A-1

When presented with genetic data, today's AOS North American Classification Committee (NACC) generally makes taxonomic decisions based on multi-locus studies rather than single-gene datasets. This practice is scientifically justified because speciation and hybridization histories are more accurately reconstructed by analyzing the combined evolutionary histories of many genetic loci rather than a single locus.

Slager et al. (2020) and the corresponding checklist proposal leading to the lumping of American/Northwestern crows by the AOS NACC in 2020 were based on results from 7,292 unlinked SNPs from the nuclear genome of 62 American/Northwestern crows, in addition to mitochondrial DNA (mtDNA) ND2 sequences.

Unfortunately, Butler (2021) and this corresponding new proposal to re-split American/Northwestern crows ignore all the nuclear SNP analyses presented in Slager et al. (2020) and limit discussion of hybridization genetics to mtDNA ND2 haplogroups.

Because mtDNA in birds is non-recombining and matrilineally inherited, mtDNA haplogroup is a binary marker that does not indicate the hybridization status of individual birds. In other words, an individual crow will have either "American" mtDNA or "Northwestern" mtDNA, even if it is a hybrid. The degree of geographic co-occurrence of haplogroups is likewise not a direct index of hybridization in that population.

Butler (2021) and the new proposal suggest that the hybrid zone is smaller than stated by Slager et al. (2020). However, this claim apparently arises from a critical misunderstanding that hybridization is limited to localities where American and Northwestern mtDNA haplogroups co-occur. The misconception is illustrated in Figure 3 from Butler (2021) and its caption, reproduced below.

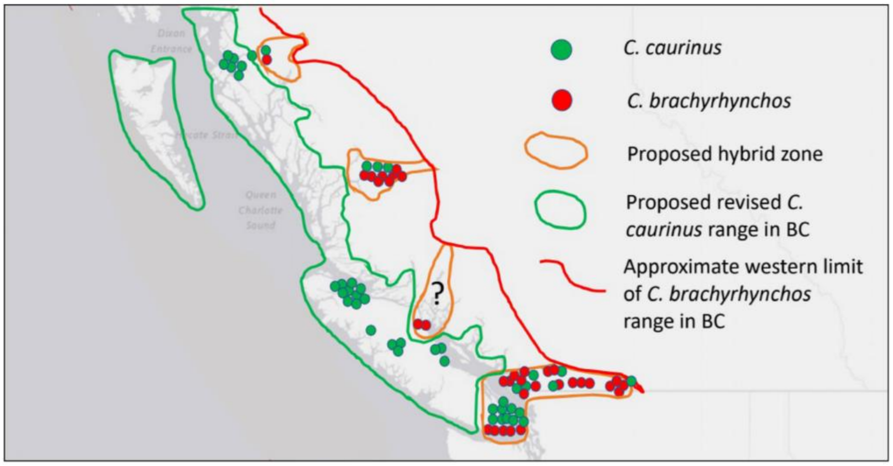


Figure 3. Distribution of *C. caurinus* and *C. brachyrhynchos* adapted from Slager *et al.*'s (2020) Supplementary Table 1, and proposed revised distribution of hybrid zone in British Columbia.

In ignoring the nuclear DNA evidence for hybridization presented in Slager et al. (2020), Butler (2021) and the new proposal have overlooked that in fact 18 of 20 crows from coastal BC sequenced for nuclear SNPs were hybrids, including 9 of the 11 crows with the "northwestern" mtDNA haplogroup and all 8 crows from Vancouver Island. Figure 1 from Slager et al. (2020) is reproduced below.

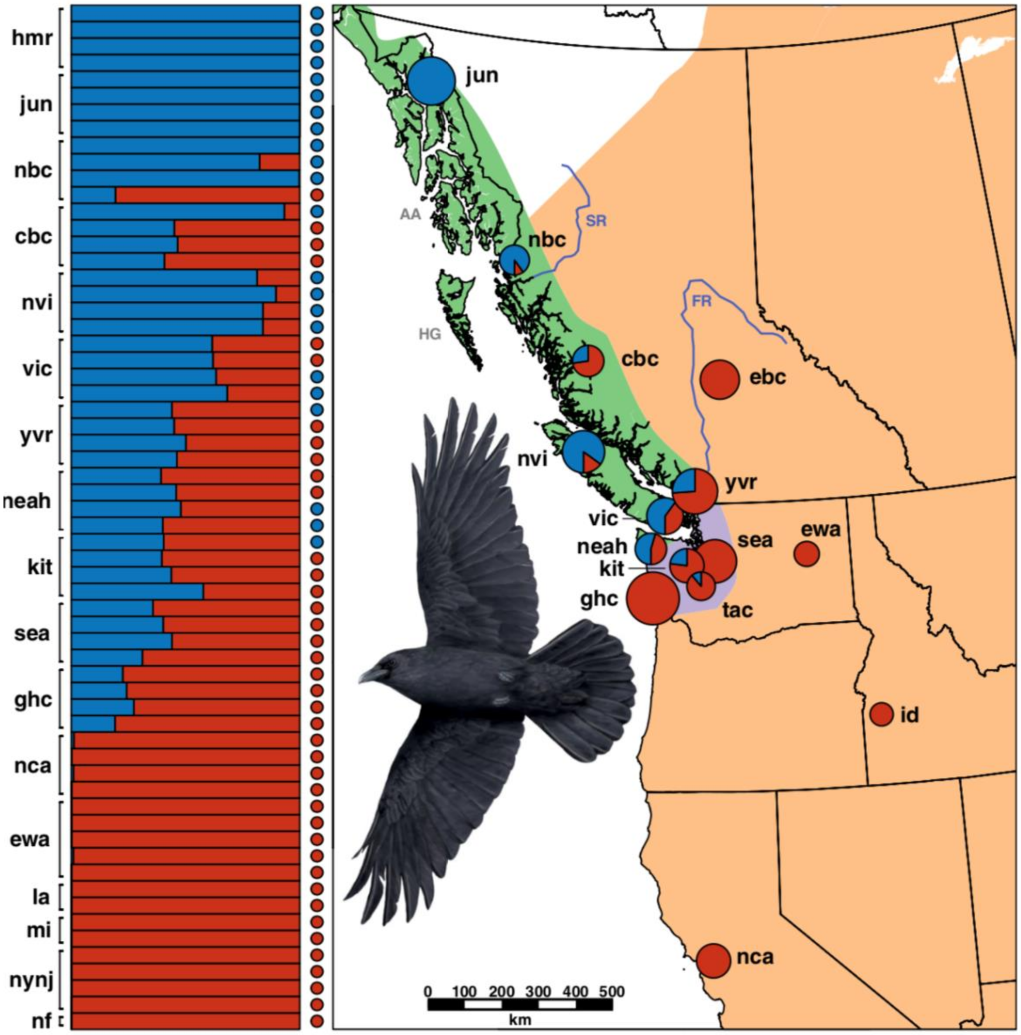


FIGURE 1 Extent of hybridization between Northwestern Crow (blue) and American Crow (red). At left, bars show nuDNA $K = 2$ ancestry proportions and adjacent circles indicate mtDNA haplogroup for the same 62 individuals. At right, locality pies depict mtDNA haplogroup proportions from the full mtDNA data set ($n = 6$–31 per locality), and background colours indicate range maps for Northwestern Crow (green), American Crow (orange), and the overlap zone (purple; BirdLife International and NatureServe, 2013). The map shows the Pacific Northwest of North America from southeastern Alaska to northern California. Sample localities outside this mapped region contain 100% Northwestern (*hmr*) or 100% American (*sca*, *la*, *mi*, *nynj*, *nf*) mtDNA haplogroups. For mtDNA haplogroup proportions across the full geographic range of American/Northwestern crows, see Figure S1. Sample IDs for bars at left run numerically from top to bottom (e.g., mi01 above mi02; see Table S1). Labels indicate locations of the Alexander Archipelago (AA), Haida Gwaii (HG), the Skeena River (SR), and the Fraser River (FR). Original crow illustration by Kevin L. Epperly [Colour figure can be viewed at wileyonlinelibrary.com]

Overall, Butler (2021) and the latest proposal offer little new information, are based on a fundamentally flawed re-analysis of Slager et al. (2020) using only a small fraction of the available data, and do not change the overall conclusions from Slager et al. (2020) that formed the basis for the NACC's 2020 decision to lump American and Northwestern crows.

Submitted by: David L. Slager, Department of Biology & Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, USA

Date of Comment: 30 September 2021

Recognize *Turdus confinis* (San Lucas Robin) as a separate species from *Turdus migratorius* (American Robin)

Effect on NACC:

This would treat our existing species, *Turdus migratorius*, as two species, i.e., resurrecting species rank for *Turdus confinis* (San Lucas Robin).

Background:

Currently treated by NACC as a subspecies of American Robin and as a subspecies "group", but the HBW/BLI lists, using the Tobias et al. scoring scheme, reinstated it as a species (*confinis* = confined to the mountains of extreme southern Baja California del Sur, Mexico).

The two groups have long been known to differ in some key plumage features. A brief history of taxonomic treatments is as follows:

- Ridgway (1907) treated the two groups as separate species. His key separated them by the well-known plumage differences in terms of having a paler head and underparts.

- Hellmayr (1934) treated *confinis* as a subspecies of *T. migratorius* with the following comment: "*Turdus migratorius confinis* Baird obviously is merely an excessively pale race of the Robin."

- This treatment was followed by Eisenmann (1955), Ripley in "Peters" (1964), and Mayr and Short (1970).

- AOU (1957) treated it as a separate species, San Lucas Robin.

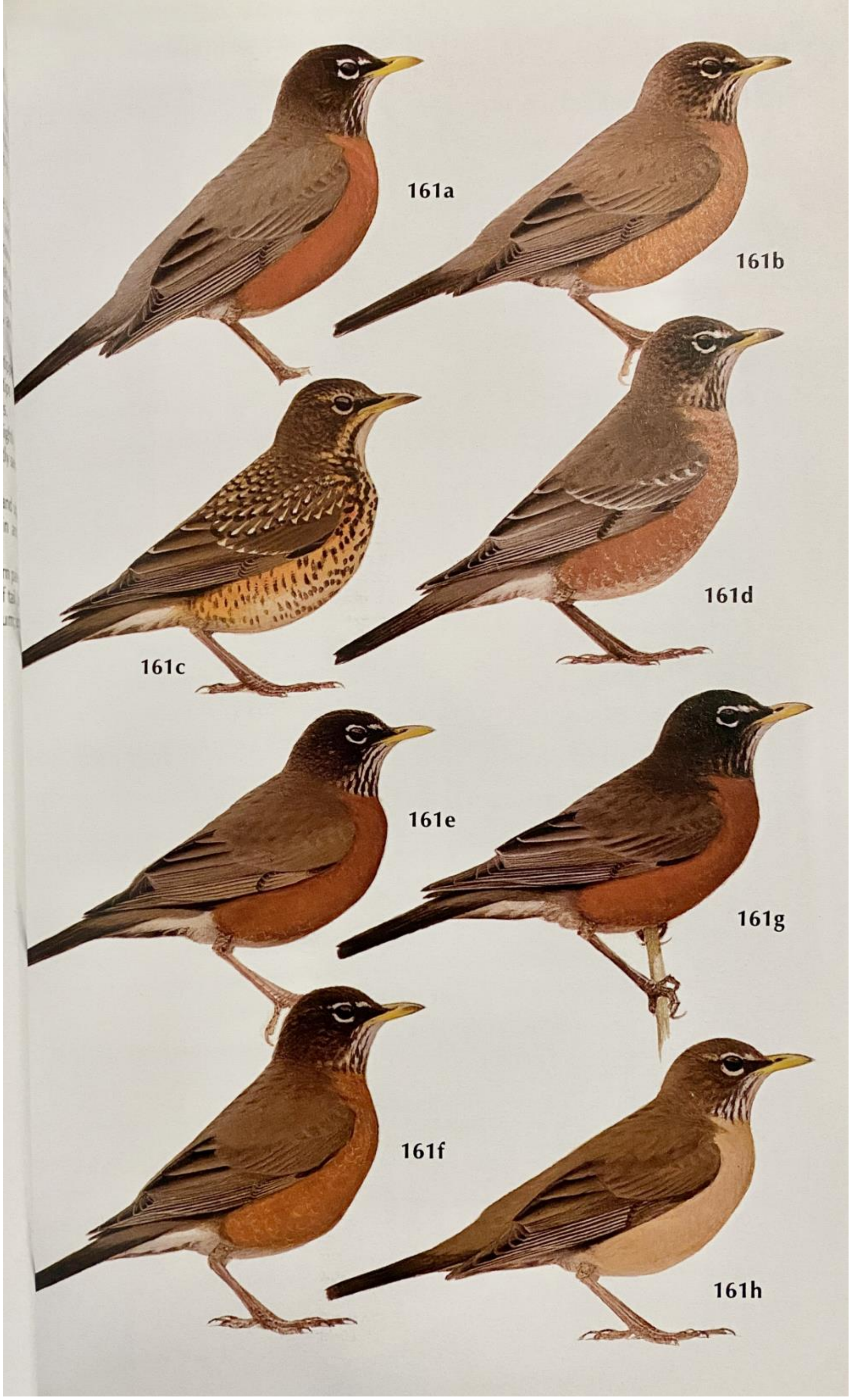
- Davis (1972, A Field Guide to the Birds of Mexico and Central America) treated them as separate species, without comment except "Considered a race of *T. migratorius* by some." Edwards (1972, A Field Guide to the Birds of Mexico) also treated them as separate species, but without comment.

- AOU (1983, 1998) treated them as conspecific, but as separate subspecies "groups", as was policy for any case in which there had been previous treatments using different species limits.

- Phillips (Known Birds Vol. 2, 1991), who reflexively disagreed with AOU on species limits at every opportunity, nonetheless maintained it as a subspecies, but added the following comment "Long considered specifically distinct, and may prove so."

- Howell & Webb (1995; Mexico guide) treated them as conspecific but *confinis* considered a separate group. As for voice, they noted that the song was "burrier and less strident in *confinis*" and that the calls were "similar".

- Clement (2000, Thrushes, Princeton U. Press) treated them as conspecific. In the VOICE section, he stated "The song of *confinis* is like the nominate but with a weaker delivery and lacking any clear notes" (but did not provide a citation). The excellent plate from that book, by Ren Hathway, is provided here to illustrate *confinis* (161h) in the context of American Robin variation:

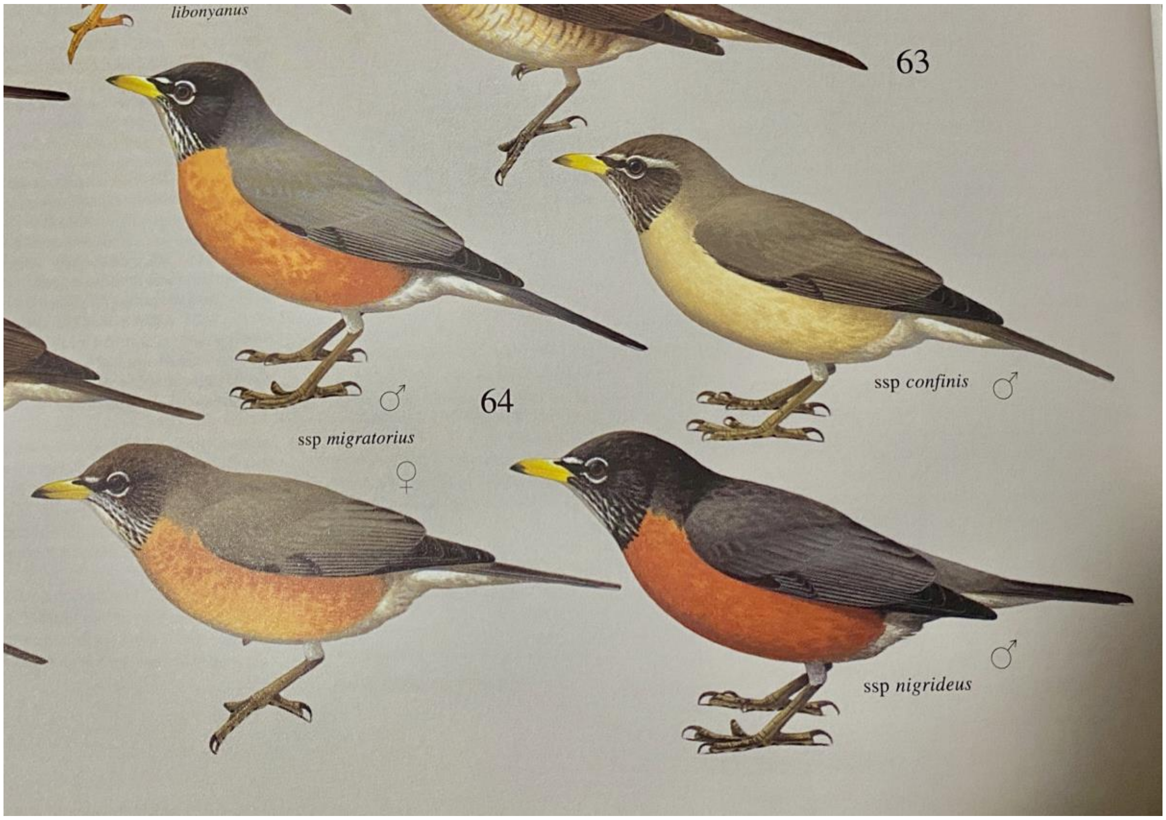


- Navarro-Sigüenza & Peterson (2004) treated *confinis* as a separate species, but their classification of birds of Mexico used the ESC.

- Collar in HBW (2005) treated them as conspecific, but dutifully mentioned that *confinis* had been treated as a separate species. Clearly, this was prior to Collar's Enlightenment and conversion to the Seven Points of Wisdom species "concept" (sorry Nigel, couldn't resist).

<u>Plumage:</u>

Here's the HBW plate, which seems to illustrate the extreme pale end of variation in *confinis*:



- Dickinson & Christidis (2014) treated them as conspecific but placed six subspecies in the *migratorius* group and *confinis* in its own group.

<u>Genetic Data:</u>

As for genetic data, I'm not sure what they could tell us on species limits in allotaxa; degree of genetic divergence is a continuous scale that spans over an order of magnitude of genetic distance between pairs of species that anyone would treat as separate species. Climate cycles have almost certainly reduced this isolated montane population to tiny sizes, thus making it easier for rapid differentiation. Regardless, I can't find a genetic dataset that included *confinis*.

For reference, here is a photo by one Pam Rasmussen: https://ebird.org/checklist/S28154856

And a bunch by my buddy and outstanding photographer Steve Mlodinow: https://ebird.org/checklist/S7809615

You can see in these photos that the bill is larger and subtly different in shape, as is also noticeable in the Hathaway plate above.

New information:

Nothing really new. Del Hoyo and Collar (2016) treated them as separate species and outlined the well-known plumage differences between the two as their rationale. From Terry's spreadsheet:

> HBW-Birdlife split: *confinis* "Previously considered conspecific with *T. migratorius*, but differs in its pale buff vs rufous breast to lower belly (3); mid-grey vs blackish-grey crown, head sides and throat streaks (2); complete vs partial white supercilium (2); somewhat longer bill (effect size 2.86, score 2); and marginally shorter tarsus (based on published evidence (Aldrich & James 1991) possibly 1); song "burrier and less strident" (Howell & Webb 1995), but at least some *T. migratorius* from Mexican mainland sound burrier than those farther N (ns), hence more vocal data needed." This was the treatment in AOU 1957, lumped in AOU 1983; adopted by WGAC.

Discussion:

Voice is the key indicator of species limits in *Turdus* and relatives, with the extreme example illustrated by the startling discovery (O'Neill et al. 2011, Condor 113: 869-880) of *Turdus sanchezorum*: by Dan Lane noticed call and then song differences among individuals of what was considered to be a single species that differed only in subtle plumage features that had been dismissed as variants of *T. hauxwelli*; Luciano Naka's genetic analysis in that paper showed that *sanchezorum* wasn't even part of the same group of *Turdus* species as *hauxwelli* . For better or worse, plumage differences are not considered sufficient criteria for species recognition, with the extreme case being the Island Thrush, *T. poliocephalus*, with 50 or so subspecies that differ dramatically in plumage and cover just about every form of plumage variation seen in the genus as a whole, but they have been treated as forming a single species in most classifications; see HBW plate.

As for *confinis*, the paler coloration is a predicted outcome of Gloger's Rule – southern Baja is among the driest, most open places inhabited by the *migratorius* lineage, as documented by Aldrich and James (1991; Auk), who used *confinis* as an example of this pattern of geographic variation and noted that the robin populations in the dry mountains of the Southwest already show paler breasts than other populations from more mesic areas. (As an aside, the Tobias et al. scheme for quantifying color differences treats the various parts of the plumage as separate characters, i.e. as if the parts of a bird were assembled LEGO style, but from a genetic standpoint, I wonder if such pigment dilution isn't just one "character" repeated throughout the plumage. The pale superciliary is longer in *confinis*, and thus is likely scored as a pattern difference …. but it nonetheless could be considered as another increase in extent of reduced pigmentation.)

Of interest to me with respect to the HBW/BLI scoring scheme is that if I'm interpreting correctly the text forwarded by Terry, 2 of the magic 7 points needs for species rank come from the slight difference in bill length. Seriously? Bill length and shape is one of the most plastic characters in the bird phenotype and thus one of the least-informative taxonomically. As just one of a thousand potential examples, bill length differences among Yellow-throated Warbler populations (which are noticeable in the field) are associated with predominant feeding substrate, yet

McKay's analysis of YTWA geographic variation indicates that no subspecies should be recognized.

Voice:

No formal analysis of differences in vocalizations has been published. As pointed out to me by Steve Mlodinow, some call notes are superficially indistinguishable; of the four cuts on xeno-canto (https://www.xeno-canto.org/species/Turdus-migratorius; all by Richard Webster), three seem indistinguishable but a fourth sounds very different (the first one on the list). If you click on the dot on the map at the tip of Baja, links to all four will appear.

The recordings in Macaulay include what might be the only online song recordings (by Peter Kaestner):
https://ebird.org/checklist/S89563091?_gl=1*1sovlet*_ga*MjE1Mzc3NTA0LjE2MzI4MDIwMDM.*_ga_QR4NVXZ8BM*MTYzMjgwMjAwMi4xLjEuMTYzMjgwMjI2Mi4x#flag-346352381&_ga=2.129947788.1016019827.1632802003-215377504.1632802003

And by Nick Roth:
https://ebird.org/checklist/S34578201?_gl=1*1pvt6tb*_ga*MjE1Mzc3NTA0LjE2MzI4MDIwMDM.*_ga_QR4NVXZ8BM*MTYzMjgwMjAwMi4xLjEuMTYzMjgwMjUwOS4zMQ..#flag-68020331&_ga=2.100570270.1016019827.1632802003-215377504.1632802003

Kaestner's recordings make it sound as if the song is indeed weaker and drier, as stated by Clement (2002), but Roth's recording of a male courting a female is much more like that of an Am. Robin, at least to my ear.

Recommendation:

So, there are some tantalizing potential differences, but these observations are not a substitute for a thorough analysis. Any taxonomic decisions based solely on cursory examination of online recordings is a really bad idea. In my opinion, any change in species limits would require a formal, published paper on comparative analogous vocalizations.

Therefore, I strongly recommend a NO on this proposal.

Note on English names:

San Lucas Robin (for Cabo San Lucas) has been in use for *confinis* for over a century, so sticking with that would be common sense if the split were adopted. No modification of our beloved American Robin would be needed, according to our guidelines, because *confinis* is clearly a peripheral isolate.

Literature Cited: (links or skeletal citations inserted throughout except for standard references)

Submitted by: Van Remsen

Date of Proposal: 28 September 2021

External comment on Proposal 2022-A-2

The various paintings (especially Hathaway) are not great, and don't capture the facial expression, which FWIW is subtly but distinctly different from AMRO: SLRO typically has a solid white eyebrow, unlike the broken pattern of AMRO, cf attached examples vs paler AMRO; that plus lack of (strong/any?) sexual dimorphism, plus differences (to my ears) in both song and call, now with lots more recordings available, would lean me towards splitting it, but as you know I don't keep lists and don't really care. It would fit into the Category Level 2 of splits = could go either way depending on philosophy, vs Category 1 = clear split, and Category 3 = possible split but more info needed.

FWIW the draft text for the in prep field guide (Howell & Dyer, Princeton) is:

*San Lucas [American] Robin *Turdus [migratorius] confinis* 23–25cm. Endemic to s. Baja, where replaces American Robin. Highland pine-oak forest, adjacent clearings, riparian corridors with taller trees. Habits much like American Robin, of which San Lucas Robin may be simply an isolated pale race. Paler underparts than American Robin, especially when faded in summer (fresh-plumaged San Lucas may be matched by palest American, which could occur as winter vagrant to s. Baja). Note unbroken whitish eyebrow, unlike American; sexes similar. Juv. browner overall with upperparts flecked buff, breast and flanks mottled dark brown. Sounds: Varied clucking calls parallel American Robin, but differ slightly in quality, shihk tuh-tuh-tuh..., etc. Caroling song similar to American Robin, but averages lower, burrier, slightly more hurried. Status: Fairly common to common in Sierra Victoria, mainly 1000–2000m, with some wandering lower in winter.

Submitted by: Steve Howell

Date of comment: 16 November 2021

Treat *Turdus plumbeus* (Red-legged Thrush) as (A) two species or (B) three species

Effect on NACC:

This would treat our existing species, *Turdus plumbeus*, as two, or three, species.

Background:

Currently treated by AOU as a single species, with two subspecies groups. It occurs throughout the Greater Antilles (except Jamaica, where there are two endemic *Turdus* species) but with an isolated population on Dominica in the Lesser Antilles (included within the Hispaniolan subspecies group). Here's the text from AOU (1998):

> "Resident [***plumbeus*** group] in the northern Bahama Islands (south to Andros and Cat Island), Cuba (and nearby cays), the Isle of Pines, Cayman Islands (Cayman Brac, with reports from Grand Cayman based on an escaped individual), and (formerly) the Swan Islands (in the western Caribbean Sea); and [***ardosiaceus*** group] in Hispaniola (including Gonâve, Tortue, and Saona islands), Puerto Rico, and Dominica* (in the Lesser Antilles)."
>
> * where it may or may not have been introduced – see Ricklefs and Olson 2009.
> Andy and Terry --- I think we should make a note of this in our distribution account

The HBW/BLI list, using the Tobias et al. scoring scheme, now treats it as constituting three species.

Taxonomic history:

- Ridgway (1907) treated the two groups as separate species and also treated *rubripes* of Cuba etc. as a third species. His key separated them by the well-known plumage differences in terms of having a paler head and underparts.

    1. *Mimocichla ardosiacea*: nominate subspecies (Haiti) + *portoricensis* (Puerto Rico) + *albiventris* (Dominica)
    2. *Mimocichla plumbea*: monotypic (Bahamas)
    3. *Mimocichla rubripes*: nominate subspecies (w. Cuba) + *eremita* (Swan Is.) + *coryi* (Cayman Brac) + *schistacea* (e. Cuba)

- Hellmayr (1934) treated the complex as consisting of two species, with the *rubripes* group included in *M. plumbea.* His footnote reads: "*Mimocichla schistacea* is so clearly intermediate to the Bahaman Thrush as to indicate conspecific relationship, and I have no hesitation in associating *M. rubripes* and allies with *M. plumbea*, the various forms constituting a natural group and replacing each other geographically."

- Ripley in "Peters" (1964) treated them all as conspecific (but now in *Turdus*) without comment (and synonymized *portoricensis* in *ardosiaceus* and *eremita* in *rubripes*)

- AOU (1983) followed "Peters" but recognized two groups:

> “Notes.—A few authors have considered the populations from Hispaniola eastward to Puerto Rico and Dominica to represent a species, *T. ardosiaceus* Vieillot, 1823 [Eastern Red-legged Thrush], distinct from *T. plumbeus* [Western Red-legged Thrush]. See also comments under *T. ravidus*.”

- Raffaele et al. (1998, A Guide to the Birds of the West Indies) treated than all as conspecific and did not mention any differences among the taxa other than plumage.

- Clement (2000, Thrushes, Princeton U. Press) treated them as conspecific but noted “Races *ardosiaceus* and *albiventris* are regarded as some as representing a distinct species – Eastern Red-legged Thrush – and further research is considered likely to support this division.” In the VOICE section, he noted distinctive calls for *coryi* and nominate *ardosiaceus* but did not place them in a comparative context. The excellent plate from that book, by Ren Hathway, is provided on the next page to illustrate the critical taxa. Note the differences in bill color, which do not seem to be taken into account by HBW/BLI. Note that the eyering colors are evidently the same.

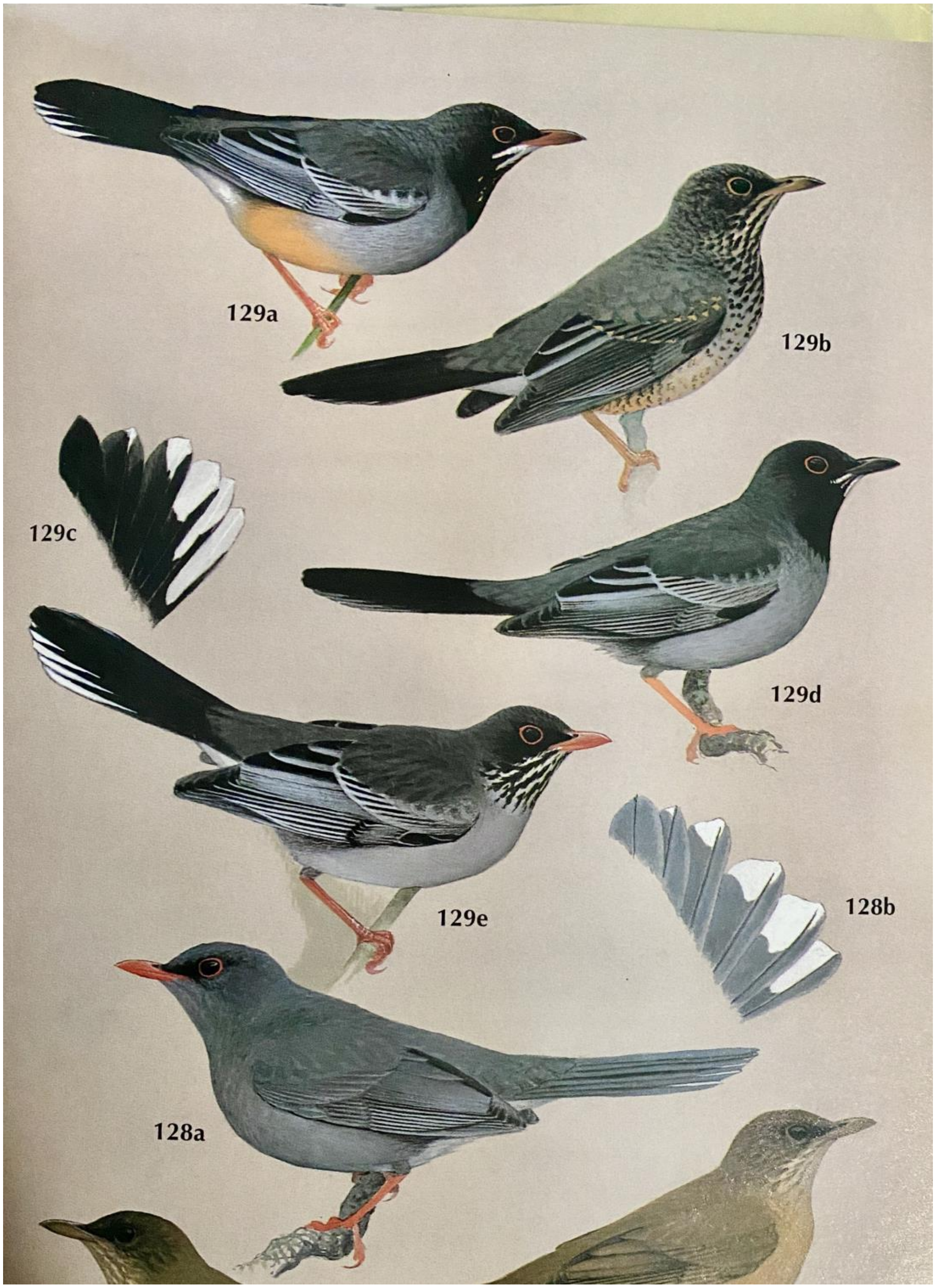
- Collar in HBW (2005) treated them as conspecific, but stated: “Has been suggested the E races *ardosiaceus* and *albiventris* warrant treatment as a separate species.” Here’s the HBW plate:

- Dickinson & Christidis (2014; H&M4) treated them as conspecific but divided the six subspecies between two groups, following AOU (1998).

(• I gave away all my James Bond West Indies stuff but can almost guarantee that he treated them all as one species.)

Genetic Data:

As for genetic data, as noted in the *Turdus confinis* proposal, I’m not sure what they could tell us on species limits in allotaxa; degree of genetic divergence is a continuous scale that spans over an order of magnitude of genetic distance between pairs of species that anyone would treat as



129a = *rubripes*
129d = *plumbeous*
129e = *ardosiaceus*
[128a = extinct *T. ravidus* from Grand Cayman, which has always been treated as part of this superspecies]

separate species. Climate cycles and catastrophic hurricanes have almost certainly reduced these insular populations to tiny sizes, thus making it easier for rapid differentiation.

Gary Voelker and colleagues' studies of *Turdus* did not include samples of both groups as far as I can tell, nor did Nagy et al.(2019). Pan et al. (2007) included few New World taxa, much less the *plumbeus* group. Nylander et al. (2008) included both *plumbeus* and *ardosiaceus* in their analysis of DNA sequence data. They found that they were sisters with what might be an above-average genetic distance between them for conspecifics but certainly not out of the range; they did not discuss species limits. Batista et al. (2020) sampled both *schistaceus* from Cuba and *ardosiacus* from Puerto Rico but evidently treated them as one taxon in their summary tree (Fig. 4).

New information:

Nothing really new. Del Hoyo and Collar (2016) not only treated them as separate species but also elevated *rubripes* to species rank; they outlined the well-known plumage differences among the three as their rationale. From Terry's spreadsheet:

> "HBW-Birdlife split into 3 species (but WGAC adopted 2-species arrangement): *T. ardosiacus* hitherto treated as conspecific with *T. plumbeus* and *T. rubripes*, but differs from former in characters given under that species (see related note/s). Differs from latter (comparing geographically and morphologically closest form *schistaceus*) in its black-and-white-striped vs black streaky throat (3); paler grey breast and flanks (1); white vs pale tan belly (2); narrower frequency range for lower-pitched notes in song, making these notes melodious rather than squeaky (1) (Boesman 2016)."

Their classification is as follows:

1. *Turdus plumbeus* (Northern Red-legged Thrush): Bahamas.
2. *Turdus rubripes* (Western Red-legged Thrush): including nominate from w. Cuba, *schistaceus* from e. Cuba, and *coryi* from Cayman Brac.
3. *Turdus ardosiaceus* (Eastern Red-legged Thrush: including nominate from Hispaniola and Puerto Rico, and *albiventris* from Dominica.

Boesman (2016) presented a few sonograms from several populations and concluded:

> "There is a slight vocal difference between *ardosiaceus* (Hispaniola/Puerto Rico) and other races (Cuba/Bahamas): *ardosiaceus* alternates 1-3 fairly melodious whistles at lower pitch with 1-2 high-pitched notes. Other races have a similar alternating series of notes, but the lower-pitched notes are not at all melodious, rather squeaky (which can be seen from the large freq. range they cover, or loud harmonics or non-harmonic frequency bands). There is however some overlap, especially birds of Bahamas (*plumbeus*) are rather intermediate. This could be given a vocal score of 1 (smaller freq. range of low-pitched notes and/or lack of loud harmonics for *ardosiaceus*). A more thorough analysis would be required to find out if vocabulary of notes is distinct among races, but a larger set of recordings would be needed to perform such analysis."

In a new volume of the BOC Checklist Series (#26), Kirkconnell. Kirwan, Garrido, Mitchell, and Wiley (2020, Birds of Cuba) treated all taxa as conspecific (and noted that there is a zone of intergradation between *schistaceus* and *rubripes* that spans several provinces).

Discussion:

Voice is the key indicator of species limits in *Turdus* and relatives, as outlined in my proposal on *Turdus* [*m*.] *confinis*. If I'm interpreting correctly the text forwarded by Terry, 6 of the magic 7 points come from plumage differences, which are not necessarily associated with species boundaries in *Turdus*, whereas only 1 comes from vocal differences.

Boesman (2016) provided the only comparative assessment of vocal differences among the groups, and noted potential differences among taxa, but he emphasized that his N was small and that further research was needed. Thus, the HBW/BLI score of "1" in terms of vocal differences is basically an assumption. *Turdus* songs are fairly complex, so further research is clearly needed. Finally, Garrido and Kirkconnell (2000; Field Guide to the Birds of Cuba) noted that the Cuban taxa frequently copy call notes of other species into its song. If this occurs on other islands as well, then the possibility that differences among islands are generated strictly by different local models for copying must at least be considered.

For voting purposes, this proposal is divided into two parts:

A. Treat the two AOS groups as separate species, i.e. *Turdus plumbeus* and *Turdus ardosiaceus*.

On this I recommend a NO. Until a formal analysis of vocalizations is published, I would regard the assessment by Boesman (2016) as suggestive but insufficient, as he himself would certainly agree. That leaves a plumage differences as the basis for taxon rank, i.e., hopeless in my opinion for allopatric *Turdus* and despite an attempt at quantification and the appearance of objectivity by HBW/BLI, basically a subjective decision that really doesn't differ from those made in the early 1900s. The only reason I can see to vote YES is that the original treatment of the two subspecies groups as representing a single species has never been justified – yet another victim of the mid-1900s Lumperama Purge. This is a reasonable position, given that astute museum scientists such as Ridgway and Hellmayr assessed the plumage differences as representing separate species. Perhaps burden-of-proof ought to be on the single species treatment. Nonetheless, I think we should wait until we have at least some better information on vocal differences, which would be relatively easy to accumulate, before making such a change.

B. Further treat *Turdus rubripes* (with *schistaceus* and *coryi*) as a separate species from *Turdus plumbeus*.

On this one, I strongly recommend a NO. With a broad zone of intergradation between the two, that is sufficient evidence for treating them as conspecific. (In the Tobias et al. scheme, hybridization counts 1 point FOR separate species status! – don't ask me to explain that one!)

Note on English names:

If the splits are adopted, I recommend following the geographically modified names on the stem "Red-legged Thrush." Most people don't like compound names, and hardly anyone is thrilled by insipid modifiers like Eastern and Western; nonetheless, I would favor using them here because retaining Red-legged Thrush in the formal English name serves to remind us that they are sisters and helps distinguish them from an exceptionally large number of unmodified "Something" Thrushes. Also, they already have some traction. Not enough in my opinion to overturn them if a really good alternative were available, but I don't see one.

Literature Cited: (links or skeletal citations inserted throughout except for standard references)

Submitted by: Van Remsen

Date of Proposal: 29 September 2021

External comment on Proposal 2022-A-3

I was surprised by the omission of one reference in this proposal: Ricklefs and Bermingham (2008), Likely human introduction of the Red-legged Thrush (*Turdus plumbeus*) to Dominica, West Indies. *The Auk* 125 (2): 299–303. This is available online at https://repository.si.edu/bitstream...nd_Bermingham_2008.pdf?sequence=1&isAllowed=y

This paper is relevant because it actually does contain a little bit of genetic information. In mitochondrial DNA, they found 16 fixed differences out of 842 bp = 1,9% between the Bahamas-Cuba-Caymans group and the Hispaniola-Puerto Rico-Dominica group (See figure 1). Based on the figure, there will be a couple of additional differences between any bird in Hispaniola and one in either Cuba or Bahamas.

I personally feel the Red-legged Thrush likely should be split in two species, but I also realize this additional information is unlikely to have a strong effect on the voting.

Submitted by: Niels Larsen (author of the Birds of the World account of Red-legged Thrush)

Date of comment: 26 March 2022

Treat *Turdus daguae* as a separate species from *Turdus assimilis* (White-throated Thrush)

Effect on NACC:

This would treat the southernmost subspecies (*daguae*) of our *Turdus assimilis* as a separate species.

Background:

This taxon is currently treated by NACC and SACC as a subspecies of *Turdus assimilis*, but as a result of anecdotal comments, NACC and Dickinson & Christidis (2014) treated it as a subspecies "group". Here's the text from AOU (1998):

> "Groups: *T. assimilis* [White-throated Thrush] and *T. daguae* Berlepsch, 1897 [Dagua Thrush]. *Turdus assimilis* and the South American *T. albicollis* Vieillot, 1818 [White-necked Thrush], constitute a superspecies (Sibley and Monroe 1990). Many authors (e.g., Wetmore 1957, Wetmore et al. 1984, Ripley in Mayr and Paynter 1964) consider them conspecific but see Monroe (1968) and Ridgely and Tudor (1989)."

I included the part about *albicollis* to explain why some older literature treats *daguae* under Middle American *Turdus albicollis*; also, *albicollis* becomes part of the problem, as you'll see below.

<u>History of taxonomic treatments</u>
Berlepsch described *daguae* as a species in *Turdus* in 1897 from lowland western Colombia, with the Río Dagua as part of the type locality, which is south of Buenaventura and NW of Cali (dpto. Cauca). Ridgway (1907) did not mention the taxon, so I assume it was not recorded in Panama until sometime after 1907. However, Hellmayr (1911; PZSL), Bangs & Barbour (1922; Bull. MCZ), and Chapman (1926: Birds of Ecuador), soon treated *daguae* as a subspecies of *Turdus assimilis* (at that time known as *Turdus tristis*).

Hellmayr (1934) treated it as a subspecies of *T. assimilis* with the following explicit rationale:

> "*Turdus assimilis daguae* Berlepsch: Differs from *T. a. cnephosa* [the adjacent subspecies in central Panama] in smaller size, shorter bill, much darker (bister brown) upper parts, and very much darker, nearly sepia brown color of the chest, sides, and flanks. ….
> "In coloration, this race comes nearest to *T. a. rubicundus*, but is still much more intensely colored. Although its much smaller dimensions and its shorter, entirely dusky bill serve to distinguish it without difficulty, yet the close similarity to the west Guatemalan form seems to afford sufficient evidence for its association with the *assimilis* group, which, as suggested by Miller and Griscom, may ultimately prove to be conspecific with *albicollis*."

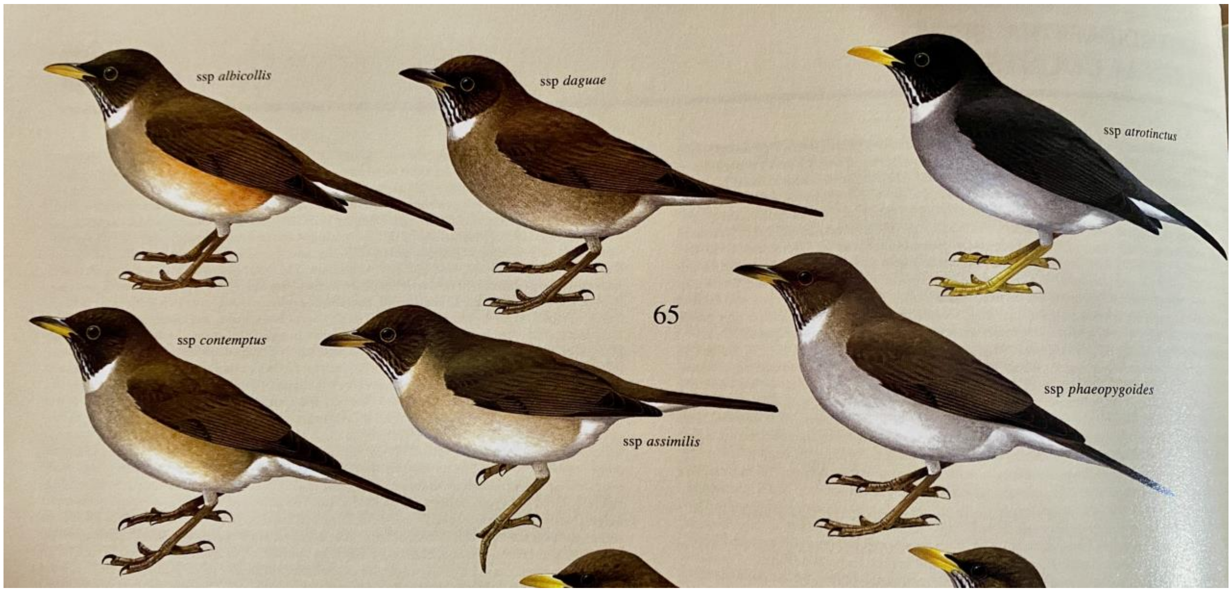
This treatment was followed by essentially all subsequent authors, including Ripley in "Peters" (1964), Meyer de Schauensee (1966), and the AOU 1983, which stated: "The populations of *T. assimilis* from eastern Panama (eastern Darien) south to Ecuador are sometimes considered a distinct species, *T. daguae* Berlepsch, 1897 [Dagua Robin]." I'm actually uncertain where this statement "sometimes" came from because I can't find a treatment from the 1900s on that did treat it as a separate species. [Anecdote: the frustration that hundreds of examples like this in AOU 1983 caused me to start lobbying when I joined the Committee in 1984 for citations for all such statements in future AOU Checklists; Burt Monroe, who wrote almost all those Notes in the 1983 Checklist, often could not remember the source of many of the statements.]

Subsequently, Ridgely & Tudor (1989) treated *daguae* as a subspecies of *T. assimilis* and mentioned only that it was not well known. Clement (2000; Thrushes; Princeton U. Press) listed it as the southern subspecies of the 10 that he recognized for *T. assimilis*; he described the plumage differences but did not illustrate it separately.

Then, Ridgely & Greenfield with the collaboration of Robbins and Coopmans (2001; The Birds of Ecuador Vol. 1) treated *daguae* as a separate species (Dagua Thrush) from *T. assimilis*, with the following text --- note that no actual data are presented:

> "*Daguae* has usually been treated as a subspecies of *T*. *assimilis* …. Now that more information is available regarding the voice of *daguae* – it is distinctly different from that of *T. assimilis* of Middle America – we consider it more appropriate to treat *T. daguae* as a separate monotypic species, differing not only in voice but also in several morphological features. *Daguae*'s voice actually more closely resembles that of cis-Andean *T*. *albicollis*, suggesting that *daguae* may be more closely related to that species."

Collar in HBW (2005) not only treated them as conspecific but also treated all of *assimilis* as conspecific with South American *T*. *albicollis.* He mentioned that *daguae* had been proposed as a separate species. Here is the relevant section of the plate:



Dickinson & Christidis (2014) treated *daguae* as conspecific with *T. assimilis* but placed *daguae* in its own subspecies group, as per AOU (1998), and cited Ridgely & Greenfield for the possible split. Angehr and Dean (2010; The Birds of Panama. A Field Guide) treated them as conspecific; their range maps nicely illustrate the substantial gap in their distributions in the lowlands of central Panama.

Del Hoyo & Collar (2016) treated *daguae* as conspecific with …. drumroll … not *T. assimilis* but with cis-Andean *T. albicollis*. This was based on Boesman (2016), who actually used the Collar (2005; HBW) species limits, i.e. broadly defined *T. albicollis*, not the two species treatment in Del Hoyo & Collar (2016). His analysis, however, shows that *T. assimilis* is clearly different from *T. albicollis* in song features, and that the song of *daguae* is actually difficult to distinguish from the eastern group of *T. albicollis* subspecies. Although Boesman would be the first to tell you that more in-depth analysis is needed, he does establish that if voice is a reliable indicator, then *daguae* belongs with *T. albicollis*. Recall also that Ridgely & Greenfield (2001) noted the similarity of *daguae* song to that of *albicollis*. That trans-Andean Chocó and cis-Andean populations are sisters is a common biogeographic pattern in Neotropical birds.

Genetic data

As for genetic data, as argued in previous proposals, I think they are of dubious value for determining taxon rank of allopatric populations, although perhaps our best estimates of divergence times.

The only study that specifically addressed the *daguae* issue was that of Núñez-Zapata and Peterson (2016), which focused on the *T. assimilis* group. Using 2 mitochondrial genes (cyt-b, ND2) and 25 individuals, their tree shows that *daguae* is strongly separated, with strong support, from the other subspecies and populations of *assimilis* (see tree on next page).

Of interest is that *daguae* is sister to *assimilis*, not the *albicollis* group, which provides evidence against inclusion of *daguae* in *T. albicollis* as in Del Hoyo and Collar (2016). However, this result could be a "gene tree/species tree" or ILS problem given the limited gene sampling, and so hopefully subsequent studies will include nuclear or genomic data. Meanwhile, this places burden-of-proof, in my opinion on moving *daguae* to *albicollis*.

Núñez-Zapata and Peterson (2016) considered the genetic data as indicating species rank for *daguae* based on genetic distance and reciprocal monophyly. However, they themselves noted the problems with using comparative genetic distances. Also, with N=6 *daguae* samples, all from three localities in NW Ecuador near the southern extreme of its range, a claim of reciprocal monophyly seems premature. All such claims are one additional sample away from being refuted. (Would someone please write a paper on the problems with "reciprocal monophyly" with respect to N and geographic sampling; certainly, some minimum number of specimens would seem required to make such a claim, depending on genes sampled, as well as some consideration of the geography of sampling given that the probability of detecting shared alleles should decrease to some degree with distance from the former contact zone.)

Batista et al. (2020) used UCEs in their broad study of *Turdus* but unfortunately did not include *daguae.*

1078 J Ornithol (2016) 157:1073–1085

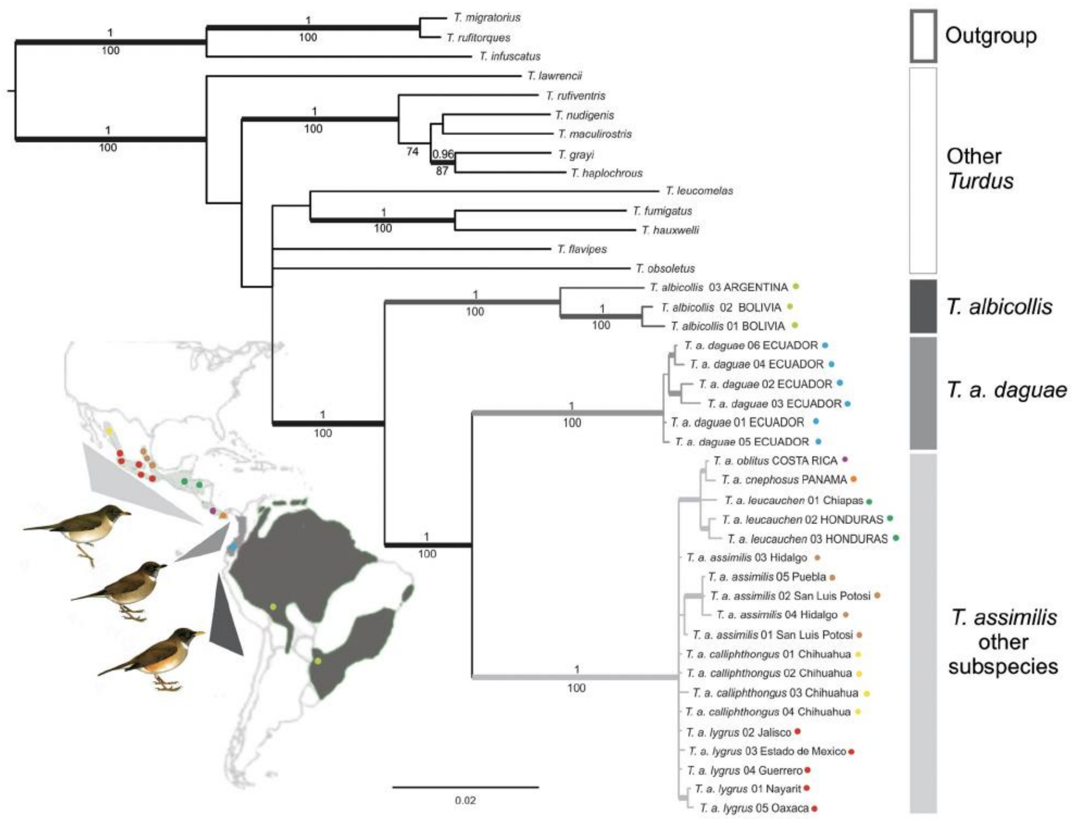


Fig. 1 Phylogenetic relationships of *T. assimilis* and related species according to ND2 and Cyt B sequences. Majority-rule consensus tree based on 18,000 trees obtained by applying the B/MCMC tree sampling procedure using the mitochondrial data set is shown. Posterior probabilities of ≥0.95 in the Bayesian analysis are indicated *above the branches*; values below the branches are ML bootstrap values of ≥70 %. Branches that received strong support in both analyses (RaxML and B/MCMC) are shown in *boldface*. *Colored circles* represent localities of the material collected and the subspecies included in the present study. Illustrations of *T. a. assimilis*, *T. a. daguae*, and *T. albicollis* were obtained from Collar (2015) with the permission of HBW Alive

Discussion:

Voice is the key indicator of species limits in *Turdus* and relatives, as outlined in my proposal on *Turdus* [*m*.] *confinis*. Between xeno-canto and Macaulay there are a sufficiently large number of recordings from throughout the range of the *assimilis-albicollis* group that someone could pick up where Boesman left off and do a formal analysis of songs and calls to analyze species limits. Until that is done, I do not see how we can change the status quo. On the one hand, a preliminary inspection of songs suggests *daguae* is closer to *albicollis* than to where we have it at present, in contrast to a genetic data set that suggests that it is close to *assimilis*. The weaknesses in both analyses make it unwise, in my opinion, to change current classification, either in terms of taxon rank or relationships.

Recommendation:

Too much uncertainty remains, in my view, to make any changes, and so I recommend a NO vote on this one.

Note on English names:

Dagua Thrush has a track record and is the only English name associated with the taxon. Although Río Dagua was an important early collecting locality, it is nonetheless a pretty obscure river in the greater scheme of things. Whether it's worth changing to something like Choco Thrush is at least worth considering. This taxon's range corresponds almost perfectly to the Chocó biogeographic region, and its plumage, darkest brown of any on the *assimilis-albicollis* group, also reflects a prevailing Gloger's Rule color trend shown by taxa endemic to the region. On the other hand, there are already 9 "Choco Somethings", so at least Dagua Thrush is novel. Because 99% of its range is in SACC territory, if split, perhaps it would be best for that committee to pick the name.

Literature Cited: (links or skeletal citations inserted throughout except for standard references)

Submitted by: Van Remsen

Date of Proposal: 1 October 2021

Reassess the taxonomy of the *Pampa curvipennis* (Wedge-tailed Sabrewing) complex: (a) lump *excellens* with *curvipennis*, and (b) split *pampa* from *curvipennis*

Description of the problem:

The *Pampa curvipennis* complex comprises three allotaxa found in eastern Mexico, Belize, and Guatemala. From north to south, *Pampa c. curvipennis* (Deppe, 1830) is found in the eastern cloud forests and adjacent foothills of the Sierra Madre Oriental from Tamaulipas to northern Oaxaca and southern Veracruz, *Pampa excellens* Wetmore, 1941, replaces *curvipennis* to the south in the Sierra de los Tuxtlas and the highlands of western Chiapas, and *Pampa c. pampa* (Lesson, 1832) is a lowland taxon widespread in the Yucatán Peninsula as far west as eastern Chiapas and Tabasco (Arizmendi et al. 2021).

The three were long considered subspecies (e.g., Ridgway 1911, Cory 1918, Wetmore 1941, Peters 1955) until Lowery and Dalquest (1951) showed skeletal differences between *excellens* and *curvipennis*, namely a decidedly larger skull in the former. This comparison, however, was based on a single specimen. Ridgway (1911) listed a single specimen from Apazote, Campeche (well within the distribution of *pampa*), as being intermediate between *pampa* and *curvipennis*, but nearer the latter. Based on this information, AOU (1983) split *excellens* with the following comment: “The morphologically distinct form from the Yucatan Peninsula and northern Central America has been treated as a separate species, *C. pampa* (Lesson, 1832) [WEDGE-TAILED SABREWING], although intergradation with *c. curvipennis* [CURVE-WINGED SABREWING] in Campeche has been reported. *C. curvipennis* and *C. excellens* are treated as conspecific by many authors; they constitute a superspecies. Further study of this complex is needed.” This is the current treatment of the complex.

New information:

A more recent series of papers have addressed genetics, morphometrics, and song of the three taxa in the group (González and Ornelas 2005, González et al. 2011, González and Ornelas 2014, Cruz-Yepez et al. 2020). In particular, González et al. (2011) used two mitochondrial and ten microsatellite markers from 160 individuals of all taxa and showed that the primary genetic break in the group is between *pampa* and *curvipennis/excellens* (see their Figs. 1, 2, and 3 on following pages). Notably, some analyses placed *excellens* as barely differentiated or embedded within *curvipennis*. Migration rates based on microsatellite data showed minimal ongoing gene flow between taxa, although somewhat higher gene flow between *excellens* and *curvipennis* (Table 4). Using mitochondrial molecular clock rates of 2% and 5% per million years, the divergence of *pampa* dated to 1.47 Mya or 0.52 Mya, whereas the divergence of *excellens* and *curvipennis* dated to 614,000 or 202,000 years.

Morphometric data from wing chord, bill length, and tail length showed the relatively larger size of *excellens* in comparison to the other two taxa, but also showed a relatively shorter bill length in male *pampa* in comparison to both *excellens* and *curvipennis* (González et al. 2011; see Fig. 4 below). Using a Jaccard similarity dendrogram (Fig. 5), González et al. (2011) found that songs clustered by taxon, but also that there were differences between populations within *curvipennis*. This intra-subspecific song structure (within *curvipennis*) was investigated by González and Ornelas (2005, 2014), who attributed their findings to a combination of geographic isolation and vocal learning.

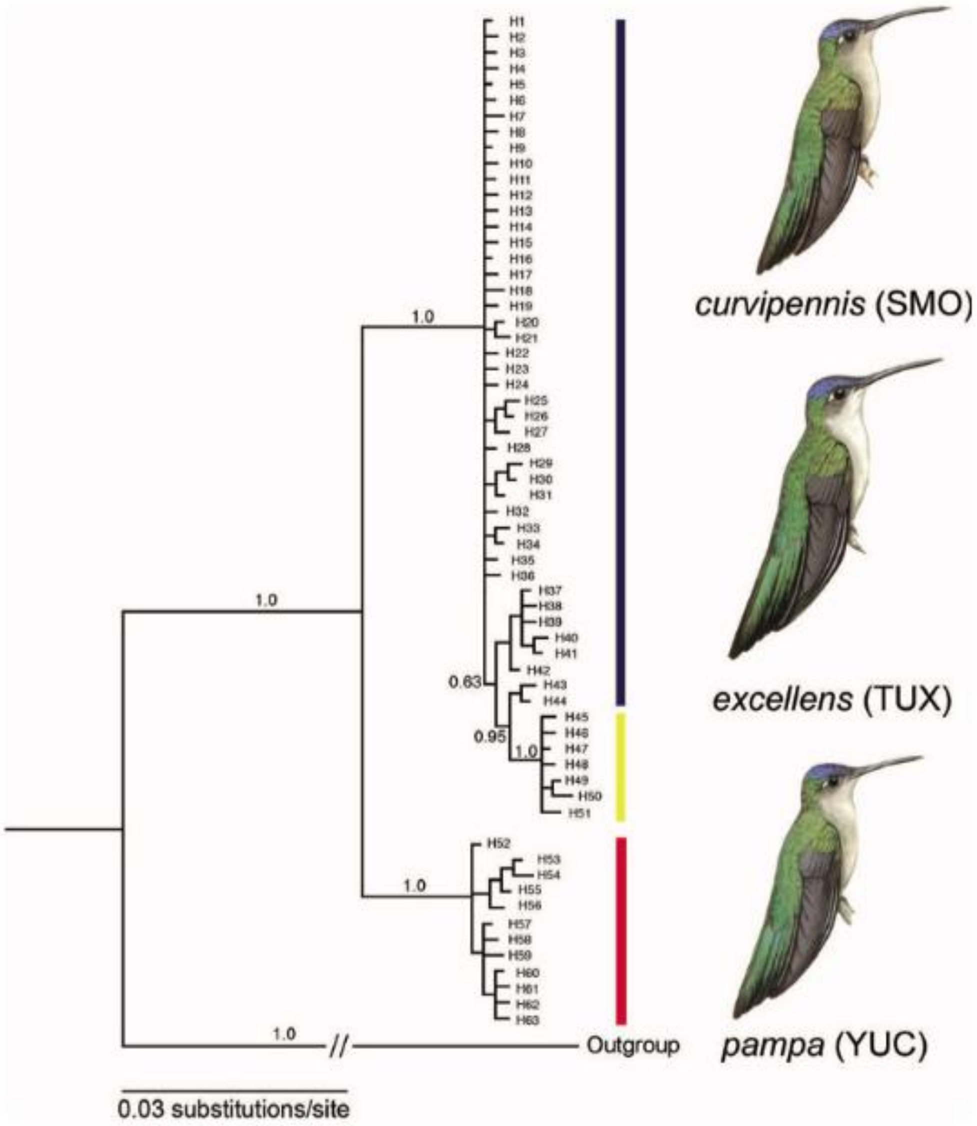


Figure 1 Phylogenetic relationships among mtDNA haplotypes based on Bayesian inference. Values above branches denote posterior probabilities, and numbers at the tip of the branches indicate distinct haplotypes. Outgroups were *Campylopterus rufus*, *C. hemileucurus*, and *C. largipennis*, and are shown collapsed into a single branch. Hummingbird illustrations were taken from color plates in the *Handbook of the Birds of the World* [32].

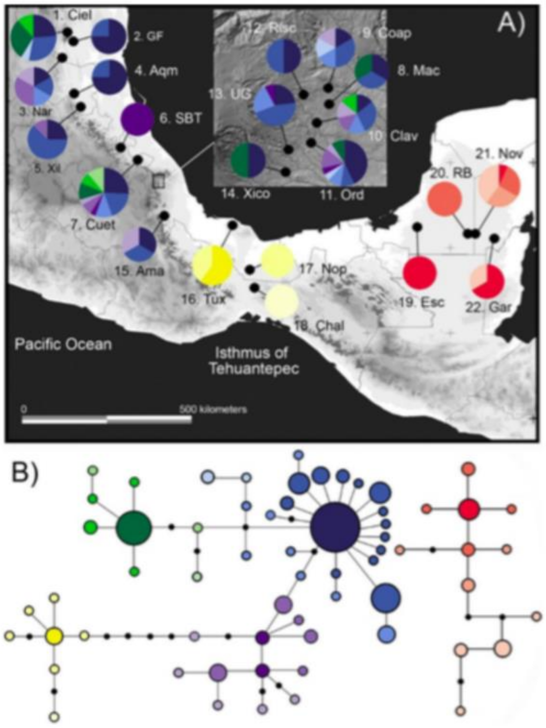


Figure 2 Sampling localities, geographic distribution, and genealogical relationships of mtDNA haplotypes. A. Pie charts indicate the frequency of occurrence of haplotypes in each population, and colors correspond to those shown in the haplotype network below. The current natural range of cloud forest (indicated by dark gray shading) is overlaid on a relief map of eastern Mexico. **B.** Statistical parsimony haplotype network derived from a combined matrix of mitochondrial genes (ATPase 6-8 and control region). Each circle represents a haplotype and its size is proportional to its frequency. Lines represent a single mutational change and black circles correspond to unsampled haplotypes.

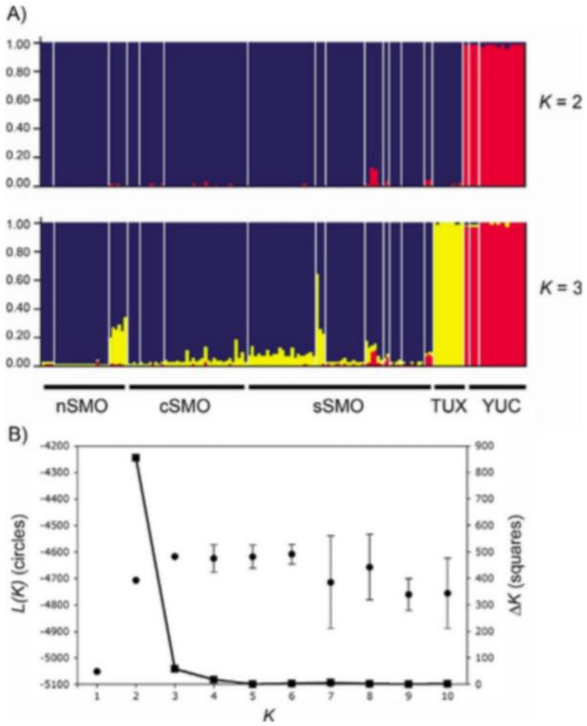


Figure 3 Spatial genetic structure determined by a Bayesian assignment analysis using STRUCTURE. A. Posterior assignment probabilities of 160 individuals of *Campylopterus curvipennis* to an optimal number of $K = 2$ and $K = 3$. Each individual is represented by a vertical line that is partitioned into K colored sections, with the length of each section proportional to the estimated membership coefficient. **B.** Mean log probability of the data ($L(K) \pm$ SD) over 10 runs for each K value (left Y axis) and values of ΔK calculated according to Evanno *et al.* [90] (right Y axis).

Table 4 Estimates of M (mutational corrected migration) from the MIGRATE analysis of microsatellites among genetic groups

	SMO	TUX	YUC
SMO	-	1.48 (0.58 - 4.22)	0.58 (-0.1 - 1.56)
TUX	1.98 (0.54 - 3.81)	-	0.49 (-0.68 - 3.39)
YUC	0.91 (0.03 - 2.29)	0.63 (-0.25 - 1.58)	-

Donor populations are in the first column. Estimates given are followed by 95% confidence intervals and none of the comparisons was significantly greater than 1.

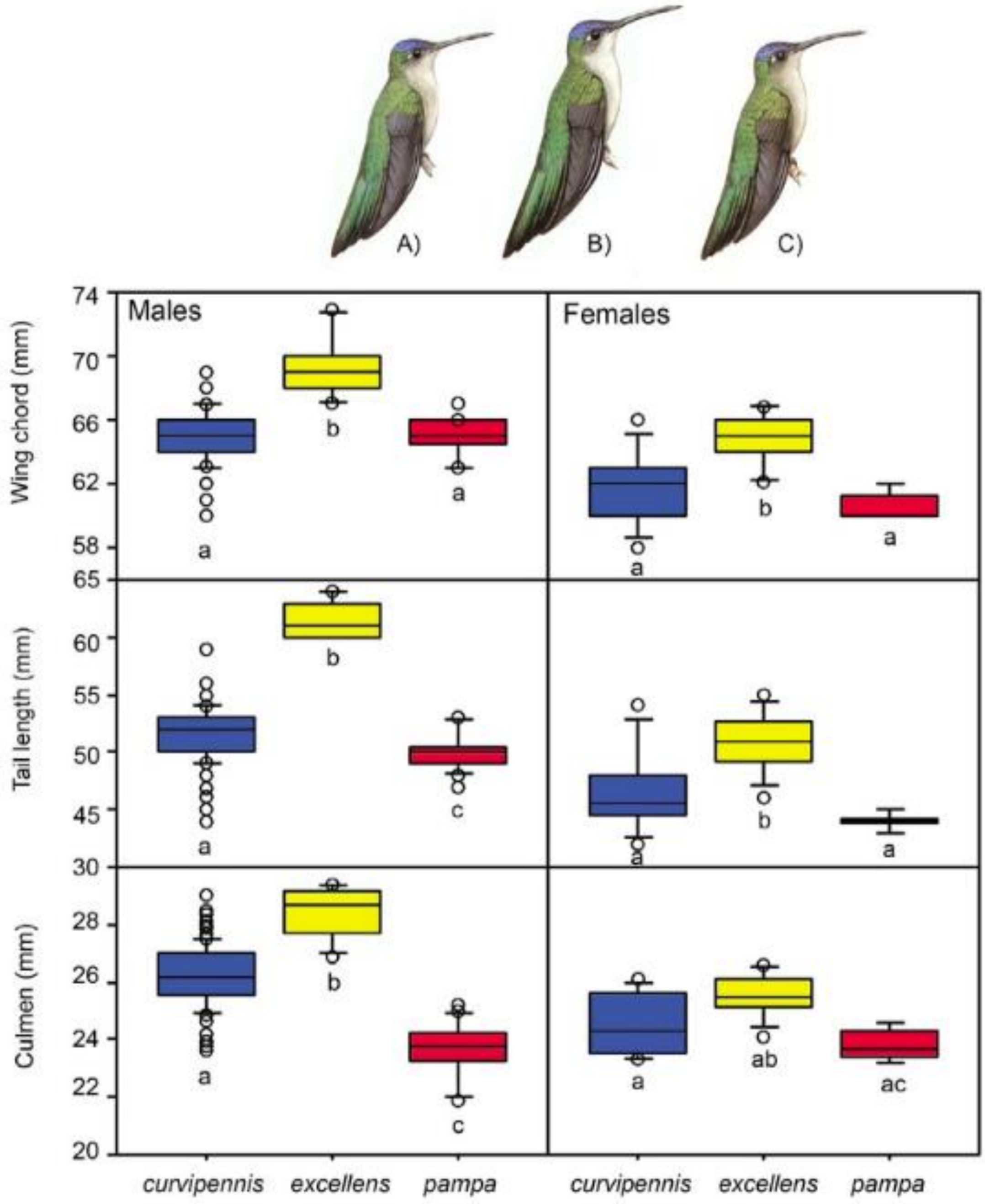


Figure 4 Morphological traits taken for males and females of *C. curvipennis* lineages. Boxplots show the 10th, 25th, 50th (median), 75th, and 90th percentiles. Values above the 90th and below the 10th percentile are plotted as open circles. Illustrations correspond to *C. c. curvipennis* (**A**), *C. c. excellens* (**B**) and *C. c. pampa* (**C**) taken from the *Handbook of the Birds of the World* [32].

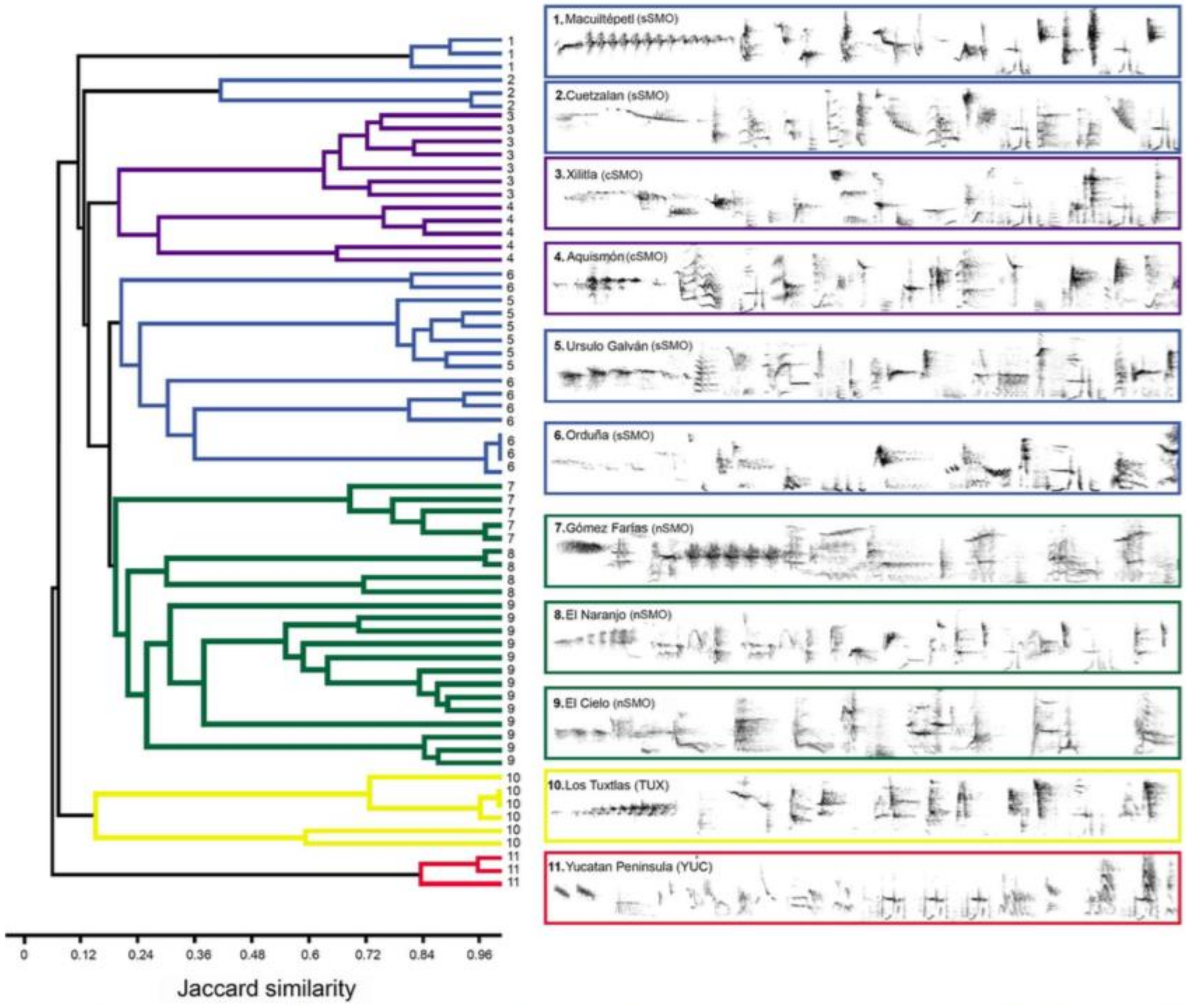


Figure 5 Dendrogram generated by cluster analysis of a presence/absence matrix of syllable types from recordings of individuals. Colored lines correspond to individuals recorded at different geographic locations: green, purple and blue correspond to sites located in the northern, central and southern parts of the Sierra Madre Oriental respectively (nSMO, cSMO, and sSMO) for the *C. c. curvipennis* lineage, yellow corresponds to the Tuxtlas region for the *C. c. excellens* lineage and red corresponds to the Yucatan Peninsula for the *C. c. pampa* lineage. Attached to the dendrogram fragments of vocalizations (4 sec) representing each sampled site are shown.

Song playback experiments focused on *P. c. curvipennis*, with no song playback experiments conducted on the other two taxa (Cruz-Yepez et al. 2020). However, those experiments showed that *curvipennis* responds equally to songs of *curvipennis* and *excellens*, but with lower response to songs of *pampa*, suggesting some degree of pre-mating isolation between *curvipennis* and *pampa*. However, the lower response to *pampa* is not very drastic, and confidence intervals overlap considerably. See figure from Cruz-Yepez et al. (2020) below.

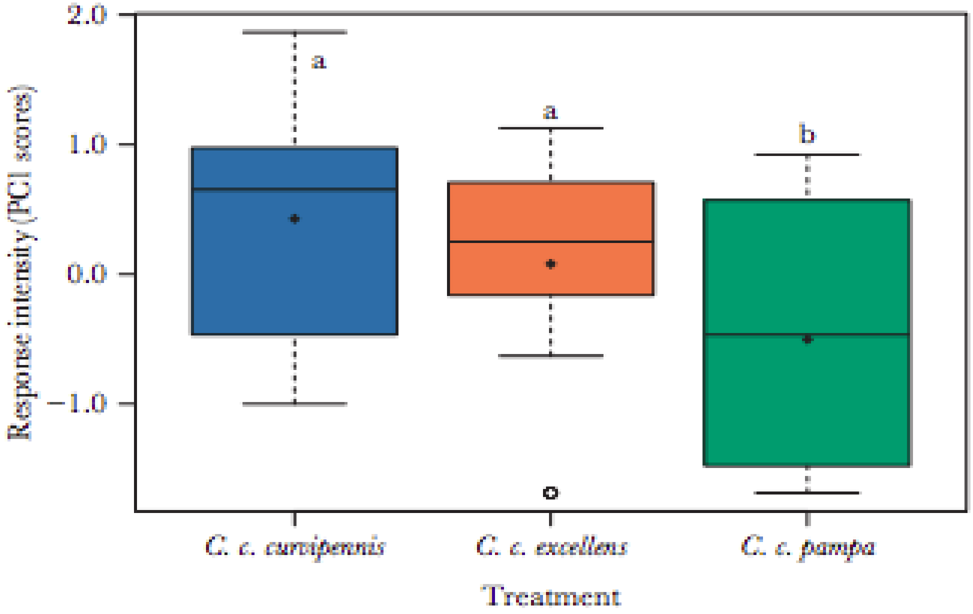


Figure 2

Response intensity (represented by PC1 scores) of *Campylopterus c. curvipennis* individuals exposed to songs of *C. c. curvipennis*, *C. c. excellens*, and *C. c. pampa*. Thick lines represent the median, and diamonds the mean. Letters indicate significant differences among treatments, result of Tukey post hoc tests.

Photos of males from the LSU collections are on the next page. In each photo, the specimens left-to-right represent the taxa in a north-to-south order: 2 *curvipennis*, 2 *excellens* from the Chiapas highlands, 2 *excellens* from Sierra de los Tuxtlas, and 2 *pampa*. Note the browner under parts and paler upper parts of *curvipennis*, the large size and pale whitish under parts of *excellens,* and the small size and darker gray underparts of *pampa*. Of note are the two *excellens* from the Chiapas highlands, which were identified as *curvipennis* by Charles Ely, but this population is typically considered to be *excellens*. These two specimens are similar in size to *excellens* from the Tuxtlas and roughly the same color below, but have a bit more brownish wash on the flanks.


LA. STATE UNIV. 11077 MUSEUM OF ZOOLOGY
MEXICO: San Luis Potosi: XILITLA ROAD
SEX ♂
DATE December 23, 1946 MARCELLA NEWMAN
LA. STATE UNIV. 11066 MUSEUM OF ZOOLOGY
MEXICO: San Luis Potosi: XILITLA
SEX ♂
DATE February 10, 1947 MARCELLA NEWMAN
COLLECTION OF CHARLES A. ELY
LSUMZ 168030
1970 COLLECTOR—CHARLES A. ELY
CAE 4460
LA. STATE UNIV. 28762 MUSEUM OF ZOOLOGY
Mexico: Volcán San Martín Tuxtla, Ver. ♂
25 August 1962 Robt. F. Andrle
LA. STATE UNIV. 28763 MUSEUM OF ZOOLOGY
Mexico: 4 mi. ENE Tapalapan, Ver. ♂
1 Sept. 1962 Robt. F. Andrle
LA. STATE UNIV. 21002 MUSEUM OF ZOOLOGY
HONDURAS
13 MAY 1956
STEPHEN M. RUSSELL
795
LA. STATE UNIV. 20560 MUSEUM OF ZOOLOGY
29 March 1955 Stephen M. Russell
356


pterus curvipennis
138
curvipennis
214
LSUMZ 168029
Collector - Charles A. Ely
LA. STATE UNIV. 28762 MUSEUM OF ZOOLOGY
25 August 1962 Robt. F. Andrle
March 1955 Stephen M. Russell
356

The primary issue here seems to be whether to place greater importance on the differentiation in song, plumage, or genetic data, as the patterns between taxa in each trait are different. In particular, *excellens* differs in morphometrics but not genetics, whereas *pampa* differs in genetics but to a lesser degree in morphometrics. Gene flow between all taxa appears to be low, although greater than zero. This is clearly a borderline case. All the differences between these taxa are small, and they are very closely related.

Recommendation:

We tentatively recommend a YES vote on lumping *excellens* with *curvipennis* based on the molecular data, and pending additional studies in the possible contact area in northern Chiapas (playback experiments and expanded genetic sampling), although we note that this is the most distinct taxon in morphometrics.

We tentatively recommend a YES vote on splitting *pampa* from *curvipennis* based on genetic differences and lower response to *pampa* song by *curvipennis*, despite the lack of playback experiments on *pampa*.

If *pampa* is split from *curvipennis*, the name Wedge-tailed Sabrewing has been used in the past and could apply here. However, as this is a split of allotaxa with approximately equivalent range sizes and Wedge-tailed has been used for the combined *curvipennis* and *pampa*, we suggest the English name of Yucatan Sabrewing for *pampa*. The English name of Curve-winged Sabrewing has been used for *curvipennis*, although this name highlights a trait shared by all sabrewings. So, while not ideal, it does have previous association with this taxon.

Effect on AOS-CLC area:

Lumping *excellens* with *curvipennis* would result in one fewer species for the AOS area. Splitting *pampa* from *curvipennis* would result in one additional species for the AOS area.

Please vote on the following two proposals:

1) Lump *excellens* with *curvipennis*
2) Split *pampa* from *curvipennis*

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Submitted by: Oscar Johnson, Louisiana State University, and Blanca E. Hernández-Baños, Universidad Nacional Autónoma de México

Date of proposal: 6 October 2021

External comment on Proposal 2022-A-5

WTSA seems like another borderline case; I recall finding some of the vocal work more sophistry than science, and don't have any strong feelings either way. For the new guide (Birds of Mexico, Howell & Dyer in prep.) we have treated all three taxa under WTSA, as follows—partly on the principle that if we split these then thousands more of equally or more valid splits would follow. Of course, this doesn't meant they're not good "species"… Good times.

***Wedge-tailed Sabrewing** *Pampa (Campylopterus) curvipennis* 12–14cm. Large, long-tailed hummer of humid evergreen and semi-deciduous forest and edge, adjacent clearings and second growth. Feeds low to high; sings mainly from mid-level perches, often in vine tangles and shady subcanopy. Distinctive if uncolorful, with stout bill, white postocular spot, pale grayish underparts, long graduated tail (longer on male, tipped whitish on female); both sexes have iridescent violet-blue crown. Imm. has buffy tips to upperparts, buff tinge to pale tail tips. Comprises 3 groups sometimes treated as species: **Curve-winged Sabrewing** *P. [c.] curvipennis* of e. Mexico foothills, **Long-tailed Sabrewing** *P. [c.] excellens* of Isthmus region, and **Yucatan Sabrewing** *P. [c.] pampa* of Yuc Pen. Long-tailed averages largest (13.5–14cm) and palest below, Curve-winged averages longer-billed and paler below than Wedge-tailed. **Sounds:** Sharp rich *chiup*, vaguely suggesting Kentucky Warbler, run into prolonged chatters or rattles when excited; high sharp *peek*. Song can be arresting: a loud, prolonged, gurgling warble interspersed with squeaky chipping; typically starts with hesitant, reedy chippering that may go on a min or longer before breaking into main song. **Status:** Fairly common. **Curve-winged** on Atlantic slope n. of Isthmus, to 1500m (mainly foothills); **Long-tailed** from Sierra de los Tuxtlas e. to w. Chis, to 1100m; **Yucatan** in Yuc Pen. (Mexico to Honduras.)

Submitted by: Steve Howell

Date of comment: 23 November 2021

Split *Haplophaedia assimilis* from Greenish Puffleg *H. aureliae*

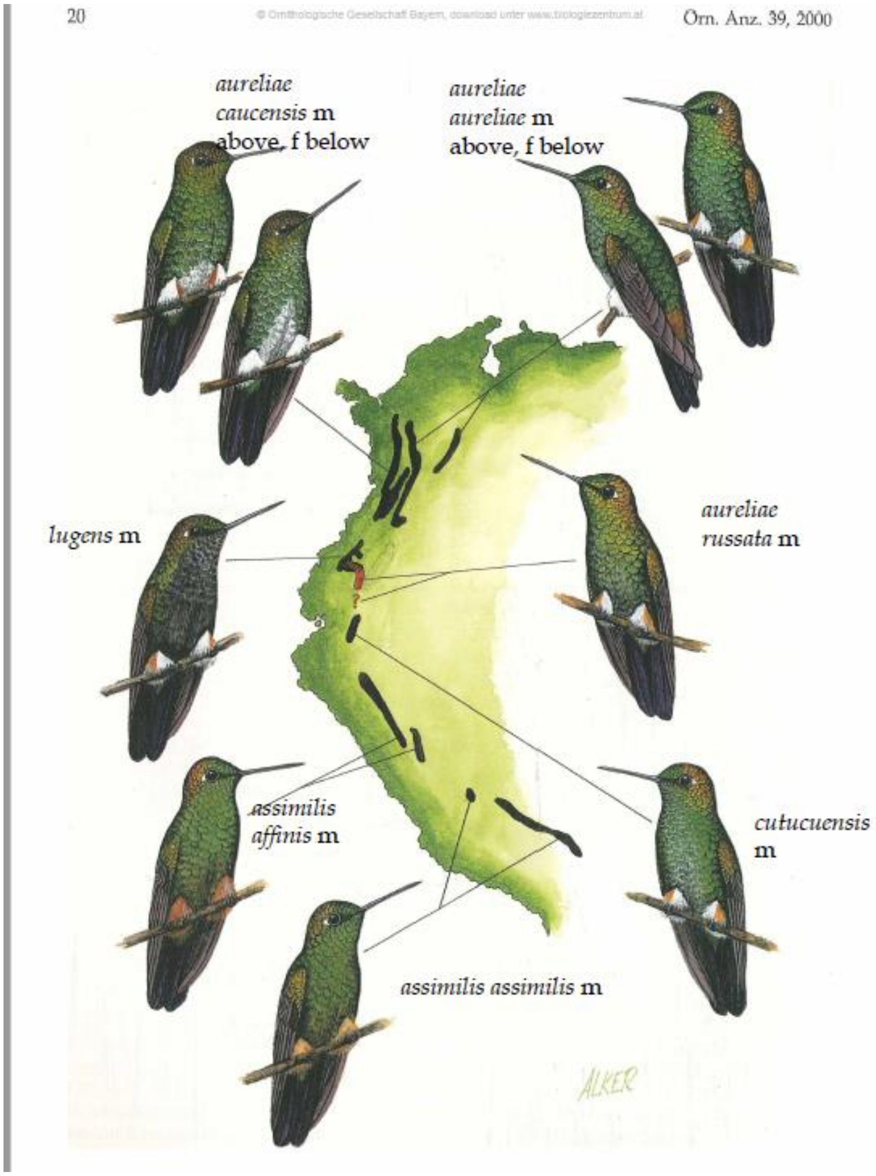
Description of the problem:

Within the NACC region the Greenish Puffleg *Haplophaedia aureliae* occurs only on a few mountains in eastern Panama (cerros Pirre, Malí, and Tacarcuna), but has long been considered widely distributed on Andean slopes from Colombia south to northern Bolivia (e.g., Wolters 1975–1982, Sibley and Monroe 1990, AOS 1998, Schulenberg et al. 2007). Numerous earlier sources (e.g., Simon 1921:188, Peters 1945) have treated *H. aureliae* as a single species, presumably leading to the NACC treatment. However, since its inception SACC has treated what we treat as *H. aureliae* as two species, Greenish Puffleg *H. aureliae* from eastern Panama at least through southern Ecuador, and Buff-thighed Puffleg *H. assimilis* of the eastern Andes of Peru and Bolivia. This was largely based on a comprehensive morphological analysis of the genus *Haplophaedia* by Schuchmann et al. (2000, https://www.zobodat.at/pdf/Anzeiger-Ornith-Ges-Bayerns_39_1_0017-0042.pdf), in which they advocated reinstatement of species status for *H. assimilis*, which was treated as *Vestipedes assimilis* by Cory (1919; *Haplophaedia* not being introduced until that same year). In addition to treating *assimilis* as specifically distinct, Cory (1919) also treated *floccus*, *russata*, and *lugens* as full species; the first two of these have long been subsumed under *H. aureliae* by subsequent authors and the latter is generally considered specifically distinct. The two subspecies in the NACC region, *galindoi* of Cerro Pirre (in c Darién) and *floccus* of Cerro Tacarcuna and its spur Cerro Malí (e Darién) and adjacent Colombia, have been subsumed within subspecies *caucensis* by some (including HBW, the accounts by Heynen 1999a, b), but both were reinstated in the HBW/BLI checklist (del Hoyo and Collar 2014).

Although Schuchmann et al. (2000) advocated specific status for both *assimilis* and *lugens*, their case for considering *assimilis* specifically distinct rested on their disjunct distribution, the all-buffy leg puffs of *assimilis* vs white or bicolored puffs in *aureliae*, and notably duller plumage than in *aureliae* (the latter described difference not being well shown in the illustrations accompanying the paper, nor in del Hoyo and Collar 2014). Nevertheless, *Haplophaedia assimilis* is also now recognized as specifically distinct by Dickinson (2003), Dickinson and Remsen (2013), Gill and Wright (2006), Gill et al. (2021), Clements et al. (2021), and HBW/BLI, in del Hoyo and Collar (2016). 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. Thus, NACC is nearly alone among major current lists in not recognizing *H. assimilis* as specifically distinct.

New information:

There does not appear to be significant new information bearing on the split of *H. assimilis*, which has been universally accepted among the four major global checklists as well as SACC. As far as I can determine, *H. assimilis* has not been sequenced (though *H. aureliae* and *H. lugens* have, and are moderately diverged; McGuire et al. 2014). However, on the SACC list (https://www.museum.lsu.edu/~Remsen/SACCBaseline03.htm), the need for a proposal to



Screenshot of Plate 1 in Schuchmann et al. (2000), with labels added.

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, buff puffs (differing in tone between the two subspecies) and overall duller plumage color that differentiate *assimilis* from the various forms of *H. aureliae*.

The following photos (thanks, Oscar!) from LSUMNZ, however, complicate the picture, and do not seem to support a major phenotypic break between *aureliae* and *assimilis* in accordance with the ranges in Schuchmann et al. (2000). Taxa are from south (left) to north (right) in both, except for *lugens* at the ends:


assimilis (2)
affinis (2)
cutucuensis
caucensis
floccus
lugens
B=93855
MUSEUM OF ZOOLOGY
TISSUE: B-43882
TISSUE B-33132
FOUNDATION OF VERTEBRATE ZOOLOGY
M. A. Carriker, Jr.
Haplophaedia lugens

Rather than supporting the distributions of morphological characters and thus taxa outlined by Schuchmann et al. (2000), the most striking difference among the series (other than the distinctive *lugens*, generally considered a separate species) seems to be between *H. assimilis assimilis* (the left two, with the buffy puffs and lack of white scaling below) and the two birds identified as *H. assimilis affinis* (from the north of the range illustrated in Schuchmann et al.'s plate 1, 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 *affinis* is illustrated there as having the most rufescent puffs. Also, as Oscar noted, the *cutucuensis* specimen (which is from the southern end of the range of any *aureliae* taxon and the next one to the north of *H. assimilis affinis*), seems indistinguishable from the two *affinis*. In response to my puzzlement, Oscar photographed the entire LSU series (below), which show all the northern Peruvian series of "*affinis*" (upper row) to be white-puffed and heavily scaled, unlike all the southern Peruvian and Bolivian *assimilis* (lower row).

In the Acknowledgments, Schuchmann et al. (2000) listed the museums at which they examined the 149 specimens used in the study, and LSU is not among them, but they did list and map an examined specimen (from the type locality; Peters 1945) from Ray-Urmaña (-6.47, -77.35) and another from nearby Chirimoto (-6.517, -77.4), both in Amazonas, which presumably were typical *affinis*. Perhaps the LSU series of "*affinis*" are actually *cutucuensis*, and the break between *H. aureliae cutucuensis* and *H. assimilis affinis* is farther south than shown in Schuchmann et al.'s (2000) map? That would seem to suggest a parapatric or possibly even sympatric distribution in this region. The seemingly strong difference (wherever it is) between white-puffed and -scaled *cutucuensis* and rufous-puffed *affinis* does not seem to indicate clinality. Whichever is the case, clearly further study is needed in this complex, which nevertheless does not necessarily support the NACC single-species position (a holdover from pre-2000 treatments).

Effect on AOS-CLC area:

If we decide to follow the SACC treatment and that of global lists, then the impacts on the NACC-area checklist would be simply a minor modification of the Distribution statement, substituting "southern Ecuador" or, as suggested by the LSU Alto Mayo area specimens, "far northern Peru" for "northern Bolivia", and also including a Notes statement regarding the split.

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, I recommend following these sources for purposes of consolidation and stability, at least until and if evidence accumulates to the contrary. It seems likely that the distributional ranges of *H. aureliae cutucuensis* and *H. assimilis affinis* (and thus the southern and northern limits of the two species, respectively) may need to be modified, but this is a matter for a more in-depth study and for SACC, as would be the preparation of a new proposal to lump *H. assimilis* with *H. aureliae* if needed [see info from new SACC proposal below]. Since the only changes to the NACC region check-list will be very minor, the benefits of following the prevailing treatment would seem to outweigh the risk of further change.

Additional information from new SACC proposal (#923) to adopt the current NACC treatment of *aureliae* and *assimilis* as conspecific:

> "When assembling information in preparation of revising the Birds of Peru in 2009, Dan Lane discovered that the Lima Museum (MUSM) had three specimens of *Haplophaedia "aureliae*," all from San Martín dept: 2 specimens from the Alto Mayo (collected in 2002 on the same expedition as the LSUMZ specimens depicted above) and one from near "Pataz" in the far SW corner of San Martin dept (about 225 km from the Alto Mayo locality). 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. After sharing this finding with lead author Tom Schulenberg, it was clear that the two taxa must turn over somewhere between the Mayo and Huayabamba drainages (the latter containing the type locality for *affinis*) without evidence of introgression. As Pamela and Oscar state above, this situation suggests that the two taxa are best considered species with respect to one another.

“Whereas the LSUMZ/MUSM Alto Mayo series was collected in 2002, postdating the publication of Schuchmann et al (2000), the single LSU specimen from Colán would have been available during the period of the study, and documented that white-tufted birds occurred south of the Marañon. Thus, the fact that Schuchmann et al. did not include the LSUMZ Museum series in their study resulted in a missed opportunity to strengthen their stance on the species limits between the *aureliae* and *assimilis* groups.

“We further suggest that the LSUMZ specimens from Alto Mayo were incorrectly labeled as “*affinis*” but represent *cutucuensis* instead, as Pamela and Oscar suggest above, adding another mid-elevation east slope Andean taxon that crosses the Marañon biogeographic barrier for a brief stretch before its distribution ends south of it.

> “Discussion and recommendation: Schuchmann et al.’s two-species treatment seems to be correct in this case, although their reasoning was weaker than the specimen material before us demonstrates, and so we recommend a NO vote on treating them as conspecific.”

[Note that the SACC recommendation for a NO vote on treating the two species as conspecific is equivalent to a YES vote on our proposal to consider the two to be separate species.]

Acknowledgements:

Many thanks to Oscar Johnson for the photos, and to Gary Stiles for advice on an earlier draft.

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Submitted by: Pamela C. Rasmussen**,** Michigan State University; information from SACC proposal by Van Remsen and Dan Lane

Date of proposal: 7 October 2021

Recognize *Trogon ambiguus* (Coppery-tailed Trogon) as a separate species from *Trogon elegans* (Elegant Trogon)

Effect on NACC:

This would treat our existing species, *Trogon elegans*, as two species, i.e., resurrecting species rank for *Trogon ambiguus* (Coppery-tailed Trogon).

Background:

This one has been on my do-list for 30 years. I've always wanted to see why our Coppery-tailed Trogon became Elegant Trogon, taxonomically and with respect to English name. So, I'm glad BLI and WGAC forced me at least to do this one.

Our *Trogon elegans* currently consists of two groups separated (predictably) by a range gap in Isthmus of Tehuantepec: the *ambiguus* group (Coppery-tailed) N of the Isthmus (SE Arizona to s. Mexico) and the *elegans* group (Guatemala to NW Costa Rica). The two groups have long known to differ in some key plumage features. Each is divided into two subspecies.

Taxonomic history:

• Ridgway (1911) treated the two groups as separate species. His key separated them by tail color (coppery to golden in *ambiguus* and subspecies *goldmani*; greenish bronzy in *elegans*) and patterning in lateral rectrices (vermiculated in *ambiguus* plus *goldmani*; barred in *elegans*)

• Cory (1919) followed Ridgway.

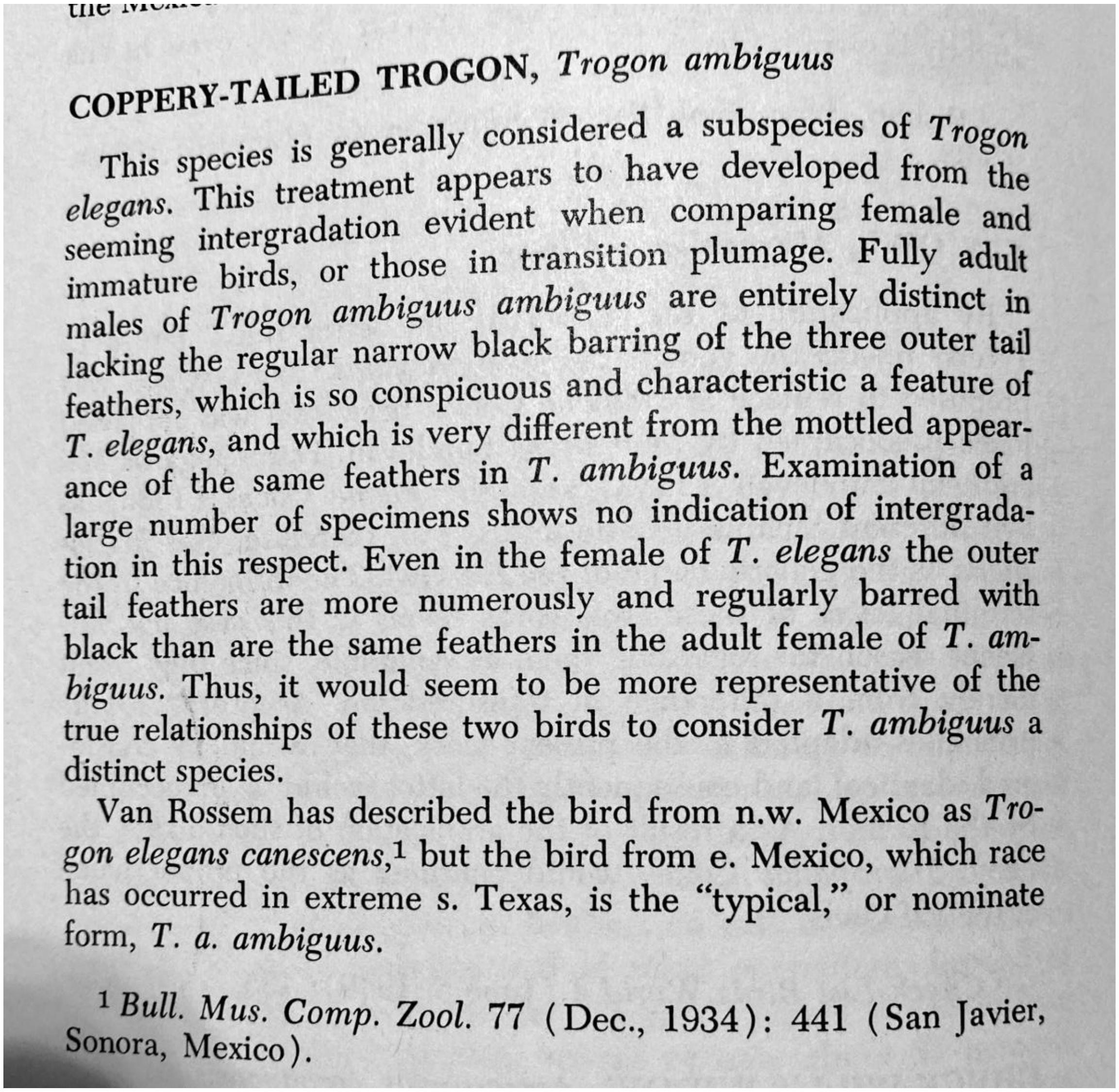
• Peters (1945) lumped the three taxa into a single species without a footnote. Whether there was anything published previous to that to back it up, I do not know. Nothing comes up in Google Scholar, but if something is mentioned within an old monograph or book, Google Scholar may not catch it.

• Eisenmann (1955) treated them as conspecific, specifically stating that he included *ambiguus* in *T. elegans*.

• AOU (1957) treated them as conspecific but called the combined species "Coppery-tailed Trogon".

• Mayr and Short (1970) treated it as an uncomplicated polytypic species (i.e., no concerns on species limits).

• Oberholser (1974) continued to treat *ambiguus* as a separate species. Here's what Oberholser wrote in his Appendix:



the

COPPERY-TAILED TROGON, *Trogon ambiguus*

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*.

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

- AOU (1983) treated them as conspecific, with only the statement: "… sometimes regarded as a separate species, *T. ambiguus* …".

- Howell & Webb (1995; Mexico guide) treated them as conspecific but mentioned the two groups. There was no mention of differences in voice between the two groups (and the description of the song sounds to me like the song of the *ambiguus* group – no surprise given that this was a book primarily on Mexico).

- AOU (1998): treated them as conspecific but recognized the two Groups:

> "Notes.—Groups: *T. ambiguus* Gould, 1835 [Coppery-tailed Trogon] and *T. elegans* [Elegant Trogon]."

- Collar in HBW (2001) treated them as conspecific but mentioned the two groups.

- Dickinson & Remsen (2013; H&M4) treated them as separate groups but also cited Oberholser (1974) for the case for returning species rank to the *ambiguus* group (apparently the only reference to have acknowledged Oberholser 1974). Knowing that this was a data-free Peters Lumperama act followed uncritically by subsequent authorities, I think we may have been tempted to reinstate *ambiguus* as a species but did not want to go against NACC treatment; also, with a substantial lowland gap between the two, Oberholser's point on lack of intermediates is nearly irrelevant.

Genetic data

As for genetic data, I'm not sure what they could tell us on species limits in allotaxa; degree of genetic divergence is a continuous scale that spans over an order of magnitude of genetic distance between pairs of species that anyone would treat as separate species. Monteros (1998) treated them as conspecific; although his GenBank accession suggests two individuals, they were not separated in the analysis and their origin was not given (as far as I could tell). A search on "*ambiguus*" within the paper produced nothing. Moyle (2006) only included 1 representative, a nominate *elegans* from El Salvador. DaCosta & Klicka (2008) included single samples from El Salvador and Mexico; they were sisters … no surprise … and the genetic distance was small, smaller than among most samples from different localities that are treated under a single species name under today's species limits; a search on "*ambiguus*" within the paper produced nothing.

New information:

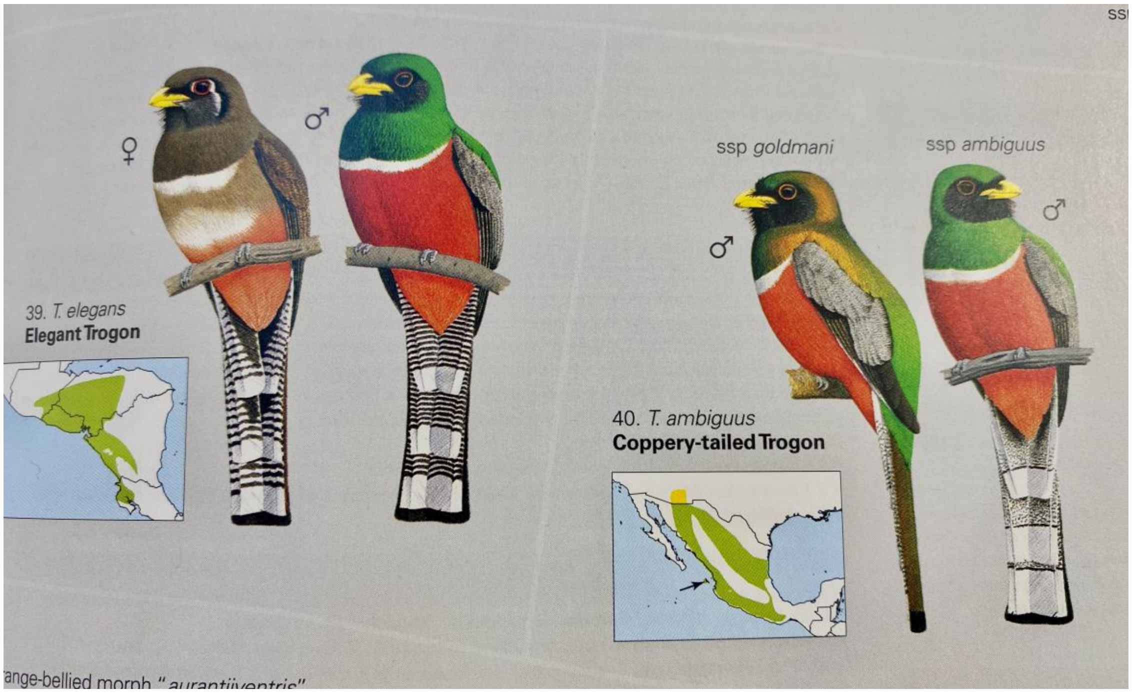
Nothing really new. Del Hoyo and Collar (2014) treated them as separate species and outlined the well-known plumage differences between the two as their rationale. From Terry's spreadsheet:

> "HBW-Birdlife split: *ambiguus* "[u]sually considered conspecific with *T. elegans*, although for long recognized as distinctive: differs in its finer-grained vermiculations on wingpanel (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)."

The plate from Del Hoyo & Collar (2016) and specimen photos from LSUMZ, provided by Oscar Johnson, are on succeeding pages.

If I am interpreting this correctly, the magic threshold of 7 points is achieved through these plumage characters, but I didn't think you could reach 7 solely on plumage characters. (Keep in mind that the 7 points threshold is based on extrapolations from 58 studies of species limits in mostly temperate passerines plus eight tropical antbirds, and including virtually no nonpasserines; see Remsen 2015 and Remsen 2016).

Voice: Nothing published per se, but xeno-canto has a lot of recordings of the song of both groups. Both share an unusually hoarse, sort-of frog like repeatable syllable that is much raspier, less mellow than other those of other *Trogon* songs. However, dabbling through the recordings suggests to me that a formal analysis would show that *ambiguus* has a faster delivery with more syllable than does *elegans*. If interested, it's easy to listen to and look at


♀
♂
39. T. elegans
Elegant Trogon
ssp goldmani
ssp ambiguus
♂
♂
40. T. ambiguus
Coppery-tailed Trogon
range-bellied morph "aurantiiventris"

sonograms of a bunch of recordings from specific localities by clicking on the locality: https://www.xeno-canto.org/species/Trogon-elegans

Here's *ambiguus* from Sonora (by Richard Webster):
- https://www.xeno-canto.org/450735

Here's *elegans* from Costa Rica (by David Bradley):
- https://www.xeno-canto.org/6773

There is some variation, and that's why a real analysis is needed, but I will predict that the differences hold up.

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 differences noted by HBW-BLI above differ among the three Amazonian subspecies of *Trogon rufus*, yet each of them intergrades wherever in contact. *Trogon rufus* being the sister lineage to *Trogon elegans*, by yardstick extrapolation these plumage characters can be predicted to be meaningless in terms of barriers to free gene flow. This illustrates one of the fundamental conceptual flaws in the Tobias et al. species ranking scheme: characters known not to be associated with barriers to gene flow in a group are nonetheless considered positive evidence in treating two taxa as species.

This is yet another case of a Lumperama decision based on nothing but plumage similarities and virtually no explicit rationale. And an analysis of plumage characters in the sister lineage show that they are not barriers to gene flow. Yet a casual cruise through online recordings hints that the lump was unjustified.

So, what do we do? We could just reverse the lump based on lack of explicit rationale for the lump. But that would appear to be endorsing the BLI/HBW split, which is based solely on the same plumage characters that have been shown to be irrelevant to species limits in the sister lineage. My recommendation would be to vote NO on this pending a formal analysis of voice. The latter would be easy to do – I think a short note in a bird journal comparing sonograms would be sufficient evidence to place burden-of-proof on treating them as conspecific.

Note on English names:

If the split were to be adopted, then the sensible names, consistent with our guidelines, would be to restrict Elegant Trogon to *T. elegans* and resuscitate Coppery-tailed Trogon for *T. ambiguus*, e.g., returning to the historical names for the species prior to their treatment as conspecific.

Literature Cited: (links or skeletal citations inserted throughout except for standard references)

Submitted by: Van Remsen

Date of Proposal: 7 October 2021

Comment on this issue from Steve Howell:

With more data than 25+ years ago (especially on voice, both songs and calls appreciably different) the trogons are best treated as good species, for which we simply state (in the Costa Rica guide appendix, Dyer & Howell in prep.):

Elegant Trogon *Trogon [elegans] elegans* (p. XXX). Differences in plumage and voice indicate that the *ambiguus* group (Mexico and sw. US; Coppery-tailed Trogon) and *elegans* group (Guatemala to Costa Rica) are best treated as separate species.

Date of comment: 23 November 2021

Treat *Lepidocolaptes neglectus* as a separate species from *L. affinis* (Spot-crowned Woodcreeper)

Effect on NACC:

This would treat our *Lepidocolaptes affinis* as two species.

Background:

Our current classification treats *Lepidocolaptes affinis* as a single species occurring from ne. Mexico to w. Panama (Chiriquí highlands). It is currently treated (Marantz et al. 2003, Dickinson & Christidis 2014) as having three subspecies, found in the mountains of Middle America: *lignicida* in ne. Mexico (Nuevo Léon to e. San Luis Potosí); nominate *affinis* from se. SLP and w. Guerrero S to Nicaragua); and *neglectus* (Costa Rica to w. Panama).

From Terry's spreadsheet:

> "HBW-Birdlife split: *neglectus* "Hitherto treated as conspecific with *L. affinis*, although possible split had been suggested on molecular grounds (Arbeláez-Cortés, Nyári & Navarro-Sigüenza 2010); differs in its fuller, buffier chin and throat (1); slightly broader, longer, brighter streaks below extending more obviously onto the belly (1); and entirely different song, a long overslurred nasal note, followed by a fast trill of some 20–30 notes, going slightly up and down in pitch, vs a long underslurred note followed by one or two shorter underslurred notes (score 4 for greater number of notes and 3 for much lower maximum frequency, 3.0–3.3 kHz vs 8.2–9.0 kHz) (Boesman 2016)."

The plumage differences, to my eye, are unimpressive. On the next page are LSUMZ specimens photographed by Oscar Johnson; the first specimen on the left is *L. a. lignicida*, the next three are *L. a. affinis*, and the two on the right are *L. a. neglectus*.

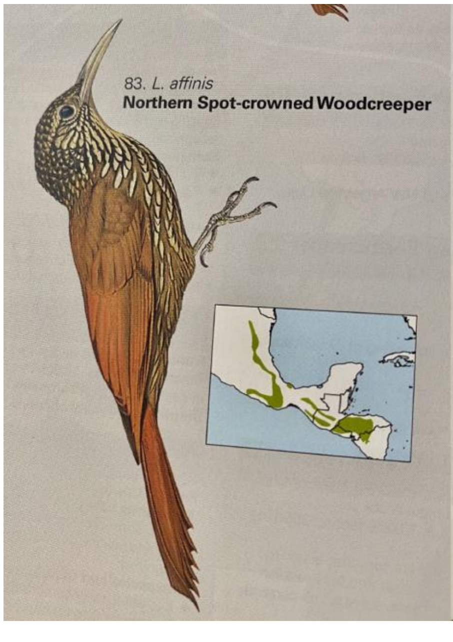
My first reaction is that I can see immediately why no classical taxonomic treatments even mentioned the possibility of two species. I can see the slightly greater extension of the streaks into the belly in *neglectus*, but I think I would have to examine specimens closely to see the difference in the throat coloration. Also, the general tawnier color of *L. a. lignicida* stands out as much to me as any differences between nominate *affinis* and *neglectus*. Only one individual was illustrated for the species in Marantz et al. (2003; HBW), in contrast to many other species in which multiple subspecies were illustrated.

Also on the next page is the plate from Del Hoyo & Collar (2016), i.e., differences emphasized (to say the least).

This is not to say that woodcreeper species, and *Lepidocolaptes* in particular, cannot show extreme plumage similarities, as reflected in the recent splits in the *Lepidocolaptes albolineatus* group by SACC.

History of taxonomic treatments: As far as I can tell, *L. affinis* has always been treated as a single species (although also including Andean *L. lacrymiger* in some classifications), from Ridgway (1911) to Dickinson and Christidis (2014), with no mention of the possibility that *neglectus* should be considered a separate species. Marantz et al. (2003; HBW), whose


LA. STATE UNIV. 11382 MUSEUM OF ZOOLOGY
MEXICO: San Luis Potosi: XILITLA REGION
2 mi. W. of village
SEX ♀
DATE January 23, 1947 ROBERT J. NEWMAN
Collection of Charles A. Ely
LSUMZ 167126
Mexico: Chiapas, Pueblo Nuevo Solistahuacán, 3 km NW
#6914
Sex-- ♀
25 March 1975
Collector - Charles A. Ely
COLLECTION OF DONALD H. BAEPLER
LSUMZ 100073
GUATEMALA: HUEHUETENANGO: SOLOMA (3 mi. N.W.)
SEX-♀
3 March 1958 COLLECTOR—DONALD H. BAEPLER
9,500 FT.
LA. STATE UNIV. 29452 MUSEUM OF ZOOLOGY
Honduras: Cortes: Finca Fe, 1 mi. NW
Jaral, 2300'
♂
22 October 1962 J. Alan Feduccia
803
LOUISIANA STATE UNIVERSITY 154010 MUSEUM OF ZOOLOGY
COSTA RICA: Prov. Cartago; 3 km ENE
Villa Mills, km 98 Pan American
Highway, 2650 m
♂
26 July 1991
T.S. Sillett 410
LOUISIANA STATE UNIVERSITY 138697 MUSEUM OF ZOOLOGY
COSTA RICA: Prov. San José; [La Georgina,
Km 95 Pan American Hwy, 2970 m]
7 January 1990 G.H. Rosenberg 2516 ♂


83. L. affinis
Northern Spot-crowned Woodcreeper


84. L. neglectus
Southern Spot-crowned Woodcreeper

species accounts are typically extremely detailed with respect to voice, made no mention of any differences in voice among the subspecies. However, Marantz et al. (2020) updated the Birds of the World account to reflect the possibility that two species are involved and noted the difference in vocalizations, but still treated all taxa as conspecific.

Vocalizations:

Howell & Webb (1995) described the voice of *L. affinis* as follows:

> "Voice. A plaintive, thin, squeaky *see-yih'* or *syeih*, a longer plaintive reedy *tw see'i tchew*, suggesting Rose-throated Becard, and longer series of similar quality, *jeer dee deet*, etc. Song a reedy note followed by a rapid laugh, *syeehr see-see-see-see-see-see-see-syn*, or *rreeer hee-hee-hee-hee-hee-hee-hee*, etc."

Stiles & Skutch (1989, Birds of Costa Rica) described the voice of *L. affinis neglectus* as follows:

> "VOICE. Call a plaintive, squeaky *deeik*; song a thin, reedy nasal note followed by a rattling trill: *deeeeeeah*, *hihihihihi*; sometimes 3 reedy whistles without a trill, *deeee-deeeeih*."

Interpreting these descriptions in terms of similarities and differences is futile, but they sound more "similar" than "different" to me. But the reason I include them will be apparent later.

New information:

Del Hoyo & Collar (2016) presented a novel taxonomic treatment by elevating *neglectus* to species rank using the Tobias et al. scoring system, as outlined in Terry's spreadsheet above. Two points were awarded to plumage differences, but those were not really needed because the vocal differences were so strong that 7 points came from interpretation of those differences, based on Boesman (2016), who presented sonograms that show that the song of southern *neglectus* is really quite different, e.g.:

Here is the song of nominate *affinis* (by Rich Hoyer):
- https://www.xeno-canto.org/97459

And another (by Dan Lane):
- https://www.xeno-canto.org/212645

Here is the song of *neglectus* (by Andrew Spencer):
- https://www.xeno-canto.org/31828

What concerns me is the description of Mexican song by Howell & Webb (1995), which I interpret to include a rapid trill ("laugh"), i.e., much like the *neglectus* song above. What also concerns me is that Marantz et al. (2000) could not find a song of nominate *affinis* to present in their account. Also concerning is that the number of songs available in xeno-canto for *affinis sensu stricto* that are usable is, in my opinion, N=1 (Hoyer's recording); the other cuts are nearly inaudible, labeled as "short song", or call notes. Although the possibility seems remote, I wonder if the true song of *affinis sensu stricto* has been recorded. Nothing I've heard fits Howell and Webb's "Song a reedy note followed by a rapid laugh, *syeehr see-see-see-see-see-see-see-syn*, or *rreeer hee-hee-hee-hee-hee-hee-hee*, etc." It seems unlikely that the super-careful

Steve Howell would have used a recording from *neglectus* to describe the song of the northern taxa. Are the vocalizations compared by Boesman analogous? I am not qualified to assess woodcreeper vocalizations, but I do know from discussions with Curtis Marantz, Bret Whitney, and Dan Lane that great care must be taken with woodcreeper songs because individuals seem capable of producing variations of the same song; also, see the discussion under Voice in Marantz et al.'s (2003) introductory chapter. For example: "Recent work has documented a higher degree of individual variation in woodcreeper song than had ever been expected." And "It seems premature to draw conclusions solely on the basis of geographical patterns in woodcreeper vocalizations." However, they also discuss the case of formerly broadly defined *Dendrocolaptes certhia*, in which the geographic variation is not variation on a theme, but completely different song types that also corresponded with plumage-defined taxon boundaries that led to a change in species limits (that we now use).

A minor point is that the song of *lignicida* may be unknown – it is represented in xeno-canto only by a single call note (by Dan Lane). Given that *lignicida* may be as different in plumage from nominate *affinis*, it seems to me that its vocalizations also should be included in any such study.

<u>Genetic data</u>
As for genetic data, as argued in previous proposals, I think they are of dubious value for determining taxon rank of allopatric populations, although perhaps our best estimates of divergence times.

Arbeláez-Cortes et al. (2010) did a survey of population structure of *L. affinis*, using 1869 bp, of which 903 were from ND2 and 966 from cyt b. Unfortunately, they did not have samples of *lignicida* (the northernmost population).

Here is the map of their sampling design, which is also a great aid for visualizing the biogeography of the situation, especially when as well-executed as this one:

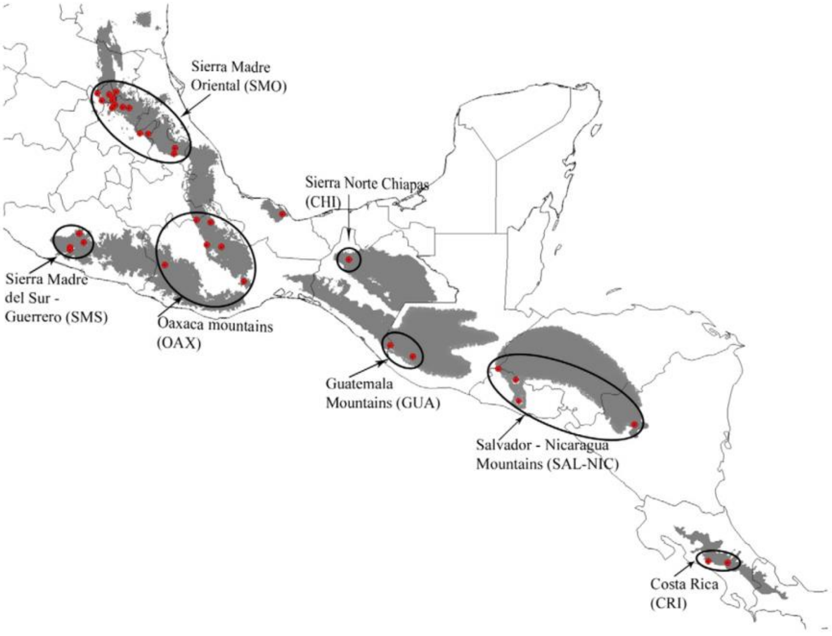


Fig. 1. Map of sampling localities for *L. affinis*. Sample origins are indicated by red dots, while populations referred to throughout the text are encircled. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Here is their tree, which shows strong geographic structure, with *neglectus* the most divergent:

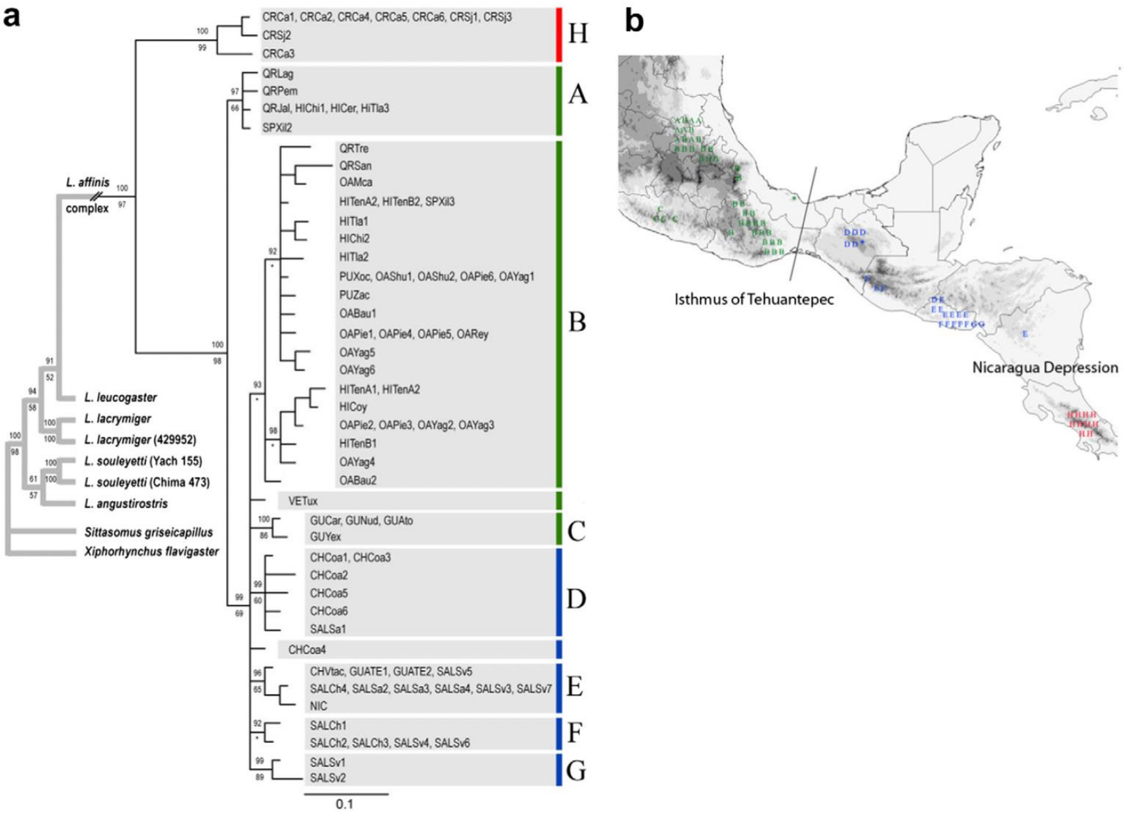


Fig. 2. (A) Bayesian phylogenetic estimates of relationships among *Lepidocolaptes affinis* haplotypes. Branch lengths are valid only for the *L. affinis* clade, while a cladogram represents relationships among *Lepidocolaptes* species. Clade colors indicate geographic origin: red = Costa Rica, blue = North-Central America South to the Isthmus of Tehuantepec, green = Mexico North to the Isthmus of Tehuantepec. Clade support is indicated above branches by *a posteriori* BI values and below branch by ML Bootstrap values (* = ML Bootstrap <50%). Capital letters depict distinct haplotype lineages. (B) Map showing the geographic location of haplotype lineages, as well as the two major lowland barriers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The paper was mainly about biogeography and historical demography, and here is the only mention of taxonomy:

> "The genetic differentiation of the lineage from Costa Rica is consistent with taxonomy (subspecies *L. a. neglectus*; Del Hoyo et al., 2003 [= Marantz et al. 2003]), and coincides with an evident demographic bottleneck. The mean genetic differentiation between *L. a. affinis* and *L. a. neglectus* (1.8%) is very similar to the values found between *L. wagleri* and *L. squamatus* (1.7%; García-Moreno and da Silva, 1997), suggesting that Costa Rican populations represent a distinct species. This result warrants further investigation on morphological and vocal variation, in order to clarify the taxonomic status of these two taxa. The Tamaulipan form *L. a. lignicida* should be examined too to test its genetic divergence given that it is morphologically very distinct from the two other forms (*L. a. affinis* and *L. a. neglectus*) that are more similar and hardly distinguishable except in long series (Bangs and Penard, 1919)." [I haven't looked up this last reference but note this with respect to the discussion of plumage above.]

This is the basis for the HBW statement in the spreadsheet.

Arbeláez-Cortes et al. (2012) included samples of both population groups in their overall analysis of relationships in *Lepidocolaptes*. If one were to use just comparable genetic distances within a genus (I wouldn't), the *neglectus-affinis* split appears closer to being at the subspecies level rather than species level:

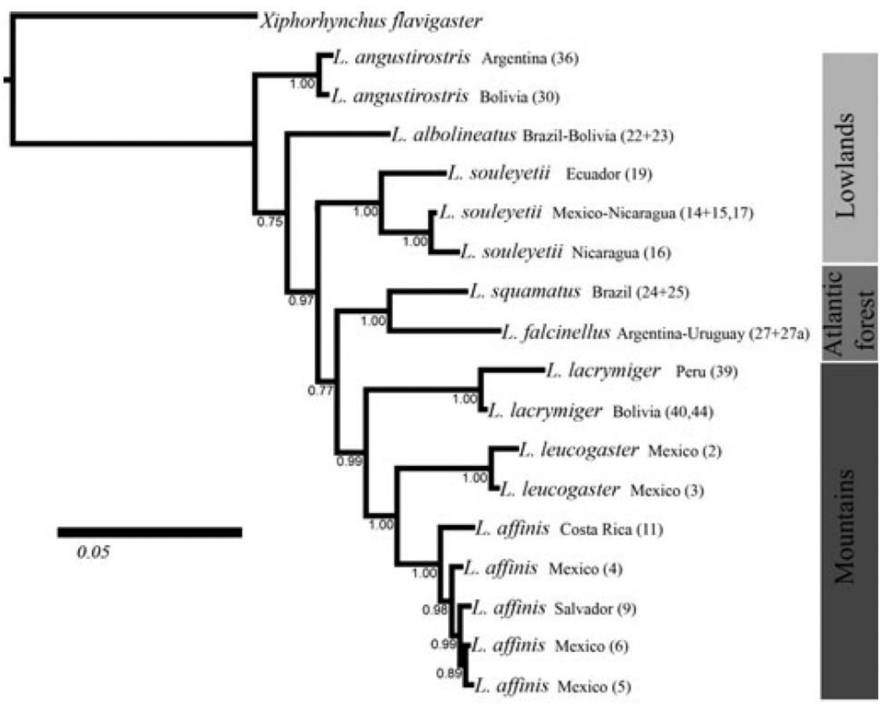


Fig. 2 Bayesian 50% majority rule consensus tree estimated for the *Lepidocolaptes* species from the COI + ND2 dataset. Bayesian posterior probabilities are indicated at each node. Numbers beside each species name are for the samples used and correspond with the numbers in Table 1 ('ID' column) and with the numbering scheme in Fig. 1.

Comments solicited from Curtis Marantz:

> "Overall, I think you are on the right track, and I found no disagreement with anything you said, except maybe the citation of Marantz et al. (2020), for which you can see the P.S. below.
>
> "I also looked at and listened to some recordings, and found that the Macaulay Library has relatively few recordings of *L. affinis* in the broad sense, with only 18 from Mexico and only 74 recordings total. The first thing that is apparent from these recordings is that the species' vocalizations are highly variable, with almost no two sounding the same (assuming they are all identified correctly!) Moreover, I found nothing in the Macaulay Library that sounds like a song from Mexico.
>
> "This said, there are differences in the vocalizations between these taxa, albeit what I consider more variations on the same theme than as different themes, as in the *Dendrocolaptes certhia* complex. As such, I would want to have available large samples of

> recordings that reflect the entire range of vocalizations before saying anything definitive about these.
>
> "The genetic samples seem to show minimal variation and pretty much in the direction expected, with the southern birds somewhat different from the northern birds, but with the entire group monophyletic and not varying all that much genetically. Moreover, the comparison with the Scaled Woodcreepers may just mean that they are not a good split, and as I recall, likewise based on very small samples of vocalizations. The photos of the specimens further reveal that these birds are only very subtly different morphologically, and likely well within the range of subspecies-level variation.
>
> "In my mind, until one has dozens, if not hundreds, of recordings, and can map out in a clear way the homologous sounds of each group under study, it is inadvisable to begin splitting woodcreepers on the basis of their vocalizations. Moreover, in Venezuela we found that populations that are not sister taxa, and which have very different vocalizations, seem to have no problem hybridizing when they come into contact.
>
> "I would recommend basing decisions on careful analyses of a wide array of vocalizations rather than a simple analysis that uses the number of elements and their frequencies, which for woodcreepers is invariably going to lead one astray. This is also why I avoided working on the *L. albolineatus* paper by Aleixo et al., because the sample of recordings that they had available was insufficient in my opinion.
>
> "Finally, having looked at literally thousands of woodcreeper songs, I would avoid putting any meaning whatsoever in the number of elements that a given song contains because this is precisely how woodcreeper songs vary motivationally, with songs given after playback or during an interaction often representing endless trills that increase and decrease in frequency almost like a wave.
>
> "P.S. By the way, I can assure you with 100% confidence that ANYTHING included in revisions to our HBW text since the books were published has zero input from me, with the lone exception being the Neotropical Birds entries for *X. guttatus* and *X. susurrans*, which I did work on shortly after finishing my dissertation around 2005. I have never been contacted by anybody at HBW or Cornell about subsequent revisions made to my accounts, so the Marantz et al. (2020) update that comments on vocalizations and suggests that two species may be involved had absolutely no input from me!"

Recommendation:

I suspect Boesman is onto something, and my gut feeling is that he may be right. But there are just too many lingering questions for me – so I would recommend a NO until we have a solid, published analysis. I see no harm in waiting until sufficient evidence is published to fortify any change in classification.

Note on English names:

HBW used Northern Spot-crowned Woodcreeper and Southern Spot-crowned Woodcreeper. If the proposal passes, or eventually passed with additional data, I think these names are acceptable. Insipid and cumbersome, but still acceptable in my opinion, in part because of lack of viable alternatives and also because the dreaded compound name retains the sister relationship between the two and thus stands out in a long list of woodcreeper names that are all Something Woodcreeper. I understand the dislike of long compound names, but I think of them as the formal English names, not the informal one we would use in the field, which would be just “Spot-crowned” or “Northern Spot-crowned” or some abbreviated rendition … just like I’ve still yet to hear anyone call a Northern Cardinal by any name other than just “Cardinal” in the field.

Literature Cited: (links or skeletal citations inserted throughout except for standard references)

Submitted by: Van Remsen

Date of Proposal: 7 October 2021

External comments on Proposal 2022-A-8

First comment:

I do not have a recording of Mexican Spot-crowned song, and in my naive youth may have described Costa Rican song in Howell & Webb, not appreciating fully the big biogeographic break. The calls, however, while variable, sound quite different between northern and southern, and in my view support a split. Indeed, Spot-crowned Woodcreeper is only the tip of the iceberg wrt splits involving numerous other ovenbirds that occur in Costa Rica, e.g., also including Wedge-billed, Olivaceous, Strong-billed, Black-banded, Spotted, and Long-tailed Woodcreepers!

Submitted by: Steve Howell

Date of comment: 23 November 2021

Second comment:

As I believe I was indeed the first to indicate significant vocal differences between the taxon *neglectus* and other taxa of the *L. affinis* complex (Boesman 2016) and given this input was the major reason for Del Hoyo & Collar (2016) to treat the former as a distinct species, I would like to comment on the present NACC proposal 2022-A-8.

The author of the proposal - while admitting he is not an expert in Woodcreeper voices - mentions several arguments to question the claimed vocal difference, which I would like to tackle one by one:

- “Howell & Webb (1995) describe the song in their field guide as “a reedy note followed by a rapid laugh, syeehr see-see-see-seesee-see-see-syn”.”

  There is no guarantee at all that this is based on a vocalization heard in Mexico. At the time of writing (1995) only voice of *neglectus* had been published in Macaulay/Ross’s CD-set “Voices of Costa Rican Birds” and the existence of two vocal groups was unknown. If field guides are used as supportive documentation (a practice which definitely requires some caution), we may as well refer to a more recent field guide such as Vallely & Dyer (2018) “Birds of Central America” (one of the few covering a region in which both groups occur, unlike Howell's Mexico guide) in which 2 vocal groups are mentioned (although admittedly an editing error did switch 'north' and 'south'…).

- "Marantz et al. (2000) could not find a song of nominate *affinis* to present in their account."

  Not sure if Marantz (2000) is in fact Marantz (2003) or a different publication, but in any case, Marantz (2003) also e.g. failed to describe the different vocalizations of *L. albolineatus* sensu lato (see Treat Lepidocolaptes layardi as a subspecies of L. fuscicapillus (lsu.edu)). We can't blame an author for not mentioning information that has not yet been revealed…

  As a matter of fact, the transcription of song in Marantz (2003) is literally identical to the one in Howell (1995) suggesting it was simply copied. If Howell's description would have been from Mexico and Marantz's description allegedly was not from the *affinis* group, we clearly have a contradiction here…

- "Also concerning is that the number of songs available in xeno-canto for *affinis* sensu stricto that are usable is, in my opinion, N=1 (Hoyer's recording); the other cuts are nearly inaudible, labeled as "short song", or call notes."

  This suggests that the claimed vocal difference is based on a single recording of the northern group (!). Besides Hoyer's recording I invite anyone to listen to and scrutinize the sonogram of the following additional 10 recordings which document the song of the northern vocal group at well-spread different locations:

  Mexico:
  XC224913 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC224911 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC224910 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC212645 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC58106 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC224915 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  ML109877111 Spot-crowned Woodcreeper Macaulay Library
  Guatemala:
  XC76640 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  Honduras:
  XC284826 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  El Salvador:
  ML82758681 Spot-crowned Woodcreeper Macaulay Library

  to be compared with song of the southern group:

  Costa Rica
  XC8910 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC166797 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC5815 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  ML319869561 Spot-crowned Woodcreeper Macaulay Library
  ML296333331 Spot-crowned Woodcreeper Macaulay Library
  ML252189451 Spot-crowned Woodcreeper Macaulay Library
  ML185968511 Spot-crowned Woodcreeper Macaulay Library

ML521736 Spot-crowned Woodcreeper (Southern) Macaulay Library
(and several more)
Panama
XC31828 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
XC271349 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
XC271348 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
ML28284 Spot-crowned Woodcreeper (Southern) Macaulay Library
ML196136051 Spot-crowned Woodcreeper Macaulay Library

Similarly, several tenfold recordings of the dominant call note of northern group (a single underslurred note) can be compared with the one of southern group (a single overslurred note)

- "I wonder if the true song of *affinis* sensu stricto has been recorded."

  It is pure speculation and against all available evidence to think that the northern group would have a song which has not yet been documented and is more similar to *neglectus*. I understand the reason of doubt, given the long underslurred whistle followed by 1-3 high-pitched shorter underslurred whistles is so different from the song of *neglectus* that it is at first hard to believe this is a homologous vocalization of a taxon so closely related. I would like to point out however that similar extreme vocal differences exist in other complexes (e.g. the *L. albolineatus* complex or the *Sittasomus griseicapillus* complex, the former split in several species, the latter since long awaiting an in depth study to do most probably the same).

  See e.g.
  Birds of the World (note on Lineated Woodcreeper)
  Birds of the World (note on Olivaceous Woodcreeper)

  Or compare e.g. songs in:
  XC272020 Guianan Woodcreeper (Lepidocolaptes albolineatus) :: xeno-canto
  XC224916 Layard's Woodcreeper (Lepidocolaptes layardi) :: xeno-canto
  previously considered the same species, or
  XC229785 Olivaceous Woodcreeper (Sittasomus griseicapillus) :: xeno-canto
  XC229784 Olivaceous Woodcreeper (Sittasomus griseicapillus) :: xeno-canto
  XC229786 Olivaceous Woodcreeper (Sittasomus griseicapillus) :: xeno-canto
  also illustrating drastically different songs!

  Even if we would for a moment assume that not all vocalizations of both groups have been recorded, then we still see that ALL known vocalizations of the northern group are different from the ones of the southern group: song and call of the southern group is based on overslurred whistles, while in northern group on underslurred whistles (for definitions under/overslurred, see Pieplow (2017)). There is thus zero overlap in vocalizations of both groups.

- "Great care must be taken with woodcreeper songs because individuals seem capable of producing variations of the same song"

  Individual variation in voice is well known and is indeed quite extensive in many woodcreepers, but it should not be confused with or used as an argument to mask species-specific vocal characteristics, and surely it is no reason to minimize the taxonomic significance of voice in this suboscine family. I believe it is safe to say that nearly every woodcreeper species can be correctly identified based solely on voice, independently of individual vocal variation. In other words, I don't see the relevance of this remark.

As a further consideration, Spot-crowned Woodcreeper sensu lato was split into Montane Woodcreeper *L. lacrymiger* and Spot-crowned Woodcreeper *L. affinis* largely based on voice (Ridgely 1994. The Birds of South America) long before genetic evidence was made available as a further support, illustrating the importance of vocal differences in this family and genus. With a dramatic increase in the availability of birdsound recordings during the last two decades, such findings can now be supported by even more extensive evidence than in these early days.

- "It seems premature to draw conclusions solely on the basis of geographical patterns in woodcreeper vocalizations"

  All recent splits of Woodcreeper complexes were supported by vocal differences in the distinct groups. As a matter of fact and as a striking and illustrative example, the geographical range of *L. duidae* was basically entirely redrawn based on voice, now extending into NE Peru and E Ecuador, whereas formerly, presumably purely based on hardly noticeable morphological differences, this was not at all the case (compare the obsolete range description of the different taxa for *L. albolineatus* in Marantz 2003 with present knowledge).

- "A minor point is that the song of *lignicida* may be unknown – it is represented in xeno-canto only by a single call note (by Dan Lane)… it seems to me that its vocalizations also should be included in any such study."

  The author seems to have overlooked the following additional recordings of this taxon from Tamaulipas, which were already mentioned and illustrated with sonogram in Boesman (2016):
  XC224913 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  XC224915 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto

- Marantz: "The first thing that is apparent from these recordings is that the species' vocalizations are highly variable, with almost no two sounding the same".

  Marantz apparently focusses on variation and inexplicably fails to see the common distinguishing features that identify each group's voice: song and call of the southern group is based on overslurred whistles, while in northern group on underslurred whistles. Southern group is a single long whistle followed by a long fast trill, song of northern group is a long whistle followed by 1-3 notes, etc.

- Marantz: "In my mind, until one has dozens, if not hundreds, of recordings, and can map out in a clear way the homologous sounds of each group under study, it is inadvisable to begin splitting woodcreepers on the basis of their vocalizations."

  Required sample size is of course a matter of discussion, but if about 100 recordings (XC+ML) are not sufficient to draw conclusions about two groups, then one may question many other taxonomic decisions from the recent past. (This doesn't mean at all

I am not in favour of large sample sizes. On the contrary, I believe my efforts to document as many bird vocalizations as possible over the last 30 years (32.000+ recordings available on-line) clearly demonstrate the importance I am giving to this.)

In this case however, I believe that chances are very slim that a larger than present sample size will uncover a hitherto undocumented territorial song or will alter significantly our understanding of song and dominant call types: *Lepidocolaptes* woodcreepers are not typical dawn singers (as opposed to many other woodcreeper species) and have a rather limited and fairly stereotypical vocabulary, mainly consisting of a song phrase and a dominant call note, which typically is uttered sporadically during the active day-time hours.

I do agree however that more recordings are needed when vocal differences are more subtle, and especially the difficult (and in my opinion unresolved) case of Buff-throated/Cocoa Woodcreeper *Xiphorhynchus guttatus/susurrans* proves that not all currently recognized woodcreeper species differ markedly in voice. Marantz's PhD work (2005) primarily focussed on this complex, and therefore he may oversee this is rather the exception than the rule, or at least that in the *Lepidocolaptes* genus vocalizations are far more stereotypical and differences rather clear-cut.

- Marantz: "Moreover, in Venezuela we found that populations that are not sister taxa, and which have very different vocalizations, seem to have no problem hybridizing when they come into contact."

  I don't see the relevance of this remark. Reasoning along these lines, one could then argue that the Woodcreeper family is a single species... (In any case, hybridization is a non-issue in allopatric populations).

- Marantz: "I would recommend basing decisions on careful analyses of a wide array of vocalizations rather than a simple analysis that uses the number of elements and their frequencies, which for woodcreepers is invariably going to lead one astray."

  I am open to any suggestions about describing objectively sounds, but before writing down my conclusions in Boesman (2016) I did analyse all on-line available recordings of all vocalizations (both song and calls) and I objectivated my findings by using standard basic sound parameters to allow quantification of differences which I believe is common practice in bioacoustical analysis for taxonomic decisions.

  I even highlighted and illustrated a somewhat aberrant vocalization, which was clearly a vocalization of a very excited bird, as can be heard in many Woodcreeper species after repeated playback:
  XC97460 Spot-crowned Woodcreeper (Lepidocolaptes affinis) :: xeno-canto
  ML6976 Spot-crowned Woodcreeper (Northern) Macaulay Library

  Both above recordings have the same pattern on sonogram (and differ from all other available vocalizations), the recordist of ML6976 in 1971 thankfully carefully noted this voice was indeed stimulated by playback…

  And finally, I placed the *affinis* complex in a broader context by comparing also with typical song of *L. lacrymiger* to check the possible hypothesis that the taxon *neglectus* would rather belong to this South American group, hypothesis that was proven wrong based on voice (besides genetic considerations).

In conclusion, I respectfully disagree that there is insufficient evidence to conclude that there are clearly two vocal groups in the *L. affinis* complex with very different voice. On the contrary, all 100+ on-line available recordings clearly indicate that both groups are readily identifiable by both song and call notes.

Whether this is sufficient evidence to treat both groups as distinct species is another matter and largely depends on the criteria used to reach such conclusion.

About the evidence there should however not be any discussion as explained above:

- Both groups differ morphologically in minor details, which however at the time were deemed sufficient to describe them as different taxa
- Both groups differ markedly in voice (we are talking here about very different voices, not differences for which a PCA is needed to plot separate groups…)
- Both groups are genetically distinct lineages
- Both groups are allopatric and thus taxonomic status in a BSC concept needs to be determined by indirect evidence different from the examination of (inter)breeding behaviour as in the case of sympatry

Similar evidence was used to upgrade a complex in the same genus (*L. albolineatus*) to 4 species (initially 5, but see Treat Lepidocolaptes layardi as a subspecies of L. fuscicapillus (lsu.edu)). I thus believe taxonomic consistency would rather favour treatment of *L. neglectus* and *L. affinis* as two distinct species.

Finally, in anticipation of the possible remark that my analysis (Boesman 2016) was not peer-reviewed, I would like to point out that this was part of a single-person effort during a single year to document 400+ cases in which vocal differences may have an impact on their taxonomic treatment (See Ornithological Notes - Birds of the World), and for which peer-reviewing was practically impossible because of time-constraints. In the five years following this effort however, the scientific community has tackled several of these cases (although unfortunately far from all of them, at the present rate it will take another few decades to do so…). Unsurprisingly, their more in-depth analysis typically led to uncovering further fine-grained structure in vocal differences. In very few cases if any however, did it lead to contradictory findings in comparison with my earlier preliminary analysis.

Submitted by: Peter Boesman

Date of comment: 30 November 2021

Recognize *Thryothorus albinucha* as a separate species from *Thryothorus ludovicianus* (Carolina Wren)

Effect on NACC:

This would treat the southernmost, isolated subspecies of *Thryothorus ludovicianus* as a separate species.

Background:

We (AOU 1998) currently treat *Thryothorus ludovicianus* as a single species but with two subspecies Groups:

> “Notes.—Groups: *T. ludovicianus* [Carolina Wren] and *albinucha* (Cabot, 1847) [Cabot's Wren]. Phillips (1986) not only treated *albinucha* as a species but also questioned whether *albinucha* belonged in the genus *Thryothorus*; however, see Griscom (1932), Lowery and Berrett (1963), and Cardiff and Remsen (1994).”

The distribution of the *albinucha* group was given as: “southeastern Mexico (Tabasco and the Yucatan Peninsula), northern Guatemala (Petén), and Belize, and locally in the interior of Guatemala (Sacapulas) and northwestern Nicaragua.”

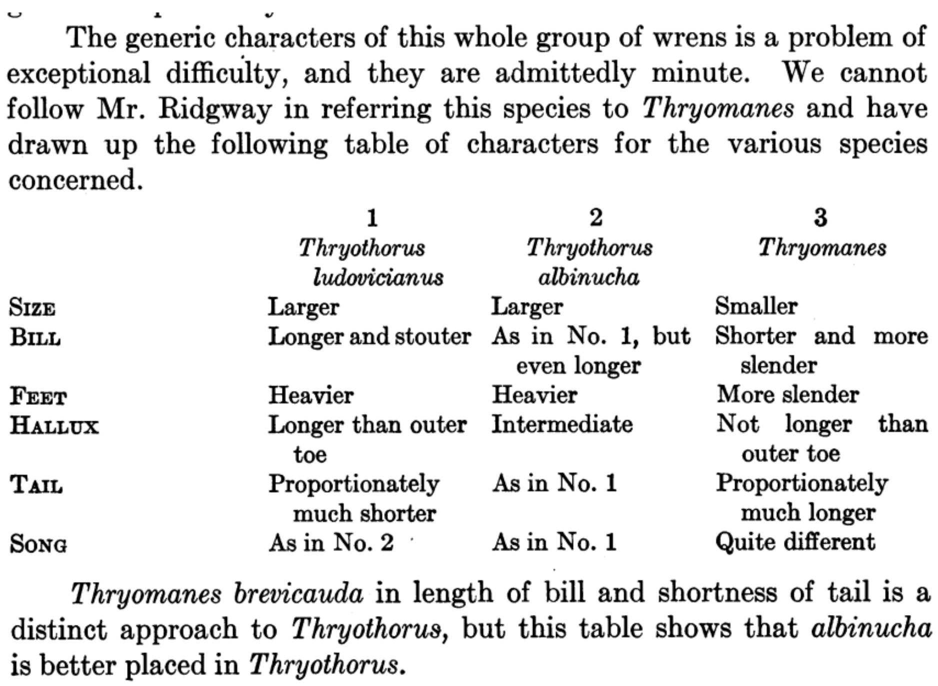
Taxonomic history:

- Ridgway (1904) not only treated *albinucha* as a separate species (Cabot’s Wren, after the describer) but also placed *albinucha* in a different genus, *Thryomanes* (including also *bewickii*). Ridgway’s key (p. 478) splits *Thryothorus* from *Thryomanes* based on whether the hind toe is longer or shorter than outer toe

- Miller and Griscom (1925) treated *albinucha* as a species but in describing a new subspecies (*subfulva*) close to *albinucha*, transferred them to *Thryothorus*, with the note on the next page (and tangentially they note that song is used here to delimit the genera – one of the first examples of this?):

- Hellmayr (1934) transferred it to *Thryothorus*, with the following footnote: “Not having seen this species, I follow Miller and Griscom in referring it to *Thryothorus*. Judging from the figure, I am inclined to believe it might be related to *T. felix*. Griscom (Bull. Amer. Mus. N. H., 64, p. 293, 1932) insists on its close relationship to *T. ludovicianus*, stating that ‘it is purely arbitrary to say that *T. ludovicianus berlandieri* and *T. albinucha subfulvus* are specifically distinct.’”

- Eisenmann (1955; The Species of Middle American Birds) treated them as separate species … so separate in fact that they are separated by 14 species in his linear sequence. He called *T. albinucha* “White-browed Wren” instead of Cabot’s Wren, as in Ridgway and Hellmayr, as part of his pogrom against possessive English names with the legalistic rationale the someone cannot “own” a species. But “White-browed”? Seriously? Not only does Carolina Wren have a mostly white eyebrow, but also several dozen species of wrens in multiple genera share this plumage feature. What was Eisenmann thinking? (Don’t get me started on what I perceive is the damage done to English names by Eisenmann.)



The generic characters of this whole group of wrens is a problem of exceptional difficulty, and they are admittedly minute. We cannot follow Mr. Ridgway in referring this species to *Thryomanes* and have drawn up the following table of characters for the various species concerned.

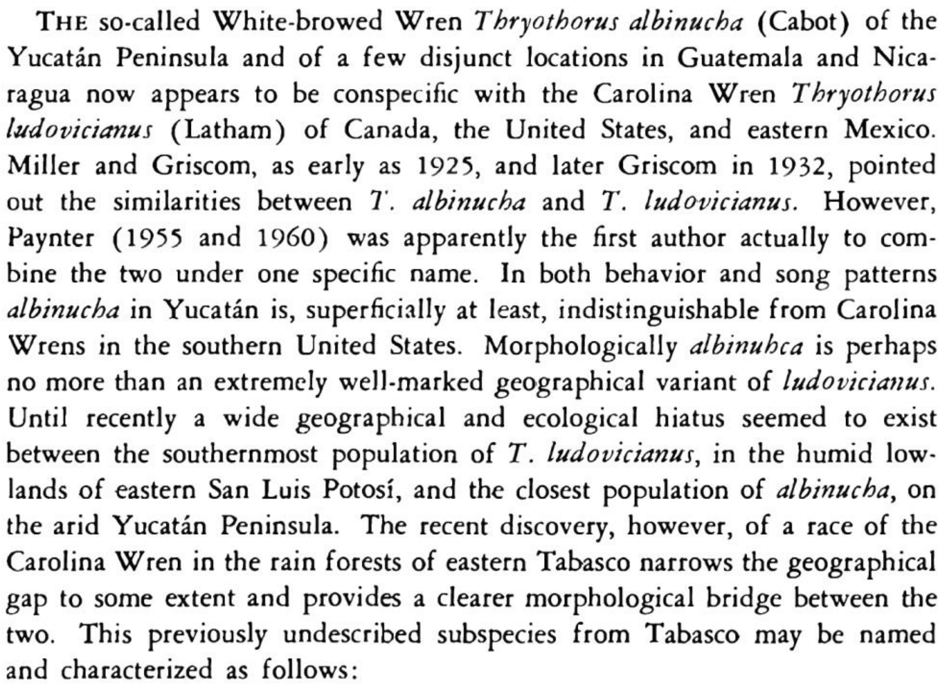
	1 *Thryothorus ludovicianus*	2 *Thryothorus albinucha*	3 *Thryomanes*
SIZE	Larger	Larger	Smaller
BILL	Longer and stouter	As in No. 1, but even longer	Shorter and more slender
FEET	Heavier	Heavier	More slender
HALLUX	Longer than outer toe	Intermediate	Not longer than outer toe
TAIL	Proportionately much shorter	As in No. 1	Proportionately much longer
SONG	As in No. 2	As in No. 1	Quite different

Thryomanes brevicauda in length of bill and shortness of tail is a distinct approach to *Thryothorus*, but this table shows that *albinucha* is better placed in *Thryothorus*.

- AOU (1957) treated them as separate species (by implication in the range statement of *ludovicianus*).

- Paynter in “Peters” (1960) treated *albinucha* and *subfulvus* as subspecies of *T. carolinensis*.

- Lowery & Berrett (1963) were emphatic about the conspecificity of *albinucha* and *ludovicianus*, especially with the discovery of a new subspecies that reduced the geographic gap between the two:



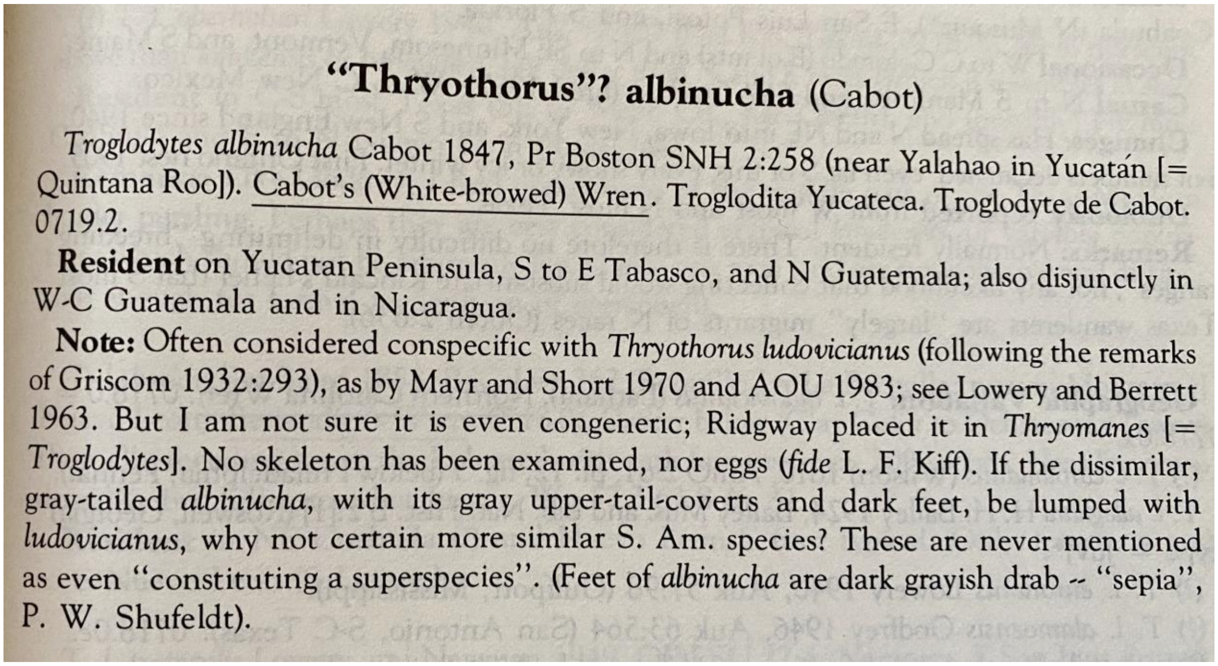
THE so-called White-browed Wren *Thryothorus albinucha* (Cabot) of the Yucatán Peninsula and of a few disjunct locations in Guatemala and Nicaragua now appears to be conspecific with the Carolina Wren *Thryothorus ludovicianus* (Latham) of Canada, the United States, and eastern Mexico. Miller and Griscom, as early as 1925, and later Griscom in 1932, pointed out the similarities between *T. albinucha* and *T. ludovicianus*. However, Paynter (1955 and 1960) was apparently the first author actually to combine the two under one specific name. In both behavior and song patterns *albinucha* in Yucatán is, superficially at least, indistinguishable from Carolina Wrens in the southern United States. Morphologically *albinuhca* is perhaps no more than an extremely well-marked geographical variant of *ludovicianus*. Until recently a wide geographical and ecological hiatus seemed to exist between the southernmost population of *T. ludovicianus*, in the humid lowlands of eastern San Luis Potosí, and the closest population of *albinucha*, on the arid Yucatán Peninsula. The recent discovery, however, of a race of the Carolina Wren in the rain forests of eastern Tabasco narrows the geographical gap to some extent and provides a clearer morphological bridge between the two. This previously undescribed subspecies from Tabasco may be named and characterized as follows:

• Mayr and Short (1970; Species Taxa of North American Birds; Publ. Nuttall Orn. Club 9) treated them as conspecific.

• Edwards (1972; Field Guide to the Birds of Mexico) treated *albinucha* as a separate species (White-browed Wren). Although he didn't compare Carolina Wren song directly to that of White-browed, his transliterations of the songs are extremely similar.

• AOU (1983) treated them as conspecific, with the two subspecies groups (but used White-browed Wren, not Cabot's Wren, as the English name, in contrast to AOU 1998)

• Phillips (1986; "Known Birds Vol. 1") wrote the following:



"Thryothorus"? albinucha (Cabot)

Troglodytes albinucha Cabot 1847, Pr Boston SNH 2:258 (near Yalahao in Yucatán [= Quintana Roo]). Cabot's (White-browed) Wren. Troglodita Yucateca. Troglodyte de Cabot. 0719.2.

Resident on Yucatan Peninsula, S to E Tabasco, and N Guatemala; also disjunctly in W-C Guatemala and in Nicaragua.

Note: Often considered conspecific with *Thryothorus ludovicianus* (following the remarks of Griscom 1932:293), as by Mayr and Short 1970 and AOU 1983; see Lowery and Berrett 1963. But I am not sure it is even congeneric; Ridgway placed it in *Thryomanes* [= *Troglodytes*]. No skeleton has been examined, nor eggs (*fide* L. F. Kiff). If the dissimilar, gray-tailed *albinucha*, with its gray upper-tail-coverts and dark feet, be lumped with *ludovicianus*, why not certain more similar S. Am. species? These are never mentioned as even "constituting a superspecies". (Feet of *albinucha* are dark grayish drab -- "sepia", P. W. Shufeldt).

(Phillips, by the way, included *Thryomanes bewickii* in *Troglodytes* … which reveals how unaware Phillips was of wren voice and behavior.)

• Cardiff and Remsen (1994), primarily as an antidote to Phillips (1986), indicated that the only recording available at the time sounded very much like a Carolina Wren.

• Howell & Webb (1995, Mexico field guide) treated them as conspecific but mentioned the two groups. In the Voice section, they described the song of the *albinucha* group as "much like Carolina Wren."

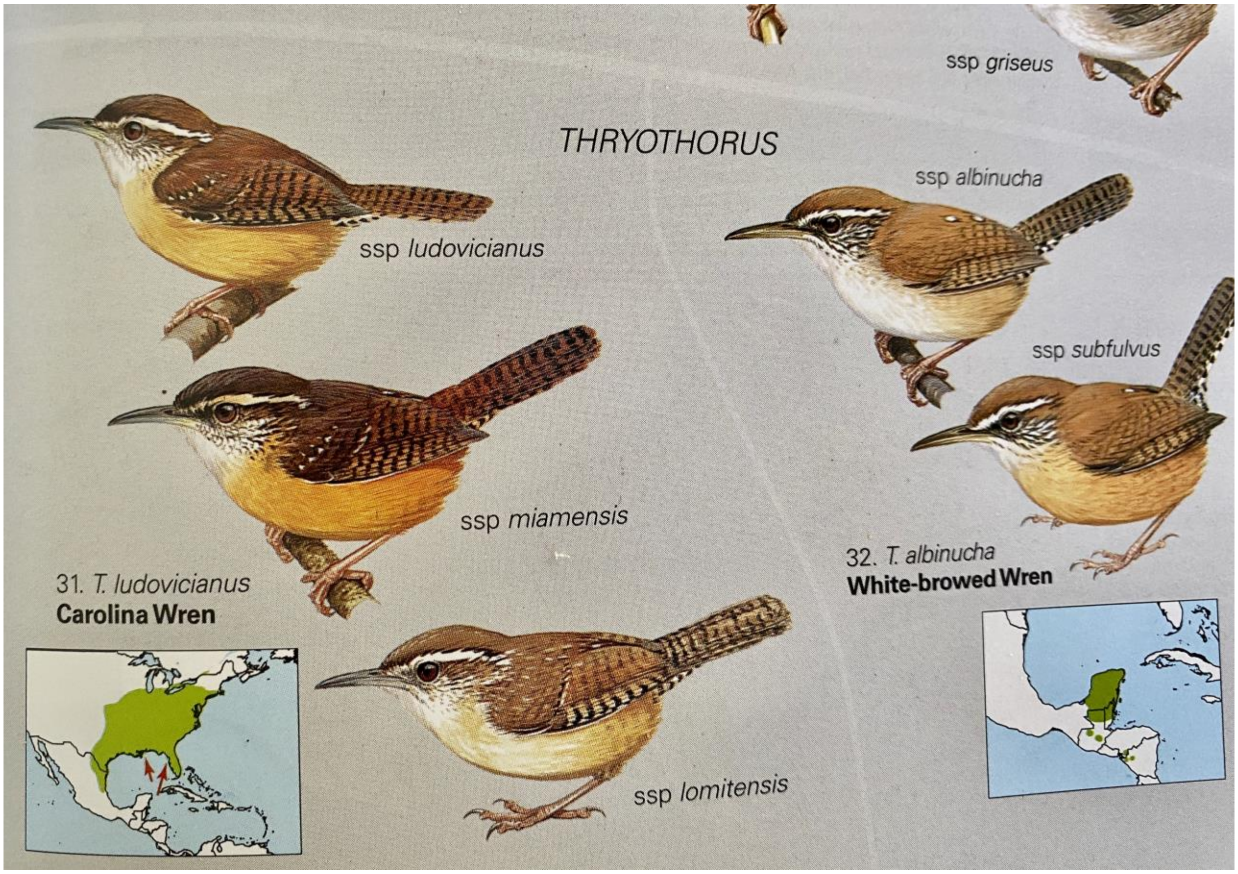
• Brewer (2001: Wrens, Dippers and Thrashers; Yale U. Press) treated them as separate species but gave no justification for this; in fact, he wrote "It may prove to be merely a well-marked, isolated race of the Carolina Wren". (Just in case you use the plate in Brewer to see what *albinucha* looks like, is incredibly misleading in portraying *albinucha* as an almost entirely grayish and whitish bird, which is inexplicable given that the bird was accurately illustrated in several places previously.)

• Kroodsma and Brewer (2005; HBW Vol. 10) treated them as separate species, but provided no justification for this; in fact, they said "Regarded by many authorities as a geographically disjunct race of *T. ludovicianus*, a view supported by recent similarities in song".

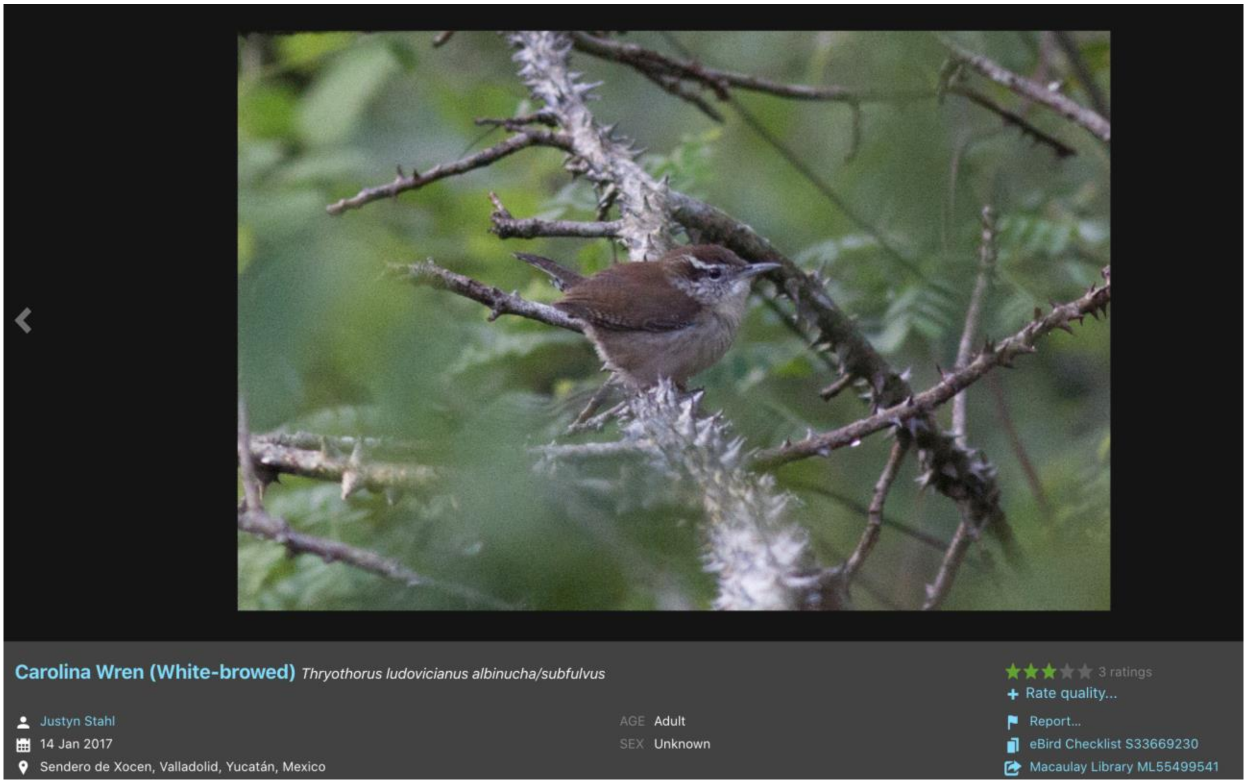
• Navarro-Sigüenza and Peterson (2004) treated *albinucha* as a separate species, but that was based on the ESC.

• Dickinson & Christidis (2014) treated them as conspecific, but as separate groups.

Plumage: To illustrate what Griscom, Lowery & Bennet, and others have pointed out, here's the HBW (2016) plate, which in my view just shows that the populations get paler the farther south one goes, with the palest being in the dry Yucatan Peninsula region:



Here are two photos from Macaulay Library, one from Yucatan (*albinucha*) and the other from Honduras (*subfulvus*). The Yucatan bird looks a little paler than a Louisiana Carolina Wren, but I would have to study the Honduras bird closely to distinguish it from a Carolina Wren in my backyard if it weren't for the somewhat grayer tail:

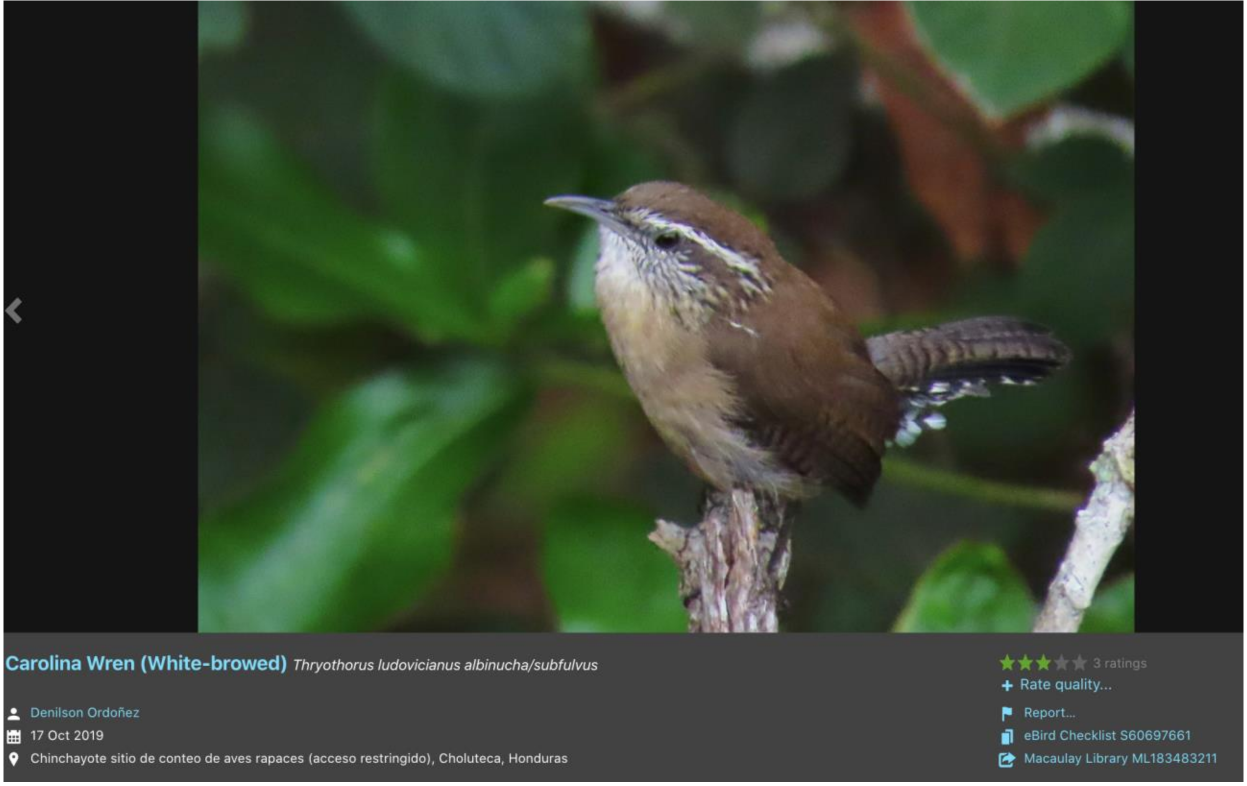


Carolina Wren (White-browed) *Thryothorus ludovicianus albinucha/subfulvus*

Justyn Stahl
14 Jan 2017
Sendero de Xocen, Valladolid, Yucatán, Mexico

AGE Adult
SEX Unknown

eBird Checklist S33669230
Macaulay Library ML55499541



Carolina Wren (White-browed) *Thryothorus ludovicianus albinucha/subfulvus*

Denilson Ordoñez
17 Oct 2019
Chinchayote sitio de conteo de aves rapaces (acceso restringido), Choluteca, Honduras

eBird Checklist S60697661
Macaulay Library ML183483211

New information:

Nothing really new. Del Hoyo and Collar (2016) treated them as separate species without comment and outlined the well-known plumage differences between the two, which was evidently their sole their rationale. From Terry's spreadsheet:

> "HBW-Birdlife split apparently based on very little: *ludovicianus* "Often considered to include *T. albinucha* as a geographically disjunct subspecies, and the two share similar songs."

Something seems to be amiss in all this because the Magic 7 Points cannot be accumulated solely on plumage scores alone, even if there were 7 "characters" in which they differed (although general lower degree of saturation of plumage cannot be regarded in my opinion as several independent characters). Either Collar made a mistake on the scoring, or we don't have all the facts on the scoring

Voice: Xeno-canto has a lot of recordings of the song of both groups.

You've all heard Carolina Wren. I would be interested to know if you would pick out these songs of *albinucha* as different:

- https://www.xeno-canto.org/118763 (Ian Davies)
- https://www.xeno-canto.org/444832 (by Manuel Grosselet)
- https://www.xeno-canto.org/437942 (By George Wagner)
- https://www.xeno-canto.org/84243 (Jelmer Poelstra))

These cuts are immediately recognizable to me as "Carolina Wren"; however, when I listen to enough cuts, I think I detect a slight difference in pitch (higher) and note complexity. Perhaps a thorough analysis would reveal consistent differences, but a thorough analysis would also have to consider potential differences in the southern populations of Carolina Wren from ne. Mexico, etc., as well as call notes. Given the large repertoire of song types within an individual male Carolina Wren and local dialects, an unusually large N would be needed to get at this.

Macaulay also has lots of recordings, accessible at https://search.macaulaylibrary.org/catalog?taxonCode=carwre2&mediaType=a&q=Carolina%20Wren%20(White-browed)%20-%20Thryothorus%20ludovicianus%20albinucha/subfulvus.

Mann et al. (2009) studied the duet of *T. l. albinucha*. They did not compare it directly to *T. ludovicianus* but did present one sonogram to show how similar they are and stated, "The songs of male *albinucha* from our study population in the Yucatan peninsula, Mexico, were very similar to those of male *ludovicianus* (Figure 2A–C)."

Genetic data:

Allopatry of these two nonmigratory groups means that they would almost certainly differ to some extent, and if no differences were found at the loci surveyed, that would only mean to me that not enough loci had been sampled. So, I'm not sure what genetic data would tell you in terms of species limits, as long as they were sisters. Some would pick some arbitrary cutoff point in % sequence divergence (bar-coding philosophy) or use comparative branch lengths within related genera to arbitrarily assign species/subspecies rank. Not me, as you already know.

The genetic data that have been published (Mann et al. 2006) show that *albinucha* and *ludovicianus* are sisters, thus refuting the hypothesis of Ridgway and Phillips, and the branch lengths separating the two are comparable to those separating several tropical wrens treated as subspecies. However, Mann et al. had only one sample of *albinucha* and one of *ludovicianus*. Mann et al. discussed the *albinucha/ludovicianus* species limits problem (including problems with playback experiments in these wrens) but did not come out strongly in favor of one treatment or the other.

Barker (2017) did not include a sample of *albinucha*.

Discussion and Recommendation:

I strongly recommend a NO on this one. In fact, I'm at a loss to explain why so many have treated these two as separate species since the situation was described accurately by Ludlow Griscom almost 100 years ago, and no contrary evidence has appeared since then. As noted above, even the Tobias-Collar scoring is questionable, or at least needs full explication.

Note on English names:

If the split were to be adopted, *albinucha* can be regarded as a peripheral isolate and thus no name change is needed for Carolina Wren (whew!). However, just in case … the two historical names as Cabot's Wren and White-browed Wren. Concerning the latter, this would be an exceptionally poor name, as outlined above under Eisenmann (1955).

Literature Cited: (links or skeletal citations inserted throughout except for standard references)

Submitted by: Van Remsen

Date of Proposal: 8 October 2021

Comment on this issue from Steve Howell:

White-browed Wren seems as good a species as many wrens that are split (such as the Plain Wren complex, although I might well lump those), and voice is often very similar in congeneric wrens such as Happy and Spot-breasted. White-browed has some calls I think are distinct from Carolina, but it's another subjective call and we don't go strongly one way or the other. It's another classic Isthmus break where different lineages are involved, but how far have they gone? I don't put much store in plumage tones with wrens, and even voice (to human ears) is difficult to appreciate. From the Belize field guide appendix (Howell & Dyer, in prep.):

White-browed [Carolina] Wren *Thryothorus [ludovicianus] albinucha* (p. XXX). Differences in voice and plumage suggest the*albinucha group* (Mexico to n. Cen America) and *ludovicanus* group (N America to ne. Mexico; Carolina Wren) may best be treated as separate species.

Date of comment: 23 November 2021

Split *Numenius hudsonicus* (Hudsonian Curlew) from *N. phaeopus* (Whimbrel)

The issue:

Numenius hudsonicus was lumped with *N. phaeopus* in the 1930s and 1940s without obvious justification. Modern data indicate that this was a mistake and that they are separate biological species.

Background:

Latham (1790, II:712) first described *Numenius hudsonicus* and at this time also used the English name Hudsonian Curlew, citing his first use of that same English name in his earlier work (Latham 1787:242-3). In the first edition of the AOU *Check-list* (AOU 1886), *Numenius hudsonicus*, the Hudsonian Curlew, was considered as a species distinct from *N. phaeopus*, the Whimbrel. This reflected earlier and contemporary treatments, such as Nuttall (1834), Audubon (1835), Coues (1872), Ridgway (1887), and also later works by shorebird experts, e.g., Seebohm (1888), and Elliot (1895). (Of historical interest is that Wilson, in his *American Ornithology*, confused it with *Numenius borealis*; see Audubon [1835] and various editions of Wilson.). Multiple authors noted that in their experience this species was distinct from *N. phaeopus*.

The two taxa were considered as species by the AOU through the 4th edition of the *Check-list* (AOU 1931), then as subspecies (*N. phaeopus phaeopus* and *N. p. hudsonicus*) in AOU (1944) and the subsequent 5th edition *Check-list* (AOU 1957, together with two other *N. phaeopus* subspecies, *islandicus* and *variegatus*, which also occur in our area of coverage). The two taxa occur as subspecific groups in the 6th and 7th editions (AOU 1983, 1998). In the 7th edition (AOU 1998), the species' groups notes related "*N. hudsonicus* Latham, 1790 [Hudsonian Curlew] and *N. phaeopus* [Whimbrel]. The two groups are genetically strongly differentiated (Zink et al. 1995) and may constitute two different species." (AOU 1998:160-161).

Hybrids between the two are not known (Gray 1958, McCarthy 2006).

This proposal considers splitting *Numenius hudsonicus* (including subspecies "*rufiventris,"* if valid, and nominate *hudsonicus*) from *Numenius phaeopus* (and its subspecies *islandicus, phaeopus, alboaxillaris, rogachevae*, and *variegatus*; Dickinson and Remsen 2013). Suggestions that *N. p. variegatus* might be specifically distinct from *N. phaeopus* (Zink et al. 1995, Livezey 2010) require further research, but at this time this seems unlikely (Sangster et al. 2011, Tan et al. 2019).

Phenotypically, the major subspecific groups *N. phaeopus* and *N. [p.] hudsonicus* are readily diagnosable by differences in plumage (e.g., *phaeopus* is distinctively white in the lower back and rump, whereas *hudsonicus* is not). Although the lumping of the two that occurred in the 20th century (Peters 1934, AOU 1944) did not provide reasoning, one can infer that these were judged to be only subspecies-level and not species-level differences. Intraspecific (subspecific) variation in shorebirds is sufficiently variable to make this an uncertain species limits characteristic (e.g., consider *Calidris ptilocnemis* and *C. alpina*), and from today's genetic and genomic perspectives this particular lumping seems to have been an error (see below).

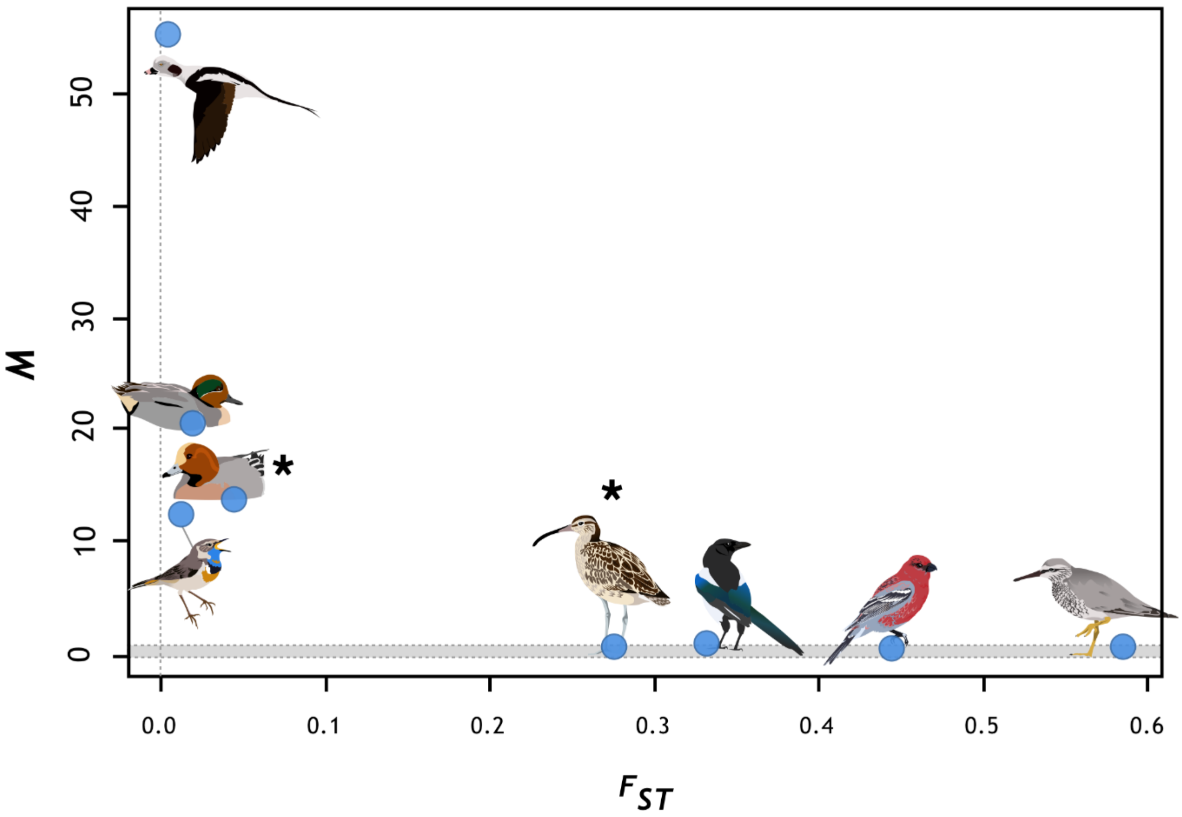
New information:

This split was considered but declined by the Committee in ~2000 (Banks et al. 2000), but we don't have a copy of that proposal available at this time (per Terry Chesser; thanks, COVID.) For clarity we'll proceed de novo.

Zink et al. (1995), using restriction fragment length polymorphisms of mtDNA, found what appeared to be species-level differences (p = 0.047) between *N. p. variegatus* from eastern Asia and *N. p. hudsonicus* from North America. Sangster et al. (2011), using phenotype and mtDNA COI sequence data from several sources showing 3.6% divergence and a monophyletic clade, elevated *N. hudsonicus* ("Hudsonian Whimbrel") to a separate species from *N. phaeopus*. Humphries and Winker (2011) corroborated the mtDNA difference, finding a relatively high level of sequence divergence in ND2 between these (then) subspecies. Although amplified fragment length polymorphisms (AFLPs) did not show significant differences in F_{ST} between the two (possibly due to small sample sizes), graphical contrasts of mtDNA vs. nuDNA divergence among this and other trans-Beringian taxa in that study suggested that taxonomically this pair was an outlier among subspecies and might be better considered full species (Humphries & Winker 2011: fig. 2).

Livezey (2010), using phenotype alone, considered *N. hudsonicus* to warrant species-level status, but he seemed to be using a phylogenetic species concept (see pp. 586, 596). In the recent revisions of the Handbook of the Birds of the World, del Hoyo & Collar (2014) did not elevate *hudsonicus* to species. Nor did Skeel and Mallory (1996, 2020).

Tan et al. (2019), using thousands of single nucleotide polymorphisms (SNPs), also found a strong difference between *N. phaeopus* and *N. [p.] hudsonicus* subspecies groups, both in principal component (PC) space and using a phylogenetic tree of their sequence data. McLaughlin et al. (2020), using over 2,300 ultraconserved element (UCE) loci, found substantial differences between *N. p. variegatus* and *N. p. hudsonicus* (F_{ST} = 0.27) and inferred long-term gene flow between them at a remarkably low 0.176 ($\pm$ 0.009) individuals per generation (or < 2 individuals every 10 generations, which with a generation time of 11.1 yrs. is less than two effective hybridization events every century). Given dispersal abilities and the annual occurrence of both taxa in Alaska (Gibson and Withrow 2015), these results suggest that reproductive isolation between the two is largely complete. Similar to Humphries and Winker (2011), McLaughlin et al. (2020) found that this taxon pair was a taxonomic outlier relative to other diverging lineages in Beringia (see their fig. 4, copied below), and they suggested that these two taxa are currently miscategorized as being just subspecies.



McLaughlin et al. (2020): Figure 4. UCE-based estimates of F_{ST} vs average migration (gene flow) rate in individuals per generation (*M*) in our eight two-population lineages, using the best-fit model results. This relationship is significant (as an exponential decay function) and demonstrates a non-continuous distribution among these lineages in Beringia in this divergence space. Two groups are apparent, one with low divergence and relatively high gene flow on the left, and one of higher divergence and low gene flow on the right. The dotted vertical line indicates $F_{ST} = 0$, and the horizontal grey band indicates *M* from 0-1 individuals per generation. Asterisks indicate two lineages that might be taxonomically miscategorized at present, given opportunities for gene flow and the amounts occurring.

Estimates of divergence dates between these forms vary from to ~1.1 Myr (mtDNA) to ~234 Kyr (UCEs; Humphries & Winker 2011, McLaughlin et al. 2020), although the latter is likely low due to gene flow and the as-yet uncalibrated nature of UCE divergence estimates at such shallow evolutionary depths.

English names:

From 1787 to 1944 (~157 yrs), the most commonly used English name for *N. hudsonicus* in the literature was Hudsonian Curlew. From 1944-2021 (~77 yrs) we used Whimbrel, uniting it with the Old World group, although the major subspecific group *hudsonicus* was termed Hudsonian Curlew in both the 6th and 7th editions (AOU 1983, 1998). If this proposed split is approved, resuming use of Hudsonian Curlew would represent the least disruption in the literature. Resuming use of a prior name (and in fact the current name of the subspecies group) has some appeal over changing it by adopting another name or inventing a new one.

Other English names have been used. For example, Seebohm (1888), Engelmoer and Roselaar (1998), Sangster et al. (2011), and Gill et al. (2021) used Hudsonian Whimbrel. Del Hoyo and Collar (2014) labeled the two major subspecific groups Eurasian Whimbrel and Hudsonian Whimbrel, as did Sangster et al. (2011) and Gill et al. (2021) in recognizing the two as species. McAtee (1948) included several other possibilities for *N. hudsonicus*. From the New World scientific literature perspective, using Hudsonian Curlew would be a resumption of using a prior name for the species and a current name for the subspecific group. People born after 1944 might consider such a resumption a name change, but from an AOU/AOS nomenclature perspective that would not be correct. Resuming use of Whimbrel for *N. phaeopus* would also be consistent with our past and current use (given it is the name for the major subspecific group; AOU 1998).

Effect on AOS-CLC area:

Recognizing *N. hudsonicus* at the species level again would require breaking its subspecific group account out of the *N. phaeopus* account and presenting the two separately. Two named forms of *N. hudsonicus* occur in our area ("*rufiventris*" and nominate *hudsonicus*), and at least two subspecies of *N. phaeopus* do, *N. p. variegatus* in the west and *N. p. islandicus/phaeopus* in the east.

Recommendation:

Evidence indicates that *Numenius hudsonicus* is a good biological species. The population genetics are particularly compelling, including both mtDNA and nuDNA. We should split it back out from *N. phaeopus*, with which it was lumped with little or no justification in the 1930s and 1940s. Resuming use of its English name Hudsonian Curlew at the species level is also warranted, as is resumption of Whimbrel for *N. phaeopus* sensu stricto, inasmuch as these are both our current names for the major subspecific groups (AOU 1998).

The vote:

a) Split *Numenius hudsonicus* (and its subspecies "*rufiventris"* and *hudsonicus*) from *Numenius phaeopus* (and its subspecies *islandicus, phaeopus, alboaxillaris, rogachevae*, and *variegatus*). Yes or No.

b) If 'a' is approved, resume using the English name Hudsonian Curlew for *N. hudsonicus* (as used in all prior *Check-lists* except the 5th edition, which did not use English names for subspecies). Yes or No.

c) If 'a' is approved, resume using the English name Whimbrel for *N. phaeopus* sensu stricto, as used in prior *Check-lists*. Yes or No.

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Submitted by: Kevin Winker, University of Alaska Museum (with input from Jack J. Withrow, Daniel D. Gibson, and Terry Chesser).

Date of proposal: 8 October 2021

External comment on Proposal 2022-A-10

Whimbrel I find unconvincing, with nothing mentioned about voice, which sure sounds similar although I haven't done any formal analysis. Winker doesn't seem to mention IOC and use of Hudsonian Whimbrel (vs. Eurasian Whimbrel, a lot more logical), or that IOC admits similar vocals need study. From the Costa Rica appendix:

Whimbrel *Numenius phaeopus* (p. XXX). Species status has been argued for New World populations (*hudsonicus* group, Hudsonian Whimbrel), based largely on genetic data (Sangster et al. 2011); although Hudsonian Whimbrel is split by IOC, in our view the case remains unproven from a biological perspective.

Submitted by: Steve Howell

Date of comment: 23 November 2021

Recognize extralimital *Leptodon forbesi* as a species distinct from Gray-headed Kite *L. cayanensis*

Note: This proposal consists of the original SACC proposal from 2007 (!) as well as information published more recently. *L. forbesi* is extralimital to the NACC area, and acceptance of this proposal would result in changes to our distributional statement and notes for *L. cayanensis*.

Original SACC Proposal 273, slightly modified:

Leptodon forbesi (Swann, 1922) was described from a single specimen obtained in Pernambuco State, northeastern Brazil. It was considered for more than a half century an invalid taxon, almost without disagreement (beginning with Hellmayr 1929). The majority of authors believed that *forbesi* was an anomalous or aberrant specimen of *L. cayanensis*, a well-known variable raptor (e.g., Foster 1971).

This treatment was affected when Teixeira *et al.* (1987) communicated the obtaining of 3 specimens in Alagoas (near Pernambuco) all similar to the type of *forbesi*, including a couple in breeding condition.

Despite acceptance of *L. forbesi* by several recent authors (Sibley and Monroe 1990, Howard and Moore 1994, Bierregaard 1994, Sibley 1996, BirdLife International 2000, Clements 2000, Ferguson-Lees and Christie 2001), the validity of the taxon seems continues to be questioned, because regular *L. cayanensis* has also been found in the same area (Silveira et al. 2003, pers. obs.).

However, two new records from Pernambuco in 2006 (see pictures, Pereira et al. 2006) and 2007 (B. M. Whitney, pers. comm.) - each time at least 2 individuals sighted - suggest that a population that matches perfectly with *forbesi* in fact exists in the Atlantic forest of northeastern Brazil (Pernambuco Center). These repeated records in this same restricted area (see another record from E. O. Willis in BirdLife International 2000), in combination with the fact that no individual similar to *forbesi* is known in the wide distribution of *cayanensis*, I think that the best treatment is to recognize *Leptodon forbesi* as a valid taxon.

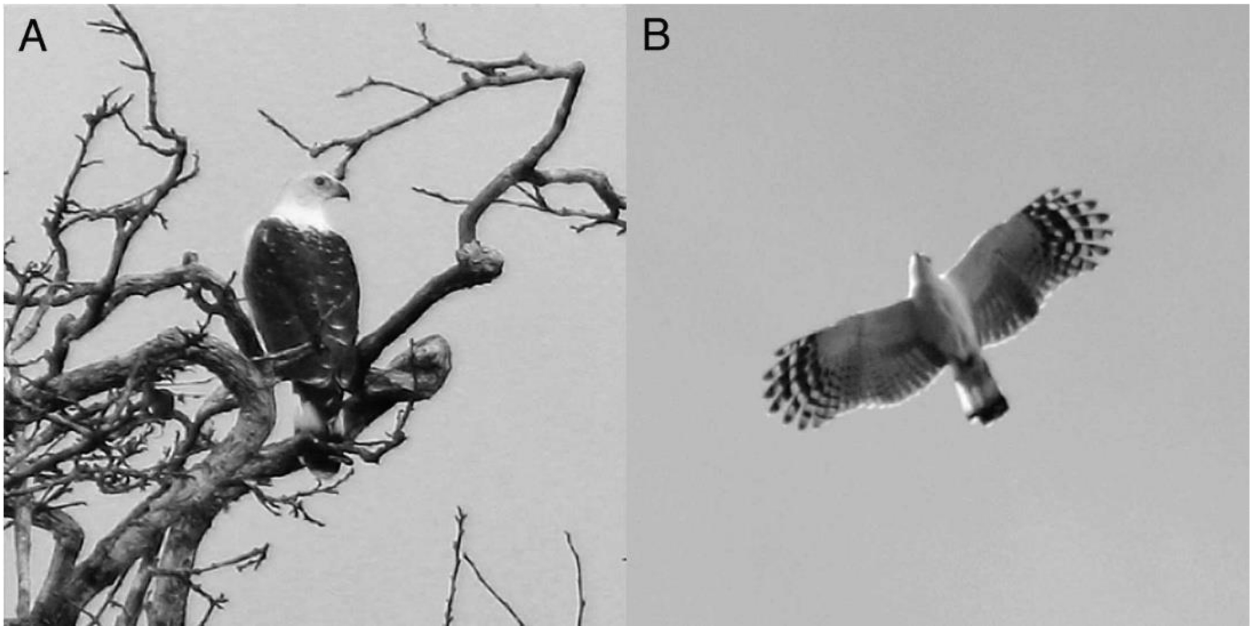
New Information:

Several years after SACC passed Proposal 273, Denés et al. (2011) published a detailed review of the biology and taxonomy of *Leptodon forbesi* and *L. cayanensis* based on museum specimens and field observations. They concluded that *L. forbesi* is a valid species distributed in the Atlantic Forest of Alagoas and Pernambuco in northeastern Brazil, and that it differs from *L. cayanensis* as follows:

> *Leptodon forbesi* can be distinguished from its congener, *L. cayanensis*, by the white color of the hind collar, instead of an inconspicuous and undelimited medium to pale neutral gray; mostly white in the underwing coverts rather than all black;

> and under surface of the secondaries predominantly white with greatly reduced black barring in comparison to the others (Fig. 2; color plate in Seipke et al. 2011).

This is their Fig. 2, showing perched and soaring individuals of *L. forbesi*:



Denés et al. (2011) noted that the range of *L. cayanensis* is typically considered to include the area of Atlantic Forest where *L. forbesi* is distributed, but all specimens from this area were found to be of *L. forbesi*. Moreover, no observations of *L. cayanensis* were made during the intensive field surveys in this region (Seipke et al. 2011), and there are apparently no documented observations of *L. cayanensis* from this area. Denés et al. concluded that the two species are allopatric.

Recommendation for NACC:

I recommend that we treat *L. forbesi* as a species separate from *L. cayanensis.* This is a well-documented split that is followed by all global lists. SACC retained the English name Gray-headed Kite for post-split *L. cayanensis*, presumably due to its vastly larger range, and I recommend that we do the same. The English name adopted by SACC for *L. forbesi* is White-collared Kite.

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Submitted by: Jose Fernando Pacheco (SACC proposal) and Terry Chesser

Date of Proposal: August 2007, modified 8 October 2021

Comments on the original SACC proposal:

Comments from Remsen: "YES. The evidence presented above clearly places burden of proof on those who question the validity of *L. forbesi*."

Comments from Stiles: "YES. Clearly the burden of proof now lies with those who would lump them - they would have to show that *forbesi*-type birds occur elsewhere within the range of *cayanensis* and that they represent some immature plumage stage, for neither of which does evidence exist at present."

Comments from Robbins: "YES. Although I wish there were more solid data, I'm willing to support elevating *forbesi* to species level."

Comments from Zimmer: "YES. Glauco Pereira's field sketches and descriptions of the birds he has recently discovered in Pernambuco match perfectly with the few specimens of *forbesi*, and do not match any known immature plumage of *cayanensis* from anywhere in its extensive range. I'd say that the burden of proof lies on those who would contend that *forbesi* is not a valid taxon."

Comments from Nores: "YES, totalmente de acuerdo. En principio sería muy raro que un inmaturo de *L. cayanensis* o de cualquier otro Falconiforme tuviera diferencias como tienen estas dos especies, especialmente en la cola. Ahora que ya han sido coleccionados y observados varios ejemplares en un área restringida dentro del rango de *L. cayanensis*, disipa, para mí, toda duda sobre la validez de la especie."

Recognize extralimital *Turdus maculirostris* as a species distinct from Spectacled Thrush *T. nudigenis*

Note: This proposal is a slight modification of SACC Proposal 385. Acceptance would result in recognition of extralimital species *Turdus maculirostris* and would necessitate changes to our distributional statement and notes for *T. nudigenis*.

Original SACC proposal:

Background:

Turdus maculirostris was described in 1883 as a subspecies of *T. ignobilis*, but two years later, its describer, Berlepsch, treated it as a species, as did Chapman (1926) in his Ecuador monograph. However, Hellmayr (1934) lumped it with *Turdus nudigenis*, with the following statement: "an exact duplicate of *T. n. nudigenis* and differing mainly by the lesser extent of the bare skin around the eye." Ripley (1964 – Peters Check-list) continued to treat it as a subspecies of *nudigenis*.

Ridgely & Tudor (1989) elevated *maculirostris* to species rank with the following note: "it lacks the wide bare ocular area so distinctive in *T. nudigenis* (the eye-ring of *maculirostris* is comparable in width to that of *T. grayi)*, differs in its forest-based habitat, and has a widely disjunct range." This treatment was followed by Sibley & Monroe (1990), Clement (2000), Restall et al. (2006), and Collar (2005) despite the absence of any formal analysis and no data on voice. In their defense, the rationale for the original lump was of the same caliber. Dickinson (2003) and Schulenberg et al. (2007) treated *maculirostris* as a subspecies of *nudigenis*.

New data:

Voelker et al. (2007) sequenced mtDNA (ND3, ND2, cyt-b) from 60 of the world's 65 *Turdus* (see SACC proposal 338). A node that unites *maculirostris*, *nudigenis*, *haplochrous*, and *grayi* received strong support (>95% Bayesian, maximum parsimony > 50%, ML bootstrap 83%. The branching pattern has *maculirostris* as sister to the other three, thus making our existing *nudigenis* paraphyletic with respect to *grayi* and *haplochrous*. However, the branching pattern has no support other than a 57% bootstrap value for a sister relationship between *nudigenis* and *haplochrous*.

Nylander et al. (2008) sequenced mitochondrial (12S, cyt-b) and nuclear (3 introns) DNA for 60 *Turdus* species. They found the same grouping and the same topology (although they did not report support values … or at least I can't find them). I am also unable to tell whether the critical section of their tree is determined solely by the one gene in common to both studies, cyt-b.

I listened to the songs and calls available at Xeno-Canto and was unable to hear any consistent differences in songs or calls between the two. However, I couldn't hear any clear differences between *grayi* and *nudigenis*, at least in terms of that mewing call; unfortunately, there does not seem to be a full song of nominate continental *nudigenis* at xeno-canto. Obviously, this doesn't mean much except that someone ought to do a formal analysis of vocalizations in this group. I am impressed with how similar these three are in terms of plumage, and in the study skins, the eye-ring of *nudigenis* isn't nearly as impressive as it would be in the field. I can certainly see why Hellmayr used the term "exact duplicate" (although I'm not sure what at "inexact duplicate" would be).

Analysis and Recommendation:

I don't think there is a strong case either way, and I have no recommendation to make. I will wait to see what others say before I vote. One could vote NO based on (1) the absence of compelling evidence to change from our current treatment, and (2) no vocal differences between the two have been documented. Keep in mind that the genetic data basically represent an mtDNA gene tree, not necessarily a species tree. One could vote YES on the basis that our current treatment rests on one sentence in Hellmayr (1934) and that if *grayi* and *nudigenis* are ranked as separate species, then *maculirostris* should also be, because in some ways it is closer in plumage and biogeography to *grayi* than it is to *nudigenis* (and is there any case of a species in *Turdus* within which there is geographic variation in eye-ring development?).

NACC Recommendation:

I recommend that we follow SACC on this. All global lists have recognized *T. maculirostris* as a valid species based on the references in the SACC proposal. SACC retained the English name Spectacled Thrush for post-split *T. nudigenis*, presumably due to its vastly larger range, and I recommend that we do the same. The English name adopted by SACC for *T. maculirostris* is Ecuadorian Thrush.

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Submitted by: Van Remsen, NACC recommendation by Terry Chesser

Date of Proposal: November 2008, modified 8 October 2021

Comments from SACC:

Comments from Stiles: "YES. Although the formal evidence for recognizing *maculirostris* is admittedly thin, it includes some genetic, morphological, habitat and distributional information. Given that the original lumping was a Petersian fiat with no explicit analysis whatever presented, I feel that what we have available now shifts the burden of proof onto the lumpers. For what it's worth, the single Colombian specimen of *maculirostris* was taken in humid Pacific foothill forest, a most unlikely habitat for either *grayi* or *nudigenis* – and a long way from the known ranges of either*."*

Comments from Nores: "NO. Pienso que no hay ningún aspecto que realmente lo separe. El apoyo genético es débil. Las diferencias morfológicas son mínimas, y el principal caracter se da en otras especies: *Turdus merula*, por ejemplo, tiene subespecies sin círculo ocular. La distribución cae tanto en especie como en subespecie, ya que hay muchos ejemplos de especies que tienen una subespecie al este de los Andes y otra al oeste. Por ej. *Trogon melanurus, Myrmotherula brachyura*, etc. Tampoco veo importante lo del hábitat. Hay también muchos ejemplos de especies en que las subespecies viven en diferentes hábitats, a veces muy distintos, como *Thamnophilus caerulescens, Melanopareia maximiliani, Sittasomus griseicapillus*, etc."

Comments from Robbins: "YES, given the two new genetic data sets coupled with the fact that *maculirostris* does have very different habitat requirements and is widely disjunct from mainland *nudigenis* (I have field experience with both) I support this split."

Comments from Zimmer: "YES. Treating it as conspecific with *T. ignobilis* makes no sense. Treating it as conspecific with *nudigenis* is more defensible, but as noted by Ridgely and others, there is a big difference in the extent of the bare ocular skin of the two species, not to mention habitat differences and range disjunction. Based on my own field experience with all of the species involved, I'd say that the vocalizations of *maculirostris* are every bit as similar to those of *grayi* as they are to those of *nudigenis*, and I don't think we want to lump those two taxa."

Comments from Jaramillo: "YES – This is a really interesting case, in particular when thinking about the vocal similarity of various taxa in this group. But then again, *Turdus* in general do not strike me as all that different overall in terms of song, calls are another story, but still taxa that appear to be good species in *Turdus* but which are closely related do tend to have rather similar calls. For example, *Turdus rufitorques* (Rufous-collared Robin), which is strikingly different visually from *Turdus migratorius* (American Robin), is surprisingly similar in calls and voice. So the similarity in vocalizations does not bother me too much in this case, although it would be nice if there were greater differences, and as Van says a study does need to be performed to better understand voice in this group. The genetic, plumage, orbital ring, and habitat differences add up to convince me that *maculirostris* should be treated as a separate species."

Comments from Pacheco: "YES. Diante do exposto, eu creio que a melhor solução seja tratá-lo em separado – o lumping foi arbitriamente implementado – até que novas informações estejam disponíveis."

Recognize extralimital *Sipia palliata* as a species distinct from Dull-mantled Antbird *S. laemosticta*

Note: This proposal is a slight modification of SACC Proposal 475. Note that at the time of that proposal, these species were still placed in *Myrmeciza*. Acceptance would result in recognition of extralimital species *Sipia palliata* and would necessitate changes to our distributional statement and notes for *S. laemosticta*. A change could also be made to the English name for *S. laemosticta*, but this is not recommended.

Original SACC proposal:

Three species of "*Myrmeciza*" antbirds are currently recognized in the *laemosticta* complex, namely *M. laemosticta*, *M. nigricauda*, and *M. berlepschi.* These species have had an unstable taxonomy, with sexes of single species treated in separate taxa, or members classified in different and often distantly related genera (see Robbins & Ridgely 1991, Zimmer & Isler 2003). Currently, only *M. laemosticta* is polytypic, with two subspecies: the nominate subspecies from lower Central America (NW Costa Rica to Darién in E Panama) and *palliata* from the Colombian and Venezuelan foothills of inter-Andean valleys (Wetmore 1972, Zimmer & Isler 2003). The taxon *palliata* includes synonymized forms *bolivari* and *venezuelae* (Robbins & Ridgely 1991) and has never been considered a separate species.

Observations and recordings by B. Whitney and A. Cuervo (published in the Colombian Andes Sound Guide; Alvarez et al. 2007) of the then-unknown loudsong of *M. l. palliata* from the Magdalena valley were indicative of their distinctiveness and degree of differentiation with respect to the loudsongs of *M. l. laemosticta*. Chaves et al. (2010) recently evaluated species limits in the *laemosticta* complex and investigated whether *M. l. palliata* merited elevation to species rank. Specifically, they conducted a quantitative analysis of vocal variation in male songs and a qualitative assessment of variation in calls and female songs and calls, coupled with a phylogenetic hypothesis for the group based on sequences of a mtDNA gene.

Fourteen vocal traits in a total of 42 individuals of the complex, as well as *M. griseiceps*, were analyzed statistically*. M. l. palliata* was vocally diagnosable from all other species and differed from *M. l. laemosticta* in three vocal characters. A multivariate analysis of songs showed that each taxon differed significantly from the others: *M. l. palliata* was vocally divergent from *M. l. laemosticta* and closer to, but distinct from, *M. nigricauda.* Vocal results were consistent with the ND2 gene tree, which showed a highly supported clade for the *laemosticta* complex with the four taxa forming a polytomy (i.e., no support for a sister relationship between *laemosticta* and *palliata*), and branches leading to each taxon were relatively long, thus indicating a comparable time of isolation. Thus, pairwise genetic distances were nearly the same among the four taxa.

Chaves et al. concluded that *M. l. laemosticta* and *M. l palliata* should be treated as distinct species under criteria of diagnosability and (inferred) potential reproductive isolation. Vocal variation indicates that *M. l. palliata* merits elevation to species rank following the standards for allopatric populations in antbirds (Isler et al. 1998), and genetic variation indicates an independent history of evolutionary isolation roughly congruent with the divergence among currently recognized species in the group. I encourage all to read the paper for further details on methods and results and to examine vocalizations in xeno-canto.

The English name Magdalena Antbird is recommended for *M. palliata* (Chaves et al. 2010). This name was previously used by Cory and Hellmayr (1924) for *Formicivora grisea hondae.* Meyer de Schauensee (1950) didn't follow Cory and Hellmayr's name for *F. g. hondae* and used "Honda Ant-Bird" instead. In both publications, Pale Antcatcher was used for *M. laemosticta palliata.* The English names proposed for these subspecies have no tradition of usage (i.e., they were only used in these publications), and taxonomic nomenclature rules do not apply for English names.

Recommendation: I recommend a YES vote to recognize *"Myrmeciza" palliata* as a separate species from *"Myrmeciza" laemosticta* and to adopt the English name Magdalena Antbird for *M. palliata.*

Recommendation for NACC:

I recommend that we follow SACC on this. All global lists have recognized *S. palliata* as a valid species based on the references in the SACC proposal. *Sipia laemosticta sensu stricto* does not occur in South America, so they did not decide whether to retain the English name Dull-mantled Antbird for the split species, but all global lists have retained this English name. Although a case could be made for changing the name in accordance with our default policy for species splits, in this case the range of *laemosticta* is larger than that of *palliata*, the English name Dull-mantled Antbird has presumably been used in the literature for Central American birds more often than for South American, and this name has been in use for *S. laemosticta sensu stricto* for the better part of a decade, if not longer. I recommend that we continue to use Dull-mantled Antbird for this species. The English name adopted by SACC for *S. palliata*, as recommended in the proposal, is Magdalena Antbird.

Literature cited:

Álvarez, M., V. Caro, O. Laverde & A. M. Cuervo. 2007. Guía Sonora de las Aves de los Andes Colombianos. Instituto Alexander von Humboldt & Cornell Laboratory of Ornithology.

Chaves, J. C., A. M. Cuervo, M. J. Miller, & C. D. Cadena. 2010. Revising species limits in a group of *Myrmeciza* antbirds reveals a cryptic species within *M. laemosticta* (Thamnophilidae). The Condor 112: 718-730. http://www.museum.lsu.edu/cuervo/pubs_files/Chaves_etal.Condor.2010.pdf

Meyer de Schauensee, R. 1950. The birds of the Republic of Colombia. Caldasia 5 (24): 645-871.

Other references in the SACC reference list or in the Chaves et al. paper.

Submitted by: Andrés M. Cuervo, NACC recommendation by Terry Chesser

Date of Proposal: December 2010, modified 8 October 2021

Comments from SACC:

Comments from Zimmer: "YES. As far as I can tell from listening to vocal samples of *palliata* (which I don't know in life) versus those of *laemosticta*, which I have recorded extensively in Costa Rica and Panama, the two taxa are diagnosably different (vocally) to an extent consistent with species-level recognition in Thamnophilidae. The vocal and genetic analyses of Chaves et al. (2010) would seem to support that conclusion. "Magdalena Antbird" seems appropriate as an English name for *palliata*."

Comments from Thomas Donegan:
"Summary: Chaves et al. (2010) demonstrate clearly that *palliata* should not be treated as part of the same species as the Dull-mantled Antbird *M. laemosticta*. However, they do not deal adequately with the elephant in the room. Esmeraldas Antbird *M. nigricauda* (of the West Andes foothills) and *palliata* (Central and East Andes foothills) are vocally almost identical, have similar habitat requirements and elevational ranges on adjacent mountain ranges and were historically treated as conspecifics. Andrés Cuervo's proposal does not discuss whether *palliata* is a good species with respect to *nigricauda* nor does it note that the vocal differences fall below that typically used as a benchmark for species rank in antbirds. Chaves et al. (2010) briefly discuss the point, but their discussion is inconsistent with the data presented and unconvincing.
"In January 2003, I made what I understand to be the first known Colombian recordings of *palliata* in Cerro de la Paz, Santander, Colombia (http://www.xeno-canto.org/recording.php?XC=24335) and then compared sonograms of this with those of *M. nigricauda* and *M. laemosticta*. At one point, I prepared a short note with a view to publication, but this was not developed further when I heard that Chaves, Cuervo and Cadena were conducting their own more detailed study, a few years ago. Chaves et al. (2010) have spent a lot of time and effort investigating the situation further and speak to their own history of study in this group. They should be congratulated for dealing with the *laemosticta* / *palliata* issue in a diligent way. The molecular data is also very interesting. However, the authors are not persuasive in concluding that *palliata* is a separate species from *nigricauda* based on vocal differences. The reasons for this are set out below.

"Vocal issues
"Isler et al. in their various papers have generally adopted a "three diagnosable differences" test for loudsongs in assessing species rank for antbirds. Chaves et al. (2010) do well to consider whether this test is appropriate for this particular group of antbirds. It has recently been shown that sympatric species of suboscine groups may show lower levels of diagnosable differences in loudsong than the traditional benchmark of three differences. Chaves et al. (2010) call for a "2 diagnosable differences" test to be applied for these *Myrmeciza* based on the differences between *nigricauda* and *berlepschi.* Some preliminary results with other *Myrmeciza* I am currently studying vocally would also support this more liberal approach, as do studies of sympatric members of the Warbling-Antbird group. However, despite what is said in Chaves et al. (2010), it is a big stretch to conclude that *palliata* and *nigricauda* meet even this "two differences" test.

"The authors do not appear to have actually elucidated two differences in loudsong between *palliata* and *nigricauda*. Their Table 1 (p.720) asserts the two differences to be in "Note shape" and "Note structure". Those 'two' variables appear on their face to be the same thing. The authors list all vocal variables that were studied in Appendix 2 (p. 729). The variable "Note structure" is described but "Note shape" is not mentioned. In Appendix 3 (p. 730) the authors go on to describe the nature of the differences shown, and cite differences in both "Note shape" (the same term not defined elsewhere) and "Change in note structure" (a variable not mentioned in Table 1 for this species pair, but which is defined in Appendix 2). The discussion of the differences between *nigricauda* and *palliata* in Appendix 3 refers to supposedly diagnosable differences referable to "Change in note structure" (although more on that below) but does not mention overall diagnosable differences in note structure.

"As can be seen from their Figure 2 (p. 721) and other recordings on xeno-canto, both *palliata* and *nigricauda* give inverted chevron shaped notes and also more "rounded" inverted-chevron-shaped notes. Some of these note shapes are given in a different order within songs in the sonograms presented in Figure 2 and some of them are skewed differently. However, note shape should only be treated as a diagnosable difference if none of the notes of the two populations are similar. It is clear that both *nigricauda* and *palliata* are capable of giving notes of the same shape: they just do so at different points in time in the sonograms presented. The only difference that the authors describe is the order in which the notes of particular structure are delivered – i.e. a difference in "change in note structure", or, more accurately "The note structure of certain notes at a particular point in time or segment within the song", not actually "Note structure". This *single* vocal difference should not be double-counted.

"Even then, Chaves et al. (2010)'s description of changes in note structure does not concord with available recordings. The sonograms of these taxa on xeno-canto show considerable variation in note shape of both *M. nigricauda* …
http://www.xeno-canto.org/browse.php?query=myrmeciza nigricauda&pagenumber=&order=taxonomy&view=3
… and "*M. palliata*"
http://www.xeno-canto.org/browse.php?query=laemosticta cnt:colombia&pagenumber=&order=taxonomy&view=3

"Appendix 3 accurately discusses the subjective differences between the sonograms shown in Figure 2, but it does not take account of individual variation in these birds. The authors describe *palliata* songs as constituting three segments. Supposedly, in the first segment, "notes of *M. nigricauda* are rounded, those of *M. l. palliata* are slurred up–down". However, XC3870 of *M. nigricauda* is as up-down in the first segment as various *palliata* recordings. In the third segment, the authors claim that "both taxa emit rounded notes (partially modulated in *M. nigricauda*). However, several recordings of *palliata* do not show any such "third segment": examples are XC10725, XC16311 and XC18154. One of these recordings was cited in the paper as being part of the sample studied. The authors also conclude that in recordings of *nigricauda*, note shapes "change from rounded to partially modulated to rounded again". However, sonograms of *nigricauda* on xeno-canto (none of which the authors studied) include more variety in note shape, with examples where the third segment involves a sharp up-down stroke (XC18884), more rounded inverted chevron (XC30289), or down stroke with a small rising initial tail (XC58961). The methodology (p. 720) asserts that the authors "examined qualitative characters through a blind inspection and grouping of printed sonograms followed by an assessment of whether the groupings matched the populations under study". But their definition of the differences in "change in note structure" between these taxa do not facilitate the blind allocation of available recordings to particular species. More detailed and convincing analysis on this issue is warranted. Given that there is a larger sample available on xeno-canto, it would be better to include these additional recordings in analyses.

"The authors also mis-describe the results of their multivariate analysis as regards *nigricauda* and *palliata*. They state as follows: "Discriminant function analysis of songs of the four taxa in the *M. laemosticta* complex revealed that each taxon's group centroid differs significantly from the others (Wilks' L = 0.003, df = 36, P < 0.0001). The analysis classified correctly 100% of individuals to their respective population designation (Table 3; Fig. 4), demonstrating that *M. l. laemosticta*, *M. l. palliata*, *M. nigricauda*, and *M. berlepschi* are all vocally diagnosable with respect to each other in multivariate space." (p. 721). This statement may be correct as regards diagnosis as between most of the species pairs studied. However, as regards *nigricauda* and *palliata* it is highly misleading. The two taxa do not appear to be diagnosable based on quantitative measures. The authors cite Table 3 (p. 724) and Figure 4 (p. 724) for the proposition that "100% of individuals" (including of *palliata* vs. *nigricauda*) could be classified correctly. However, in Figure 3 (p. 723), *nigricauda* and *palliata* overlap for all vocal variables. Table 3 (p. 724) shows the weight given to the variables in the analysis; and in Figure 4 (p. 724), *palliata* and *nigricauda* cluster together and would not appear diagnosable in the (x=10-11, y=-12 to -10) part of the range. The authors cite a Wilks lambda test, but that compares the statistical significance of differences between centroids, not dealing with diagnosability. To consider diagnosability using multivariate analysis, one should demonstrate that recorded values for the two groups fall either side of a curve or line, depict 95% or higher ellipsoids on the diagram which should not overlap or carry out other statistical tests. Figure 4 shows *palliata* and *nigricauda* clustering together, so it is doubtful that those sorts of analyses would show diagnosability.

"Assuming that the authors were inadvertent in asserting that *palliata* and *nigricauda* are fully diagnosable in multivariate space, and given that there are no diagnosable differences in the quantitative variables, we are considering here only subjective differences in note shape. When comparing those to differences between sympatric taxa, it should not be only the *existence* of a difference that is relevant, but the *degree and nature* of the difference. The authors consider the vocal differences between *palliata* and *nigricauda* to be similar to those between *berlepschi* and *nigricauda*, which are sympatric. However, recordings of *berlepschi* show more fundamental differences in "note structure". *M. berlepschi* recordings involve down strokes, with only a tiny rising "tail" in some instances and no significant "change in note structure". See Figure 2 (p. 721) and also other recordings available on xeno-canto: http://www.xeno-canto.org/browse.php?query=myrmeciza berlepschi&pagenumber=&order=taxonomy&view=3

"In contrast, both *palliata* and *nigricauda* songs consist of a series of up-down strokes or "chevrons" of varying shape. As discussed above, perhaps only the "second segment" shows diagnosable differences in note shape. The degree of those differences is not very impressive compared with those between *nigricauda* and *berlepschi* and are not accurately described by Chaves et al. (2010).

"Finally, the authors refer to differences in call. Although this is not analysed in detail, various examples of sonograms of calls are presented in Figure 5 (p. 724). The authors' selection of published sonograms is quite surprising. Similarly structured calls do not appear to have been presented. Chaves et al. (2010) show the *palliata* call being a flat rasp, with that of *nigricauda* being a very different up-down stroke. However, another of my recordings, XC31829 (and also XC10724 by Nick Athanas) are of calls of *palliata* and they are up-down strokes, with much more similar note shape to the sonogram of the call presented by Chaves et al. (2010) of *nigricauda*. The calls of *nigricauda* and *palliata* sound rather similar, with the call of *nigricauda* perhaps being a little raspier.

"A conservative approach under a comparative BSC approach of the nature adopted in Remsen (2005), Helbig et al. (2002) and similar papers would therefore be to lump *palliata* with *nigricauda* on the basis of the vocal data presented.

"<u>Sampling gaps</u>

“The authors have overlooked to study some very interesting and important specimens. It has never been suggested that *laemosticta*, *palliata* or *nigricauda* exist in sympatry and Chaves et al. (2010) do not suggest this either. However, the three forms occur in very close proximity in the central to northern section of the West Andes and surrounding region. Some of them may indeed be sympatric or parapatric. The authors do not discuss whether or not the taxa intergrade in this region.

“The closest materials studied by Chaves et al. (2010) for *laemosticta* are from Panama, *palliata* from the northern Central Andes and *nigricauda* from the southern-central part of the West Andes. *M. nigricauda* is generally not considered to extend further north in range than the locality sampled by the authors in major texts. However, the literature may not be correct in this respect. Project Biomap (www.biomap.net) data include a specimen of *nigricauda* from the Baudó mountains in Chocó department (ANSP 147226) and another from Remedios, Antioquia in the northern foothills of the *Central* Andes (Colegio San José, Medellín, 0021B). I have not seen these specimens or any photograph of them, but per information on Biomap, the Remedios skin’s identification was confirmed by Tomás Cuadros who noted that it represented a significant range extension.

“Based on these specimens, *M. nigricauda* may range further north and east than is generally thought and could be sympatric or parapatric with *M. (x.) palliata*. Or it may not if these are database or identification errors. The Baudó specimen, whatever it is, falls in an important sampling gap. There are now several lower elevation localities in the northern West Andes foothills and Baudó mountains that are safe to study for sound recording or other field studies. There is a specimen of *palliata* which one of the authors (Andrés Cuervo), Paul Salaman and myself collected in 1999 from the northern end of the Central Andes below Anorí (close to Remedios) which is close to these other localities, and this one was sampled by the authors. Chaves et al. (2010) should have studied the other specimens mentioned above before concluding that *palliata* and *nigricauda* are two species. If *palliata* and *nigricauda* are sympatric and do not intergrade then they must be split, *but the specimens mentioned above must first be studied to confirm whether or not this is the case*.

“Plumage

“Plumage differences are notable in the context of Thamnophilidae, with differences in the mantle colour and throat pattern of males and wing bars of females. However, these are not so great such that the two forms were historically treated as conspecifics, including as recently as by Hilty & Brown (1986). Certainly, *palliata* is closer in plumage to *laemosticta* than it is to *nigricauda*. It would be nice to see some data on biometrics before concluding that phenotype supports the split of *palliata* from *nigricauda* and the authors do not justify this split with regard to plumages.

“Molecular data

“One could also treat *palliata* as a species because *nigricauda* would otherwise be paraphyletic based on the molecular data and applying phylogenetic species concepts. SACC has accepted some splits in the past where there is paraphyly but little vocal support (e.g. Ecuadorian Thrush, although the disjunct distributions were also relevant there). Genetic differences (7%) are pretty impressive and more or less equal as between *laemosticta, nigricauda* and *palliata*. On the other hand, the *laemosticta* to *palliata* node is not very strongly supported (0.73 / 61) and there are “good” species that show greater intraspecific mtDNA variation than these.

“Conclusion

“Chaves et al. (2010)’s vocal data strongly support moving *palliata* from *laemosticta* to *nigricauda* but do not support splitting *palliata* from *nigricauda*. At least, it would be sensible to take the following steps before making this split: (i) studies of voice, the specimens referred to above, and molecular samples from the “gap” in the northern West Andes and Baudó; (ii) a more convincing study and accurate description of the differences (if any) in what I would term “The note structure of certain notes at a particular point in time or segment within the song”; (iii) a study of differences in the calls involving comparison of more appropriate examples, a larger sample and statistical analysis; and (iv) more information on the strength of molecular support for *palliata* plus *nigricauda* not being monophyletic. Splitting *palliata* from *nigricauda* may be warranted (particularly if they are sympatric) but it may not be. I just don’t know. In the absence of the information mentioned above, I would suggest a prudent course of action would be to reject this proposal for the time being and treat *palliata* as a subspecies of *nigricauda*. *M. nigricauda* was described before *palliata* (1892 vs. 1917) so the former name has priority, resulting in no change being necessary to the SACC list.

“These criticisms are presented with a heavy heart – not least because the last thing that Colombian ornithology needs at the moment is another argument. However, these are genuinely held concerns about the methods, discussion and new taxonomy in Chaves et al. (2010)’s paper. The SACC ought to be made aware of these concerns. I would though warmly welcome any observations that the authors or others may have in response to these comments.”

<u>Comments from Bret Whitney</u>: “I was a formal reviewer of the Chaves et al paper, and accepted it with minor revision, which objected mainly to their too-strict interpretation of the “three-character yardstick” as it was presented in Isler et al. (1998), and it was toned-down for publication. I think Thomas Donegan has also adopted an overly rigid interpretation of the “three-character yardstick”: we clearly stated that, for some groups, especially those for which other data sets provided support for significant divergences, less than three characters might be appropriate. I greatly appreciate Donegan’s criticisms, based in part on appropriate data not used by Chaves et al.; they are generally well-formulated and reasonable, and I find the bit about the geographic proximity of the three forms to be a sticking point, worth a focused trip to record and collect some specimens in an apparent, or at least potential, contact zone. That said, the Islers have formulated an objective and convincing test for the diagnosability of male loudsongs (albeit from a somewhat different sample than that employed by Chaves et al.), and on that basis I am willing to accept that, until further field collecting can be conducted, and a larger sample of vocalizations analyzed, the best course forward is the split of *palliata* and *nigricauda*. At present, I consider that decision an advancement in our understanding of the taxonomy of this poorly known complex, but it is always subject to revision should further collecting and analysis point to a different arrangement. To Donegan’s “heavy heart”, I suggest that ornithologists knowingly sharing a focused interest in the same groups of birds, and especially those gathering complementary data, make an effort to collaborate to produce the best publication, or set of publications possible. Then it’s left to the rest of us, who know a lot less about most of these individual situations, to try to make the best of the best.”

<u>Additional comments from Andrés Cuervo, Daniel Cadena, Juan Camilo Chaves and Matt Miller</u>: “We welcome the comments offered by Thomas Donegan on our *Myrmeciza laemosticta* paper in which he questioned our recommendation of elevating *M. l. palliata* to species rank (a hypothesis people started to think about ever since Bret Whitney obtained the first recordings of songs of *palliata* in Colombia in 1992) by pointing out that this taxon could be rather treated as a subspecies of *M. nigricauda* based on song similarity.

“To reach the conclusion that the divergent taxa *nigricauda* and *palliata* are nothing else but populations of the same biological species, one would have to ignore complementary evidence in current existence and propel vocal similarity as the sole basis for that interpretation. As Donegan points out, multiple lines of evidence should be considered including better sampling in areas of potential geographic contact and examining more vocal data than what we had at hand by mid 2008. We believe this would be very worthwhile. Potential intergradation, which would eventually support a lump between *nigricauda* and *palliata*, when based on inexistent data is mere speculation at this point. Thus, we cannot comment on this more other than to say that complementary studies and new specimens and recordings would be desirable. For the purpose of evaluating this proposal we are left with the available vocal and molecular data. We assume that the important baseline taxonomic and distributional work by Robbins and Ridgely (1991) is being taken into consideration as well.

“Regarding Donegan’s specific criticisms, we accept up front that the qualitative differentiation between the samples of *palliata* and *nigricauda* studied by Chaves et al. could be subtler than we surmised and that we could have done a better job at characterizing it verbally. However, an independent assessment by Mort and Phyllis Isler led to the conclusion that songs of these taxa can indeed be diagnosed qualitatively. The Islers went a step further to suggest that female songs are also likely diagnostic. We did not emphasize the latter finding in the paper much owing to what we thought was a reduced sample size.

“The multivariate statistical analysis (and the genetic analysis, for that matter) should be taken as a complement to the “yardstick” approach based on individual diagnostic features. This analysis specifically seeks to derive composite variables that summarize vocal variation and tests whether predefined groups can be discriminated by variation in the data. These results are summarized in the paper’s Fig. 4 and do reflect that quantitative vocal differentiation exists between *palliata* and *nigricauda*, although there is marginal overlap. However, the decision of whether taxa are vocally diagnosable should not be based solely on a cursory examination of this graph (which does not show other dimensions of the discriminant function). More telling is the fact that nearly all recordings were correctly classified by our discriminant function to their respective taxon. Note we say nearly all because following Donegan’s criticism we have reanalyzed our data and have to admit we found a mistake: the truth is that all *nigricauda* recordings but one were assigned to *nigricauda* (the other was assigned to *palliata*), and all *palliata* recordings but one were assigned to *palliata* (the other was assigned to *nigricauda*). We thank Donegan for leading us to realize a mistake crept in to our paper and we stand corrected. Regardless, the results of the DFA suggesting differentiation are complementary to the gold-standard methodology to establish species limits in antbirds (M. Isler, P. Isler, B. Whitney), which is based on diagnosability in individual traits (the issue discussed in the paragraph above). In any event, we expect that as more recordings become available and more vocal types are compared, we will get a more robust idea of the magnitude of vocal differentiation and its biological implications and we do encourage further work on this system.

“Donegan states that we should have studied a number of museum study skins listed in the Project Biomap database before concluding that *palliata* merited species rank, but we note that: (1) most of the relevant specimens (e.g. from the Baudó mountains) were indeed examined in a careful review of the complex by Robbins and Ridgely (1991) – except one male from Mutatá, NW Antioquia (J. Haffer specimen at ICN) that is inseparable from *palliata* specimens, (2) the Biomap’s record from Remedios, NE Dept. Antioquia, turned out to be a misidentified specimen (we have determined it is not even a *Myrmeciza* of this group but a male *Cercomacra tyrannina*), and (3) independent of the inclusion or not of an analysis using specimens in our study, the results from the vocal and genetic analysis are verifiable and we think that the conclusions are sound.

"In sum, we suggest that even if every point raised by Donegan was correct, then the information available taken as a whole indicates that *palliata* and *nigricauda* are differentiated lineages that have been evolving independently to the extent that the inferred potential reproductive isolation is likely. Direct tests of such a hypothesis obviously require additional fieldwork, but the current data are consistent with reproductive isolation of the two taxa, not the reverse. A separate proposal (or better, a new, more comprehensive study) based on current or new information for merging *palliata* with *nigricauda* could be presented elsewhere or to the consideration of this committee following formal analyses. Consequently, we think that the most conservative hypothesis of species limits in this group at this point is to maintain *palliata* as a separate species from any other taxa of this complex."

<u>Additional comments solicited from Mort and Phyllis Isler:</u> "In response to Thomas Donegan's thoughtful comments and the Acting Chair's request to consider his comments, we undertook an independent review of the vocal characteristics of *Myrmeciza laemosticta palliata* (henceforth *palliata*) and *M. nigricauda* (henceforth *nigricauda*).

"Procedure: Mort examined spectrograms and extracted a typical loudsong or multiple loudsongs if there was obvious variation, including what appeared to be male and female songs, from every available recording of *palliata* (n =10) and every available recording of *nigricauda* from Colombia and a random sample of *nigricauda* recordings from Ecuador (n = 11, locations available on request). Recordings were allocated to taxa on the basis of recordists' identifications and geography. 39 loudsongs in all were extracted. Each was printed on a page with no identifying data that were handwritten on the backside of the page.

"The unidentified loudsongs were given to Phyllis who had not yet read the Chaves et al. 2010 paper and had no idea of the results. She was asked to sort them into groups on the basis of qualitative characteristics and to identify the distinctive characters that she used.

"Phyllis sorted the 39 loudsongs into two primary groups and five subsets. After she finished, we turned the pages over to check the taxon. The two primary groups corresponded to *palliata* and *nigricauda*, i.e., every loudsong was sorted correctly to taxon (100 percent). The loudsongs of *nigricauda* were further sorted into two subsets, the smaller of which (n = 3) was later identified as a female loudsong, identified as such in one recording. The loudsongs of *palliata* were sorted into three subsets. Again a small (n = 5) subset was identified as the female loudsong. The other two subsets of *palliata* differed only in the presence or absence of a high-pitched terminal note.

"Phyllis stated that she used two characters to distinguish the two primary groups: (1) differences in note shape and (2) differences in the sequence of change of note shape. With regard to the latter, she pointed out that in one group the note change was gradual and subtle whereas in the other group the note shape change was abrupt and substantial. The sequential placement of different types of notes is independent of their presence or absence, and in our 1988 and sequential papers, we have treated them as such. Although Phyllis' description of change in note shape differed somewhat from that of the paper, the independent "blind" test supported the finding of the paper of a difference in two distinct qualitative characters between *palliata* and *nigricauda*.

"Moreover, based on our brief review, it appears that other vocal distinctions between *palliata* and *nigricauda* will be found in future studies. Principally, despite the small samples, it seems certain that female loudsongs differ diagnostically from male loudsongs and that female loudsongs differ between the two populations at least as much as males, and probably more. The authors describe differences in female loudsongs, but conclude that sample sizes are too small to include them as characters in the diagnosis. We understand this conservative position, but we would have given them more weight in the analysis as a second type of vocalization because of the apparent consistency of the female loudsongs that we see in our (slightly larger) samples. Unfortunately, female loudsongs illustrated in the paper (Fig. 6 which does not identify sources) do not seem to typify (represent central tendencies) female loudsongs in our inventory that appear to differ somewhat more dramatically between the two taxa. Because female loudsongs were not included in the analysis, in our opinion the statement in the paper that evidence is provided that two characters may be sufficient to support species status is not supported by this study. (By the way, we treat the three diagnostic vocal character yardstick as a "point of reference, not a requirement" [Isler et al. 1998], and in principle we would not object to a strong case for two character finding.)

"Finally, beyond note shape characteristics, we observed visually that pallida and *nigricauda* loudsongs appear to differ in note frequency, in particular the frequency of the highest point in the note (peak frequency). Consequently, we measured peak frequencies of the initial note and the middle (central in time) note of samples of *palliata* (n = 10) and *nigricauda* (n = 11). Peaks of *palliata* notes started lower and increased, whereas peaks of *nigricauda* notes started higher and typically decreased in the central notes of the vocalization. The peak frequency of initial *palliata* notes was 4157–4958 Hz (mean 4157 ± 235) and of *nigricauda* 5041–5809 Hz (mean 5372 ± 271), although there is a recording in our collection identified as *Myrmotherula schisticolor* by the recordist but which appears to be *nigricauda* in which the peak of the first note is 4507 Hz. We also computed the difference in peaks between the initial and middle notes. Peaks of *palliata* notes increased from 184–635 Hz (mean +442 ± 140), whereas those of *nigricauda* decreased from 33–317 Hz (mean -202 ± 116) excluding an example in which the first note was lower pitched than the second note and therefore slightly lower pitched (33 Hz) than the middle note. We do not present these preliminary data as a formal diagnosis, but they provide support to the conclusion that male loudsongs of the two populations are distinct.

"Thomas Donegan also raises issues regarding the multivariate analysis, differences in calls, geographic distribution, plumage distinctions, and the molecular analysis presented in the paper. The authors have responded to most of these comments, and all agree that additional studies of the complex would be useful.

"In summary, we recommend that the committee accept the authors' recommendation that *Myrmeciza palliata* be considered specifically distinct on the basis of vocal differences between it and the other three species in the complex. We conclude that two distinct qualitative characters distinguish male loudsongs and may be supported by differences in quantitative frequency measurements. Furthermore, differences in female loudsongs, unevaluated in the paper, appear certain to provide additional evidence that *palliata* and *nigricauda* have evolved to species status under the Biological Species Concept."

<u>Additional comments from Thomas Donegan</u>: "The Islers have done considerable work on my point (ii) above: (study of qualitative vocal differences). There are apparently diagnosable differences in the second section of the song as per my comments above; and the Islers have now also come up with a further "change in note structure" difference that Chaves et al. (2010)

did not elucidate. Based on that study, the *nigricauda / palliata* split is supported. Bret Whitney nicely summarises the reasons for doing this.

"It is pleasing that the authors have looked into some of the records at range extremities. When I heard of the Isler study last week, I also decided to look further into these issues, obtaining a photo of the "*nigricauda*" specimen at Colegio San Jose supposedly identified by Cuádros (new catalogue number CSJ-a 2219). It is indeed of a male *Cercomacra parkeri/tyrannina*, probably the latter based on elevation. The curator is now correcting their database and labels. As noted in my earlier comments, the specimens needed to be checked before coming to any conclusions! Separately, Reserva Natural de Aves "Las Tangaras" in the northern West Andes may be an ideal candidate locality for future studies, as it lies between known localities for *nigricauda* and *palliata* in the northern West Andes. There are no records of these birds there to date in the few studies that have taken place, only *M. berlepschi* in lower elevation forest below the reserve. That locality deserves further study for these birds.

"One response to Bret Whitney's comments: the discussion set out above was not based on a rigid interpretation of the "three characters" yardstick, but on the authors only describing a single difference and not describing it in a manner consistent with the sample. The Islers have now come up with two better-defined diagnosable qualitative differences in loudsong, which are consistent with available recordings. The Chaves et al. "two differences" yardstick is consistent with studies of *Hypocnemis* (Isler et al. 2007) - assuming the observed differences in call stand up to analysis. Moreover, it may be supported once a forthcoming publication on some other *Myrmeciza* including *Myrmeciza goeldii / melanoceps* is out. In a study of these and related species, including analysis of over 140 loudsongs for each of *goeldii* and *melanoceps* and tens of other vocalisations, there would appear to be only a single diagnosable difference in loudsong – also in "the note structure of certain notes at a particular point in time or segment". This pair is also apparently allopatric lowland *Myrmeciza* species with broadly similar calls. As a disclaimer, the paper is still being finalised, there are strong bare-skin as well as plumage differences and they are in a different section of the paraphyletic *Myrmeciza* tree. But this would otherwise seem a very analogous situation to *M. nigricauda / palliata* in a more closely related group than *Hypocnemis* and one that will give support to Chaves et al.' proposals in light of the Isler study.

"I would thank the authors and others for considering my concerns in such a detailed, sensible and collegiate manner, and would now support this proposal, if not entirely for the reasons set out in the Chaves et al., paper, then for the reasons set out in this discussion. The authors and Islers should also be encouraged to produce a short note for *Condor* making a few corrections and discussing some of the additional points in this exchange of communications. This proposal may have taken up a lot of space on the SACC website, but hopefully it makes for interesting reading, and everyone involved in this discussion now seems to be in agreement.

"[Thanks to Danny Zurc (Museo de Ciencias Naturales de La Salle, un proyecto cultural del Instituto Tecnologico Metropolitano) for the photograph of the CSJ specimens; and Alonso Quevedo and Trevor Ellery for information on birds at Las Tangaras.]"

<u>Comments from Stiles</u>: "YES, especially given the additional information provided by the Islers that resolved Donegan's (reasonable) doubts regarding vocalizations. Perhaps unfortunate that Chaves et al. did not discuss plumage characters, because males of *palliata* and *nigricauda* differ strongly, females more subtly but consistently, adding another set of characters favoring species status."

Comments from Pacheco: “YES. Após é a análise adicional dos Islers, a partir das construtivas colocações de Donegan.”

Comments from Robbins: “YES. The process that has occurred during the evaluation of this proposal is precisely how we want the Committee to function. All parties should be congratulated not only in the new insights that were brought to bear on this perplexing problem, but also in the manner in which it was presented.”

Comments from Nores: “YES. Song differences (Xeno-canto) are noticeable. Moreover, the molecular analysis by Chavez et al. (2010) clearly shows a highly supported clade for the *laemosticta* complex with the four taxa forming a polytomy.”

Comments from Pérez-Emán: “YES. As indicated by Mark, the evaluation of this proposal is a clear example of a constructive peer-reviewed process leading to a stronger documentation of the evidence supporting species status in this group. As Donegan pointed out, a short note including some of the issues raised here and providing the new evidence seems to be warranted.”

(a) Recognize *Herpsilochmus frater* as a species distinct from Rufous-winged Antwren *H. rufimarginatus*, and (b) adopt the new English names Rusty-winged Antwren for *H. frateri* and Rufous-margined Antwren for *H. rufimarginatus*

Note: This proposal is a combination and slight modification of SACC Proposals 870 and 904. Acceptance would result in recognition of *Herpsilochmus frater* and would necessitate replacement of our account for *H. rufimarginatus* with a new account for *H. frater*.

SACC 870: Treat *Herpsilochmus frater* as a separate species from *Herpsilochmus rufimarginatus*

Background:

Herpsilochmus rufimarginatus was described by Temminck in 1822 (type locality Rio de Janeiro, Brazil). Subsequently more taxa were described: *scapularis* (Wied, 1931, Bahia, Brazil), *frater* (Sclater, 1880, Sarayacu, Ecuador) and *exiguus* (Nelson, 1912, Cana, Panama). Cory and Hellmayr (1924) assigned them to the same species *H. rufimarginatus* but considered *scapularis* junior synonym of nominate. Later, Peters (1951), however, considered *scapularis* a valid taxon, and this treatment with 4 subspecies was repeated by Zimmer & Isler (2003).

As for distinctiveness of the various taxa, Zimmer & Isler (2003) described some morphological and vocal differences without quantification and suggested that more than one species may be involved.

New information:

1. Marcelo da Silva (2013) investigated in detail the morphology and voice of the 3 Brazilian taxa. His findings are in his Master thesis; unfortunately, no follow-up peer-reviewed paper was published.

The main results were:
a. *rufimarginatus* is morphologically the most distinctive taxon (see his Tables 1 and 2 on the next page), and
b. *rufimarginatus* is vocally the most distinctive taxon (see his Table 4 on the next page)

Limited unspecified playback experiments were also carried out, in which playing *rufimarginatus* loudsong in NE Brazil did not elicit response from that population.

2. Independently, Boesman (2016) made a brief analysis of all 4 taxa (including also *exiguus*). He used in part different sound parameters, and also concluded that *rufimarginatus* clearly stood out vocally vs. the other taxa (with measurements indicating several non-overlapping ranges).

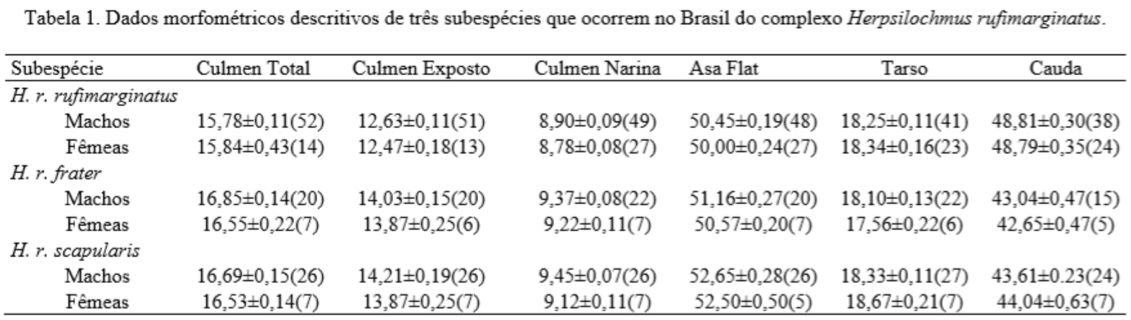


Tabela 1. Dados morfométricos descritivos de três subespécies que ocorrem no Brasil do complexo *Herpsilochmus rufimarginatus*.

Subespécie	Culmen Total	Culmen Exposto	Culmen Narina	Asa Flat	Tarso	Cauda
H. r. rufimarginatus						
Machos	15,78±0,11(52)	12,63±0,11(51)	8,90±0,09(49)	50,45±0,19(48)	18,25±0,11(41)	48,81±0,30(38)
Fêmeas	15,84±0,43(14)	12,47±0,18(13)	8,78±0,08(27)	50,00±0,24(27)	18,34±0,16(23)	48,79±0,35(24)
H. r. frater						
Machos	16,85±0,14(20)	14,03±0,15(20)	9,37±0,08(22)	51,16±0,27(20)	18,10±0,13(22)	43,04±0,47(15)
Fêmeas	16,55±0,22(7)	13,87±0,25(6)	9,22±0,11(7)	50,57±0,20(7)	17,56±0,22(6)	42,65±0,47(5)
H. r. scapularis						
Machos	16,69±0,15(26)	14,21±0,19(26)	9,45±0,07(26)	52,65±0,28(26)	18,33±0,11(27)	43,61±0.23(24)
Fêmeas	16,53±0,14(7)	13,87±0,25(7)	9,12±0,11(7)	52,50±0,50(5)	18,67±0,21(7)	44,04±0,63(7)

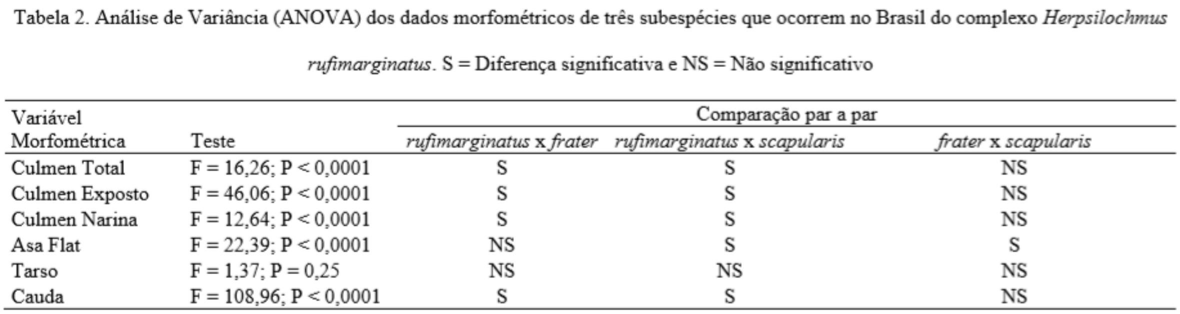


Tabela 2. Análise de Variância (ANOVA) dos dados morfométricos de três subespécies que ocorrem no Brasil do complexo *Herpsilochmus rufimarginatus*. S = Diferença significativa e NS = Não significativo

Variável Morfométrica	Teste	Comparação par a par		
		rufimarginatus x *frater*	*rufimarginatus* x *scapularis*	*frater* x *scapularis*
Culmen Total	F = 16,26; P < 0,0001	S	S	NS
Culmen Exposto	F = 46,06; P < 0,0001	S	S	NS
Culmen Narina	F = 12,64; P < 0,0001	S	S	NS
Asa Flat	F = 22,39; P < 0,0001	NS	S	S
Tarso	F = 1,37; P = 0,25	NS	NS	NS
Cauda	F = 108,96; P < 0,0001	S	S	NS

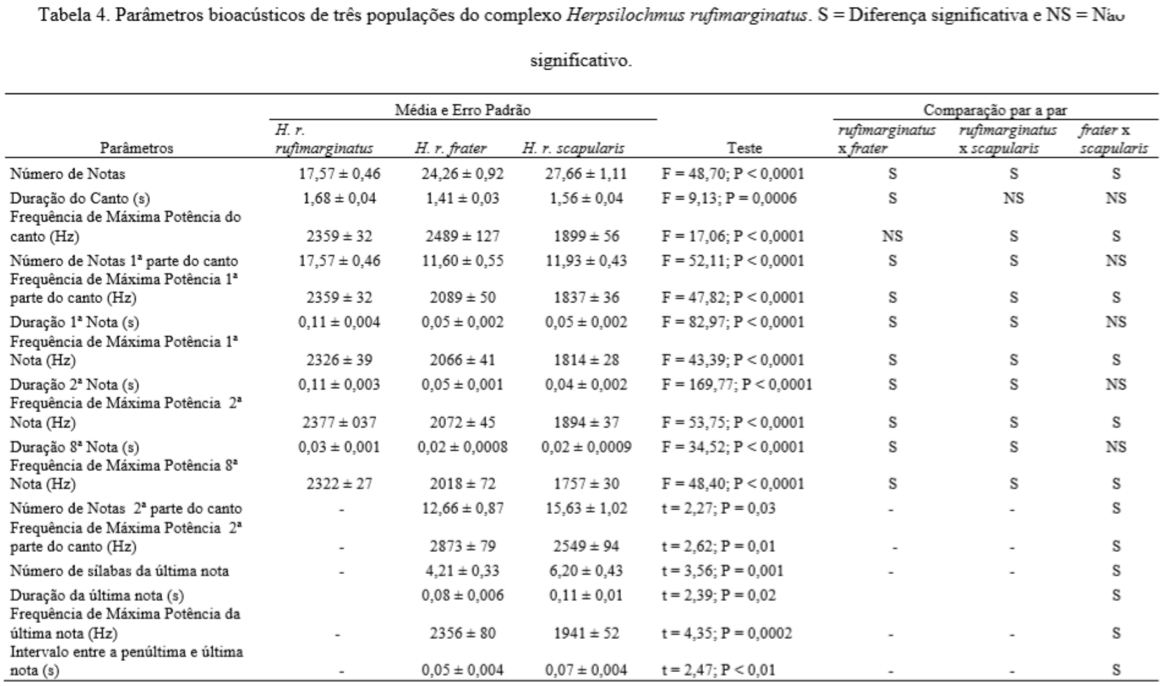


Tabela 4. Parâmetros bioacústicos de três populações do complexo *Herpsilochmus rufimarginatus*. S = Diferença significativa e NS = Não significativo.

Parâmetros	Média e Erro Padrão			Teste	Comparação par a par		
	H. r. rufimarginatus	*H. r. frater*	*H. r. scapularis*		*rufimarginatus* x *frater*	*rufimarginatus* x *scapularis*	*frater* x *scapularis*
Número de Notas	17,57 ± 0,46	24,26 ± 0,92	27,66 ± 1,11	F = 48,70; P < 0,0001	S	S	S
Duração do Canto (s)	1,68 ± 0,04	1,41 ± 0,03	1,56 ± 0,04	F = 9,13; P = 0,0006	S	NS	NS
Frequência de Máxima Potência do canto (Hz)	2359 ± 32	2489 ± 127	1899 ± 56	F = 17,06; P < 0,0001	NS	S	S
Número de Notas 1ª parte do canto	17,57 ± 0,46	11,60 ± 0,55	11,93 ± 0,43	F = 52,11; P < 0,0001	S	S	NS
Frequência de Máxima Potência 1ª parte do canto (Hz)	2359 ± 32	2089 ± 50	1837 ± 36	F = 47,82; P < 0,0001	S	S	S
Duração 1ª Nota (s)	0,11 ± 0,004	0,05 ± 0,002	0,05 ± 0,002	F = 82,97; P < 0,0001	S	S	NS
Frequência de Máxima Potência 1ª Nota (Hz)	2326 ± 39	2066 ± 41	1814 ± 28	F = 43,39; P < 0,0001	S	S	S
Duração 2ª Nota (s)	0,11 ± 0,003	0,05 ± 0,001	0,04 ± 0,002	F = 169,77; P < 0,0001	S	S	NS
Frequência de Máxima Potência 2ª Nota (Hz)	2377 ± 037	2072 ± 45	1894 ± 37	F = 53,75; P < 0,0001	S	S	S
Duração 8ª Nota (s)	0,03 ± 0,001	0,02 ± 0,0008	0,02 ± 0,0009	F = 34,52; P < 0,0001	S	S	NS
Frequência de Máxima Potência 8ª Nota (Hz)	2322 ± 27	2018 ± 72	1757 ± 30	F = 48,40; P < 0,0001	S	S	S
Número de Notas 2ª parte do canto	-	12,66 ± 0,87	15,63 ± 1,02	t = 2,27; P = 0,03	-	-	S
Frequência de Máxima Potência 2ª parte do canto (Hz)	-	2873 ± 79	2549 ± 94	t = 2,62; P = 0,01	-	-	S
Número de sílabas da última nota	-	4,21 ± 0,33	6,20 ± 0,43	t = 3,56; P = 0,001	-	-	S
Duração da última nota (s)		0,08 ± 0,006	0,11 ± 0,01	t = 2,39; P = 0,02			S
Frequência de Máxima Potência da última nota (Hz)	-	2356 ± 80	1941 ± 52	t = 4,35; P = 0,0002	-	-	S
Intervalo entre a penúltima e última nota (s)	-	0,05 ± 0,004	0,07 ± 0,004	t = 2,47; P < 0,01	-	-	S

(‘Erro padrao’ is Standard error, not SD!)

3. In a vivid discussion on xeno-canto (https://www.xeno-canto.org/forum/topic/5265), involving Dan Lane, Jeremy Minns and myself, there was a general consensus that *rufimarginatus* was vocally the most distinct taxon.

4. A comparison of calls has not been performed, but seems to be quite complex at first sight, e.g., taxon *frater* has at least 4 different call types, one of which is rarely heard (and possibly not even over its entire range) but quite similar (not identical) to the main call of *rufimarginatus*. A large set of recordings of call notes would thus be required, not only to document the full vocal array for every taxon and evaluate (possibly subtle) differences, but also to determine relative frequency for every call type (without even touching the topic of respective functions…).

5. The vocal group identified as *rufimarginatus* occurs along the Atlantic side from Paraguay and Argentina in the south to Bahia in the north (the most northerly sound recording presently on XC being just north of Salvador), whereas the population north of the rio Sao Francisco was assumed to be *scapularis*.

Taxonomic names:

1. Marcelo da Silva (2013) zoomed in on the specific case of *scapularis*. The type locality 'Bahia' is unprecise, but in any case, it must have been a locality south of the rio Sao Francisco, and (given that there is uniformity in morphology and voice with birds further south) in fact had earlier been named *rufimarginatus*; thus, he considered *scapularis* a junior synonym of *rufimarginatus*. Da Silva, therefore, suggested that a holotype be redefined for the northern population occurring from Alagoas to Rio Grande do Norte, but he did not name this taxon (p. 84).

2. The XC discussion mentioned above also mainly focused on this topic, reaching a similar conclusion: *scapularis* is a junior synonym of *rufimarginatus*.

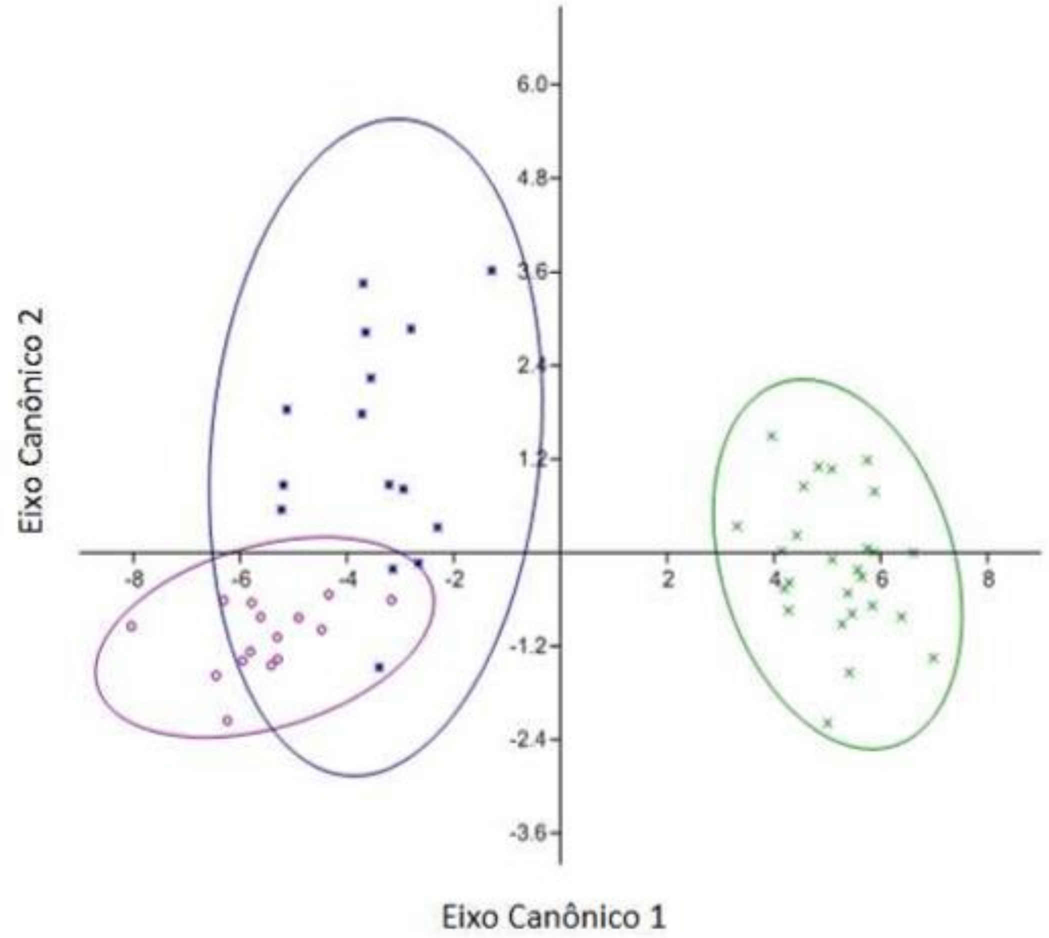
Discussion:

The taxon *rufimarginatus* is thus readily identifiable by ear (loudsong), differing significantly in a variety of sound parameters. It is also morphologically the most distinct taxon. For the sake of uniformity, it would have been more transparent if the Isler criteria had been applied for this member of the antbird family, as 3 significant sound parameters are considered a yardstick for species level (Isler 1998). Nevertheless, this slightly different approach also clearly illustrates the vocal distinctiveness of this taxon (see Fig. 6 on next page).

Clinal variation is not an issue here; comparing the most northerly loudsong available on XC (XC482426) with the most southerly of the NE Brazil population (XC80216) shows the same vocal break.

No genetic data are presented, but this is not different from the majority of taxonomic changes in the antbird family during the last two decades, given that their voice is innate and very stereotypical, allowing clear-cut assessments based on voice. Geographically isolated by the rio Sao Francisco, nominate *rufimarginatus* can be considered an allopatric population, and thus there is hardly any chance of contact with other populations. Genetic divergence is to be expected, independent of the reproductive barrier created by vocal difference. Distance to the Amazonian *frater* population is even larger.

Figura 6. Representação dos dois primeiros eixos da análise de função discriminante realizadas com caracteres vocais de espécimes de três subespécies que ocorrem no Brasil do complexo *Herpsilochmus rufimarginatus*. O "x" representa *H. r. rufimarginatus*, estrela *H. r. scapularis* e o círculo *H. r. frater*.



For the sake of completeness: although the population in extreme NE Brazil was clearly less different from *frater*, da Silva also suggested to elevate this taxon to species rank. This is clearly another topic, not in the least because this would definitely require the description of a new taxon. Meanwhile, the best option is likely to include this population in the taxon *frater*, awaiting further investigation.

Part B. English name:

As for the English name, del Hoyo & Collar (2016) used the names Northern and Southern Rufous-winged Antwren (albeit with incorrect ranges for both species and without solving the issue of *scapularis)*. Given that *rufimarginatus* occurs further north than they assumed, this

North/South distinction is less convincing but still a viable option (and more accurate than calling them eastern/western). Keeping 'Rufous-winged Antwren' in the name is very meaningful, as they are the only *Herpsilochmus* species with rufous in the wing, a genus which otherwise shows very few obvious field characters. Maintaining 'Rufous-winged Antwren' for only one of them would only cause confusion (old vs new treatment).

Recommendation:

A. Treat *Herpsilochmus frater* (including subspecies *exiguus*) as separate species from *Herpsilochmus rufimarginatus* (monotypic). (The name *scapularis* becomes invalid.)
B. English name: Southern Rufous-winged Antwren (*H. rufimarginatus*) and Northern Rufous-winged Antwren (*H. frater*) (if a NO vote is given, alternative naming is required)

Peter Boesman, July 2020

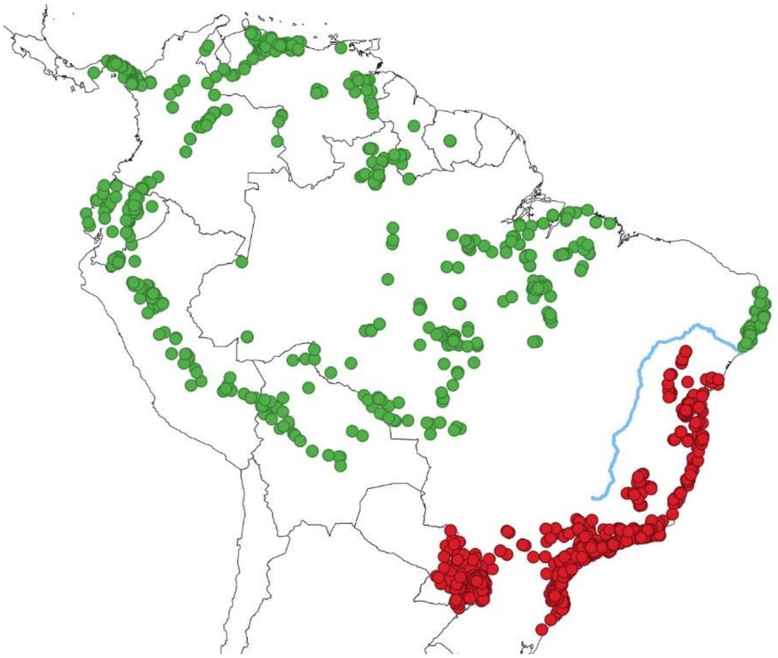
Comments on SACC Proposal 870:
Comments from Stiles: "YES on the split. NO on Northern vs. Southern: too much ambiguity here. I'd propose Atlantic vs. Western for *rufimarginatus* and *frater*-*exiguus*, respectively. The distribution of *rufimarginatus* (as described: it would be nice to have a range map!) seems to be characteristic of the Atlantic-forest species of Brazil, whereas *frater*-*exiguus* extends westward through Venezuela and Colombia to the Darien in Panama as well as into Amazonia."

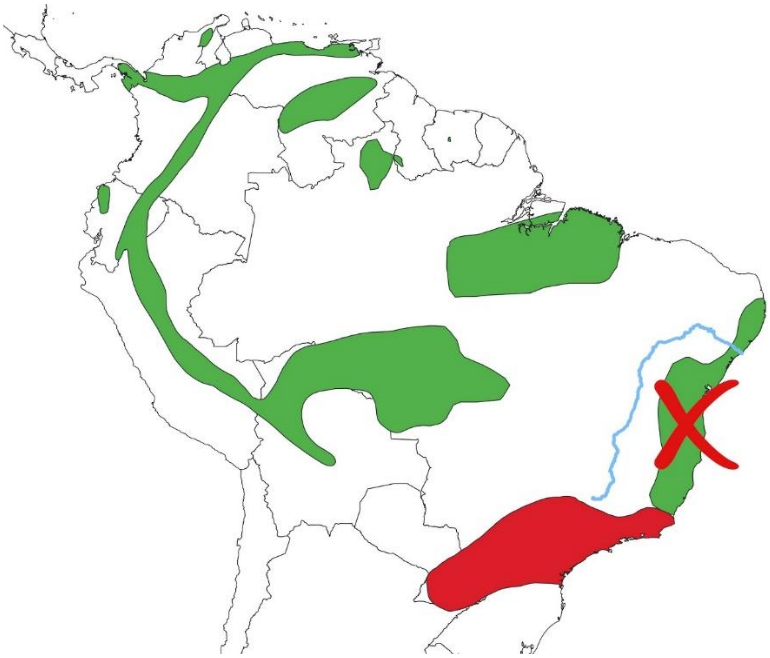
Comments from Robbins: "YES. After listening to multiple cuts of song of these, I vote yes to recognize *frater* as a species. It would be nice to have a genetic data set for this clade, but the differences in song of *frater* vs. nominate are so striking that there is no need to wait for those data."

Comments from Rafael Lima: "I would like to comment about the English names and provide a map to help with Proposal 870 (*Herpsilochmus rufimarginatus* complex).

"I made a map using eBird points to illustrate the issue [maps are on the next page]. The birds of the "Amazon Group" are green and the birds of the "Atlantic Group" are red. Note that the birds north of the São Francisco River (Pernambuco Center of Endemism) belong to the "Amazonian Group", so Stiles's suggestion of the English names Atlantic vs. Western is not a good idea. I agree with the names suggested by Boesman.

"The other map I made with the IUCN shapefile (the same one used by HBW Alive). Note that (as Peter has already noticed), when HBW Alive split two taxa (based on Boesman 2016), they made a mistake on the map. Since the catalog of Olivério Pinto (1978), the name "*H. r. scapularis*" has been attributed simultaneously to the population of Bahia (south of the São Francisco River) and the population of Pernambuco Endemism Center (north of the São Francisco River). This misinformation was followed by the printed HBW volume and is still in Birds of the World. The taxon "*scapularis*" really caused confusion in the literature, because it was assigned to completely different populations (north and south of the São Francisco River)."





<u>Comments from Areta</u>: "YES. The work by Silva is convincing, and the distribution of vocal types is clear. At first hear, I agree with Dan Lane´s comments that the population from Alagoas-Pernambuco seems to belong to *frater* and not to a new species, but this will need to be properly published before we can make any decision. For the time being, it seems more reasonable to consider them as part of *frater*.

“Regarding the common English names, I don´t understand the discussion of Eastern-Western vs. Southern-Northern. Both species have overlapping longitudes and latitudes (as Rafael´s map clearly shows), so from that perspective neither is great (and it would make it complicated in the event of more splits). Also, these are among the most boring possible names! Since vocalizations were key for the split, I would suggest a reference to their songs might be better. Something along the lines of Churring Rufous-winged Antwren (*frater*) and Piping Rufous-winged Antwren (*rufimarginatus*). I admit I don´t like these long names in any manner, but if Rufous-winged has to stay, then a reference to a feature of the birds and not to their ranges seems better.”

Comments solicited from Mort Isler: “I recommend a YES vote because of the clear distinctions between songs of *frater* (including *exiguus* and "*scapularis*" north of the R. São Francisco) and *rufimarginatus* (including "*scapularis*" south of the R. São Francisco). I say that with the hope that future proposals will be better supported.

“Most bothersome, I could not identify the locations of the recordings of *scapularis* used in Silva's analysis. I could not find yellow dots representing *scapularis* on Figure 9, and the only list of recording locations (Appendix 2) puts them in his recommended taxa (including the unsubstantiated proposal for a new species). The introduction provides the range of *scapularis* as Rio Grande do Norte to Minas Gerais, but based on the vocal data, this could not be the *scapularis* used in the analysis. I have assumed in making my recommendation that *scapularis* used in the analysis was limited to locations north of the R. São Francisco. My Portuguese has declined with age, so I apologize if I missed it, but delineations of study populations should include recording locations.

“I appreciate the clarity of Peter Boesman's notes for HBW Alive, and I understand that they were only submitted as supporting data, but they are insufficient for making taxonomic decisions for multiple reasons including small sample size, lack of locational data, and absence of distributional data. I only mention this as a concern that others may think the information sufficient.

“I am sad that a more complete analysis of the *H. rufimarginatus* complex was not available. Peter expressed the same concern in his proposal regarding the absence of calls of the populations analyzed, and it obviously would have been desirable that the entire complex had been considered.

“I have read the proposals for English names, and I hope that any available molecular phylogenies will be consulted before "Rufous-winged" is used in constructing names. The songs (and possibly the calls) differ to an extent that the assumption that *frater* and *rufimarginatus* are sister species should be confirmed.”

Comments from Pacheco: “YES. The vocal repertoire of the populations north of the São Francisco River are those of the *frater*/Amazonian pattern, whereas to the south of the São Francisco River - including all of Bahia (therefore involving "*scapularis*") - it is possible to hear something identical to that sung in the typical range of *H*. *rufimarginatus* (Rio de Janeiro). Rafael did a good job of clarifying where this correct break is.”

Comments from Claramunt: “YES. The evidence clearly points to species-level taxa.”

Additional comments from Areta: “After reading Mort´s comments, and having myself proposed some preliminary alternatives, I think that keeping Rufous-winged for the nominate, and finding a new name for *frater* would be desirable. I propose Rusty-winged for *frater*, and Rufous-winged for *rufimarginatus*. Seems to be the less disruptive option, as one stays the same and the other one would adopt a new name bearing resemblance to its previous name. Alternatively, if both names must change, I would not use "Rufous-winged" as a common theme.
”A final note: I also agree in that Boesman´s notes are good to have an overview of the situation, but the lack of precise catalogue numbers, geographic data, date of recording, and other missing data, make them insufficient to inform taxonomic decisions *per se*.”

Comments from Zimmer: “YES. The vocal differences between nominate *rufimarginatus* and the remaining taxa in the complex are pretty obvious to anyone with comparative field experience, so this one has been begging for attention for some time. Mort Isler and I mentioned (HBW Volume 8, 2003) the likelihood that more than one species was nested within *rufimarginatus*, but in the absence of a comprehensive analysis encompassing the entire complex, we didn’t want to get out over our skies. I might take this opportunity to second Mort’s comments on this Proposal, and note that we still don’t have a comprehensive analysis for the entire group, nor even one that takes into account the various calls. In spite of this, I think the distinctions between the loudsongs of *rufimarginatus* relative to *frater* are great enough, particularly taking into account the biometric differences, that we can at least advance the ball downfield by making this one change, and then hope for a more comprehensive analysis providing resolution regarding taxon-limits in the rest of the group, as well as a molecular-based phylogeny to resolve the relationships of the various taxa not only to one another, but also to other species within *Herpsilochmus*. In the absence of such analyses, it’s worth noting, as some people have already commented, that populations from NE Brazil north of the rio São Francisco are clearly closer vocally to *frater* than they are to all populations south of the São Francisco. So, pending a comprehensive analysis of the entire complex, the north of the São Francisco population should, provisionally, be placed with *frater*, whereas populations from south of the São Francisco should be placed with nominate *rufimarginatus*. (B) “NO” to the proposed English names of “Northern” and “Southern” modifying the group name of Rufous-winged Antwren. Until the taxon-limits are sorted out for the remainder of the group, we are left with the reality that we could be looking at a two-species treatment (*rufimarginatus* versus *frater* + *exiguus* + “*scapularis*” north of the São Francisco). If things shake out that way, then, as Nacho notes, both species would have ranges that overlap in latitude and longitude, negating the utility of “Northern/Southern” and “Eastern/Atlantic versus Western”. The quality of the songs is the most obvious difference between *rufimarginatus* and everything else in the complex, and thus, I find Nacho’s suggestion of “Churring Rufous-winged Antwren” (for *frater/exiguous*/northern “*scapularis*”) and “Piping Rufous-winged Antwren” (for *rufimarginatus*) compelling, despite the length and awkwardness of the names. Of course, as Mort has pointed out, we can’t assume that *rufimarginatus* is sister to *frater* (*sensu lato*) just because they both have rufous in the wings. It could prove more closely related to one of the other *Herpsilochmus* species found in Eastern or South-Central Brazil, in which case we would ultimately be dropping the group name of “Rufous-winged Antwren” and could just go with “Piping Antwren” and “Churring Antwren”. We could also end up in a scenario wherein the complex proves to be a monophyletic group, but either *exiguus* or northern “*scapularis*” is shown to merit splitting from *frater*. In that case (3 species), names describing the voices would not work so well, and we would probably need to revert to English names descriptive of the range (e.g. "Western Rufous-winged" for *exiguus*; "Amazonian Rufous-winged" for *frater*; "Sooretama Rufous-winged" for *rufimarginatus*). There are lots of moving parts here, and in the absence of knowing how the taxonomic dust will settle, I would suggest retaining the compound group name, and using the modifiers suggested by Nacho (Piping and Churring)."

Comments by Lane: "YES. The voices of these two groups are worlds apart (by *Herpsilochmus* standards, anyway), and I think a split is warranted. Also, I am glad that the proper names are used here! As Peter says, the case for placing the name *scapularis* under *rufimarginatus* here, and using "*frater*" for birds in NE Brazil, is hashed out in da Silva's 2013 dissertation, the Xeno-canto forum here <https://www.xeno-canto.org/forum/topic/5265> and in the comments and map by Rafael Lima above. Thus, even though there has been a mistaken tendency for much previous literature (e.g., HBW) to use "*scapularis*" for NE Brazilian birds, the name belongs to those in Bahia, not to those farther north. Therefore, *frater* is the oldest name for the population with the song type sung by NE Brazilian birds, and it is thus the correct species name for the daughter species once these two groups of taxa are separated. As for English names, I think a separate proposal will need to be drafted to address them."

Comments from Jaramillo: "YES – Pretty interesting, I had no idea that this separation existed. Weirdly enough, this was the first antwren I ever witnessed in my life, Misiones, Argentina.
"NO on English names, but I am very keen on a yes to the Churring and Piping. I don't think there is a need to maintain the "rufous-winged", but I would be fine if this is a prerequisite from other committee members."

Comments from Schulenberg: "B. NO. The recent Harvey et al. paper in Science (Harvey et many al., 2020, The evolution of a tropical biodiversity hotspot, Science 370: 1343-1348, https:/doi.org/10.1126/science.aaz6970) seems to make clear (Figure 1 - if you can read it) that *frater* (represented by two samples, from Panama and Amazonas, Brazil) and *rufimarginatus* (also two samples) are sister species. Note, however, that in Column G, of their supplementary table listing the specimens sampled, they identify a specimen from Minas Gerais as *scapularis* - apparently their name for what SACC refers to as *frater* - but by location I assume this is a nominate *rufimarginatus*. or, to put it another way, since the Minas Gerais sample is sister to their sample of undoubted *rufimarginatus* from Paraguay, there will be some explaining to do if the Minas specimen is * not * *rufimarginatus*.

"So. we can put aside concerns that *frater* and *rufimarginatus* may not be sister taxa; it seems to be established that they are. That said, as usual I'm going to have a hard time voting for any pair of names in the form of "Xxxx Rufous-winged Antwren"; we just don't need yet more long compound bird names. I'm not thrilled with Piping Antwren and Churring Antwren, not because I object to basing the English name on the songs, but because I'm not sure that these two adjectives best describe the quality of each song (especially in the case of 'Piping'). I don't have better descriptive terms in mind, however, and could accept Piping and Churring if no one comes up with anything better."

Comments from Bonaccorso: "A. YES. The differences in song and morphology seem to point to two different species. However, I am not entirely comfortable with the lack of genetic data and diagnostic plumage characters."

Comments from Stiles: "A (the split of *frater* from *rufimarginatus* passed, but B (the E-name) did not; I gather that a 6:3 NO margin exists but am not entirely sure just what would be rejected as some did (or did not) favor conserving Rufous-winged as the name for both species, with the modifiers referring to the vocalizations of the loudsongs. I would prefer against using vocalizations, as all did not agree on the best adjectives for these – they are subjective in any case and could cause problems should *frater* be split in the future. Proposal 904 is a rerun of this one (see below)."

SACC 904: Establish new English names for *Herpsilochmus frater* and *Herpsilochmus rufimarginatus*

Background:

Part B of Proposal 870A raised the issue of English names for the two species resulting from the split of *H. rufimarginatus*. As noted therein, retaining "Rufous-winged Antwren" as the stand-alone English name for one of the two daughter species should not be viewed as an option, given that our standard procedure is to create new names for each daughter species, and, that I don't think either the "relative range size" or "differential usage" arguments are strong enough in this case to warrant an exception to our English naming guidelines. Although the geographic range of *frater* (including subspecies *exiguus*) is significantly larger than that of *rufimarginatus*, the latter is arguably more common and familiar over its still rather extensive latitudinal range than the former is over much of its range (e.g. it is a rather uncommon and patchily distributed bird over much of the Amazon Basin).

Boesman, in the Proposal 870A, did suggest that retaining "Rufous-winged Antwren" as a shared group name for *frater* and *rufimarginatus*, was desirable, since these are the only *Herpsilochmus* species with rufous in the wing. This was the strategy employed by del Hoyo & Collar (2016), who used "Northern Rufous-winged Antwren" for *frater*, and "Southern Rufous-winged Antwren" for *rufimarginatus*. Others have advocated using "Western Rufous-winged Antwren" for *frater* + *exiguus* + "*scapularis*" (from N of rio São Francisco), and either "Eastern" or "Atlantic" Rufous-winged Antwren for *rufimarginatus* + "*scapularis*" (from S of rio São Francisco). Besides creating the kind of boring, bulky, compound names that few like and many despise, neither of these sets of names are ideal, because, as Nacho pointed out, the ranges of the two species overlap one another in latitude and longitude, rendering almost any geographic modifiers as non-exclusive at best, and confusing at worst.

As has been pointed out by Nacho, and others, the two species of "Rufous-winged Antwrens" are most obviously distinguished from one another by their songs, which led Nacho to suggest the names "Churring Rufous-winged Antwren" for *frater*, and "Piping Rufous-winged Antwren" for *rufimarginatus*. A couple of us expressed support for using modifiers such as "Churring" and "Piping" (with, or without the hyphenated group name of "Rufous-winged") that allude to the vocal distinctions between the two species, although, as Tom noted, neither of those names (especially "Piping") really captures the vocal quality of either species. I've spent some time thinking about different modifiers that would more accurately describe the vocal differences, and haven't come up with anything better. One reason not to construct names based upon vocal differences is out of concern that *frater* could ultimately prove to include more than one species, resulting in a three-species treatment in which English names based upon vocal differences could be rendered confusing or meaningless.

Recommendation:

Meanwhile, after mulling all of this over a fair bit, I have come around to the idea of formulating new names that reflect the distinctive rufous panel in the wings common to both species, and skipping the hyphenated group-name. I would suggest the following novel names, any of which could be fairly applied to either *frater* or *rufimarginatus*:

1) Rusty-winged Antwren (Nacho had previously suggested this as an alternative for *frater*).
2) Ferruginous-winged Antwren
3) Blaze-winged Antwren

I like the idea of using "Blaze-winged" for one of the taxa, even though it doesn't refer specifically to the rufous color of the wing-panel. One of the many dictionary meanings of "blaze" is "a very bright display of light or color", and that would certainly apply to the eye-catching rufous wing panel of these birds. I also like that it is a more novel name (we do have a Blaze-winged Parakeet in our domain, and invokes the wing panel without falling into the confusing hairsplitting of "rusty" versus "rufous" versus "ferruginous" trap.

Given the complexities of this case, and the desire to move this along, I would suggest that we go with ranked-choice voting, as we have done with a few other English name Proposals recently. Therefore, voting members should rank each option 1-2-3-4-5, with 1 being the favored option. I assume that anyone voting for "something" + the compound group name of "Rufous-winged Antwren" as their 1st choice for one of the taxa would do the same for both taxa. In the event that the compound group names win out, then that will necessitate a follow-up Proposal to vote on the modifiers (fingers crossed that doesn't happen!).

Herpsilochmus frater:

Option 1a: Rusty-winged Antwren
Option 1b: Ferruginous-winged Antwren
Option 1c: Blaze-winged Antwren
Option 1d: Churring Antwren
Option 1e: "something" (Western/Northern/Churring/something else) Rufous-winged Antwren
Option 1f: something else (e.g., Rusty-margined: see Lane comments)

Herpsilochmus rufimarginatus:

Option 2a: Blaze-winged Antwren

Option 2b: Ferruginous-winged Antwren
Option 2c: Rusty-winged Antwren
Option 2d: Piping Antwren
Option 2e: “something” (Eastern/Atlantic/Southern/Piping/something else) Rufous-winged Antwren
Option 2f: Rufous-margined Antwren

Kevin J. Zimmer, January 2021

Comments on SACC 904:

Comments from Lane: “None of the options provided really make me very enthusiastic. Here are my top picks for the two daughter species:

> *“H. frater*: "Barking Antwren" or "Cackling Antwren" (two of its most distinctive vocalizations are the bark and descending cackle calls which are unmatched by other *Herpsilochmus*... I don't find "churring" to be a particularly good descriptor of the vocalizations of this species, I'm afraid). If voice-based names don't sit well with committee members, how about "Circumbasin Antwren" (to draw attention to its curious largely circum-Amazonian distribution)?
>
> *“H. rufimarginatus*: To me the obvious first choice is "Rufous-margined Antwren" as it is a direct translation of the scientific name, and although similar to the previous name for the combined species, is plenty distinct.”

Comments from Stiles: “Here, I like Dan´s suggestion of Rufous-margined for *H. rufimarginatus* – it is accurate and goes with the Latin name, also retains some connection with Rufous-winged, the former name for the species prior to the split. For *frater*, I prefer Rusty-winged over Ferruginous-winged over any name based on vocalizations, which are decidedly subjective (and if *frater* gets split later, and the vocalizations of the taxa do not match, things could get confusing). Least preferred: anything combined with Rufous-winged for both.”

Comments from Schulenberg:

“*Herpsilochmus frater*: I rate these (descending order of preference) as

1 Rusty-winged Antwren
2 Ferruginous-winged Antwren
3 Blaze-winged Antwren
4 Churring Antwren
5 "something" (Western/Northern/Churring/something else) Rufous-winged Antwren
6 something else (e.g., see Lane comments)

Herpsilochmus rufimarginatus:

1 Rufous-margined Antwren

2 Piping Antwren
3 Blaze-winged Antwren
4 Ferruginous-winged Antwren
5 Rusty-winged Antwren
6 "something" (Eastern/Atlantic/Southern/Piping/something else) Rufous-winged Antwren

<u>Comments from Stiles</u>: “E-names for *Herpsilochmus* spp. I would suggest reworking the lists of suggested names including “Rufous-margined” for *rufimarginatus* to facilitate things, perhaps omitting from the lists the “something Rufous-winged”, which most disliked in any case.”

<u>Comments from Jaramillo</u>: “See below for my top choices. Rusty-winged is confusingly similar to Rufous-winged, but I think that is OK in this situation. Mentally it may invoke the right looking bird if you were previously used to Rufous-winged. So that is good for the field observer. Blaze-wing is memorable, unique, I like it.

Herpsilochmus frater: Option 1a: Rusty-winged Antwren
Herpsilochmus rufimarginatus: Option 2a: Blaze-winged Antwren

<u>Comments from Donsker</u>: “Here's how I would rank vote them:

Herpsilochmus frater:
1. Rusty-winged Antwren (1a)
2. Ferruginous-winged Antwren (1b)
3. Blaze-winged Antwren (1c)
4. Rusty-margined Antwren (1f)

Herpsilochmus rufimarginatus:
1. Rufous-margined Antwren (2f)
2. Rusty-winged Antwren (2c)
3. Ferruginous-winged Antwren (2b)
4. Blaze-winged Antwren (2a)

“I'm not fond of using the vocal alternatives or "Something" Rufous-winged Antwren.”

<u>Comments from Stiles</u>: “Here are my choices:

for *frater*: 1-Rusty-winged (1a); 2.5-Rusty-margined (1f), 2.5-Ferruginous-winged (1b); 4-Blaze-winged (1c); 5-Churring (1d); 6-compound name (1e)

for *rufimarginatus*: 1-Rufous-margined (2f); 2.5-Ferruginous-winged (2b); 2.5-Blaze-winged (2a); 4-Rusty-winged (so as to not conflict with this as my first choice for *frater*) (2c) ; 5-Piping (2d); 6-compound name (2e).

“I definitely would dump the compound names, and the vocalization-type names seem too subjective. Ferruginous-winged seems a bit clunky and Blaze-winged to me seems more to indicate a flash of color when the wings are opened.”

Comments from Jaramillo: “See below for my top choices. Rusty-winged is confusingly similar to Rufous-winged, but I think that is OK in this situation. Mentally it may invoke the right looking bird if you were previously used to Rufous-winged. So, that is good for the field observer. Blaze-winged is memorable, unique, I like it.

Herpsilochmus frater:
Option 1a: Rusty-winged Antwren
2. Blaze-winged Antwren (1c)
3. Ferruginous-winged Antwren (1b)
4. Rusty-margined Antwren (1f)

Herpsilochmus rufimarginatus:
Option 2a: Blaze-winged Antwren
2. Rusty-winged Antwren (2c)
3. Ferruginous-winged Antwren (2b)
4. Rufous-margined Antwren

Comments from Zimmer: “Here’s how I would rank the proposed English names:

Herpsilochmus frater:

1. Rusty-winged Antwren (1a)
2. Blaze-winged Antwren (1c)
3. Ferruginous-winged Antwren (1b)
4. Rusty-margined Antwren (1f)

Herpsilochmus rufimarginatus:

1. Blaze-winged Antwren (2a)
2. Rufous-margined Antwren (2f)
3. Ferruginous-winged Antwren (2b)
4. Rusty-winged Antwren (2c)”

Comments from Lane:

“For *H. frater* (ranked from top choice down):

1. Rusty-winged Antwren
2. Ferruginous-winged Antwren
3. Barking/Cackling Antwren
4. Blaze-winged Antwren
5. Churring Antwren

“For *H. rufimarginatus*:

1. Rufous-margined Antwren
2. “something” (Eastern/Atlantic/Southern/Piping/something else) Rufous-winged Antwren
3. Piping Antwren
4. Rusty-winged Antwren
5. Ferruginous-winged Antwren

6. Blaze-winged Antwren

"'Blaze-winged' to me suggests a white or fiery-colored (yellow, red, orange) patch in the wing, which neither daughter species has, and so it's a bit misleading."

Recommendation for NACC:

Only one of these species (*H. frater*) occurs in our area and it is only found in eastern Panama, so I recommend that we follow SACC on the species split and the English names, both on the evidence and because these are largely or exclusively South American birds. The split was unanimously approved by SACC, as was the English name "Rusty-winged Antwren" for *H. frater*. Votes on the English name for *H. rufimarginatus* were more varied, but 5 of 7 voters listed "Rufous-margined Antwren" as their first choice. Clements/eBird and the IOC list have made this split and have also adopted these English names, but HBW-Birdlife uses the compound names "Southern Rufous-winged Antwren" for *H. rufimarginatus* and "Northern Rufous-winged Antwren" for *H. frater* (for which they use the scientific name *H. scapularis*, but see discussion above about this).

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Submitted by: Peter Boesman (SACC 870), Kevin Zimmer (SACC 904), and Terry Chesser (NACC recommendation)

Date of Proposal: July 2020 and January 2021 (SACC proposals), 8 October 2021

Recognize extralimital *Pyrocephalus nanus* as a species distinct from Vermilion Flycatcher *P. rubinus*

Note: This proposal is a slight modification of SACC Proposal 818. Although SACC only accepted one of four proposed splits, the entire proposal is reproduced here. Acceptance of the split that SACC accepted, which is what is proposed for NACC, would result in recognition of extralimital species *Pyrocephalus nanus* and would necessitate changes to our distributional statement and notes for *P. rubinus*.

Original SACC Proposal: Split *Pyrocephalus rubinus* into multiple species

Background:

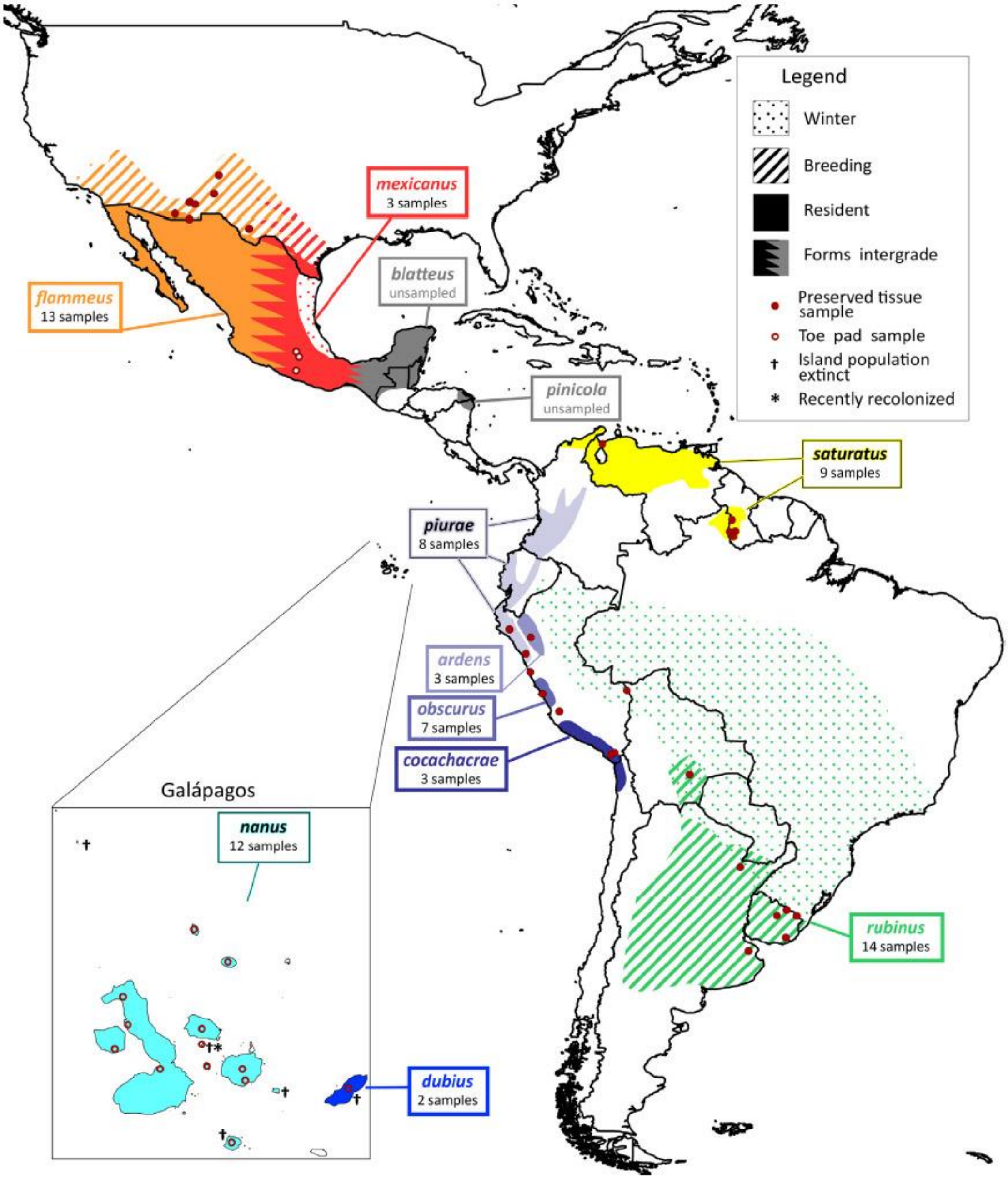
The Vermilion Flycatcher is a widespread, common species that forms a monotypic genus. It is not a species that has stood out taxonomically, other than it often gets called out as unusual for a tyrannid because the male is so brightly and distinctively colored. What has also caught the attention of some is that while male plumage of various geographical forms is similar, the plumages of females are not, with some being quite distinctive … specifically, those from the Galapagos islands.

Pyrocephalus rubinus is very widespread and it shows substantial geographic variation with 12 traditionally recognized subspecies (see distribution map on next page), much of it based on differences in female plumage. Although no suggestions to separate the species into multiples has been made in the past, it is worthwhile to note that a largely ignored paper by DeBenedictis (1966) notes the radically different voice of one of the Galapagos populations. DeBenedictis described the aerial display and vocalization of one population (Isabela Island) in the Galapagos and confirmed that it is fundamentally distinct from mainland populations. Rather than a rising series of notes as on the mainland, the Galapagos population gives a single repeated note. Based on this paper, one would think that the single species status of *Pyrocephalus rubinus* would have been called into question, but as mentioned above this note has largely been ignored, although recent authors have suggested that *P. rubinus* is more than one species (Ellison et al., 2009; Farnsworth and Lebbin, 2004.). Recordings of the Galapagos birds have not been widely available. In his first trip to Galapagos, A. Jaramillo was able to obtain poor recordings of the Isabela population of the Vermilion Flycatcher and confirmed the description of the vocal display as noted by DeBenedictis (1966).

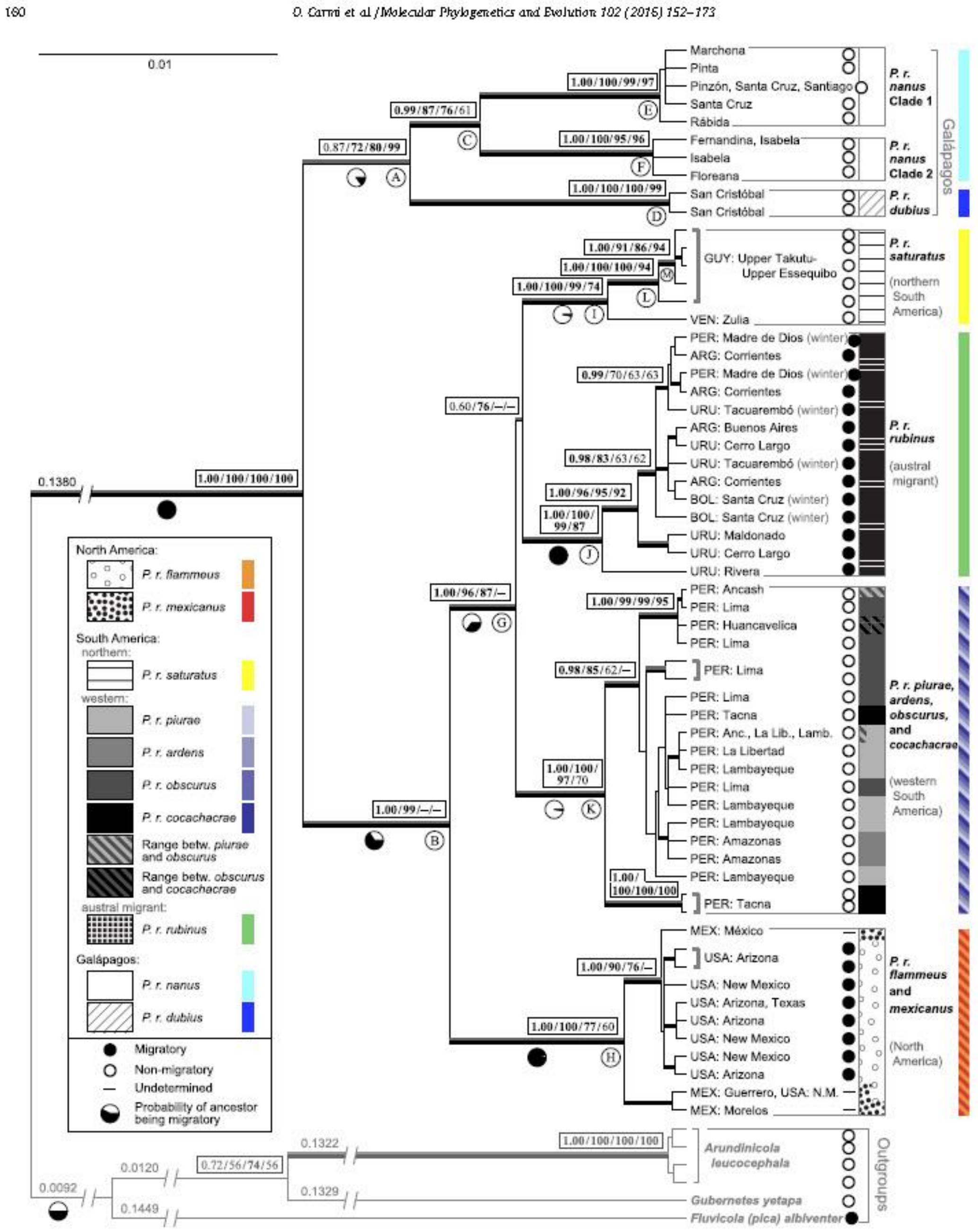
New Information:

Carmi et al. (2016) took a fresh look at *Pyrocephalus*, with molecular datasets, to clarify the relationships of taxa within the genus. A total of 85 individuals was sampled, from 10 of the 12 named subspecies in Dickinson and Christidis (2014). Two mitochondrial protein-coding genes (ND2 and Cyt *b*) were sequenced as well as two nuclear loci (ODC and FGB5).

The mitochondrial DNA tree (see figure on page after next) shows that *Pyrocephalus* is monophyletic and is separated by a very deep branch from closest relatives. Seven clades show up in the data, including three from the Galapagos Islands. These seven clades from two sister groups, one of the three clades from the Galapagos, and the other of the remaining four clades from the continent. In the Galapagos, one clade corresponds to the subspecies *dubius* from San Cristobal Island, the geologically oldest island in the archipelago with a member of *Pyrocephalus*. The other two correspond to *nanus*, one clade from the older northern islands (Pinta, Marchena, Santiago, Rábida, Pinzón, and Santa Cruz) and the other from the younger southern and western islands (Fernandina, Isabela, and Floreana). The continental clades separate into two groups: a South American group and a North American group. The South American clade further separates into the austral migratory *rubinus* group, the populations along western South America, and those in northern South America.



The nuclear allele networks (see figure on next page) show a different pattern. In the ODC network, one allele (d) was found throughout continental populations. Of the five alleles that differed from allele d by more than one substitution, three were found in Austral *rubinus*. The possible root of the allele network was closer to two of these *rubinus* alleles. A total of seven alleles was unique to *rubinus*. One allele was unique to *nanus* from the Galapagos. The highest allele diversity was found in *rubinus*. In the FGB5 network there were three groups of alleles, one of several alleles found in the North American clade, one of birds from the Western South



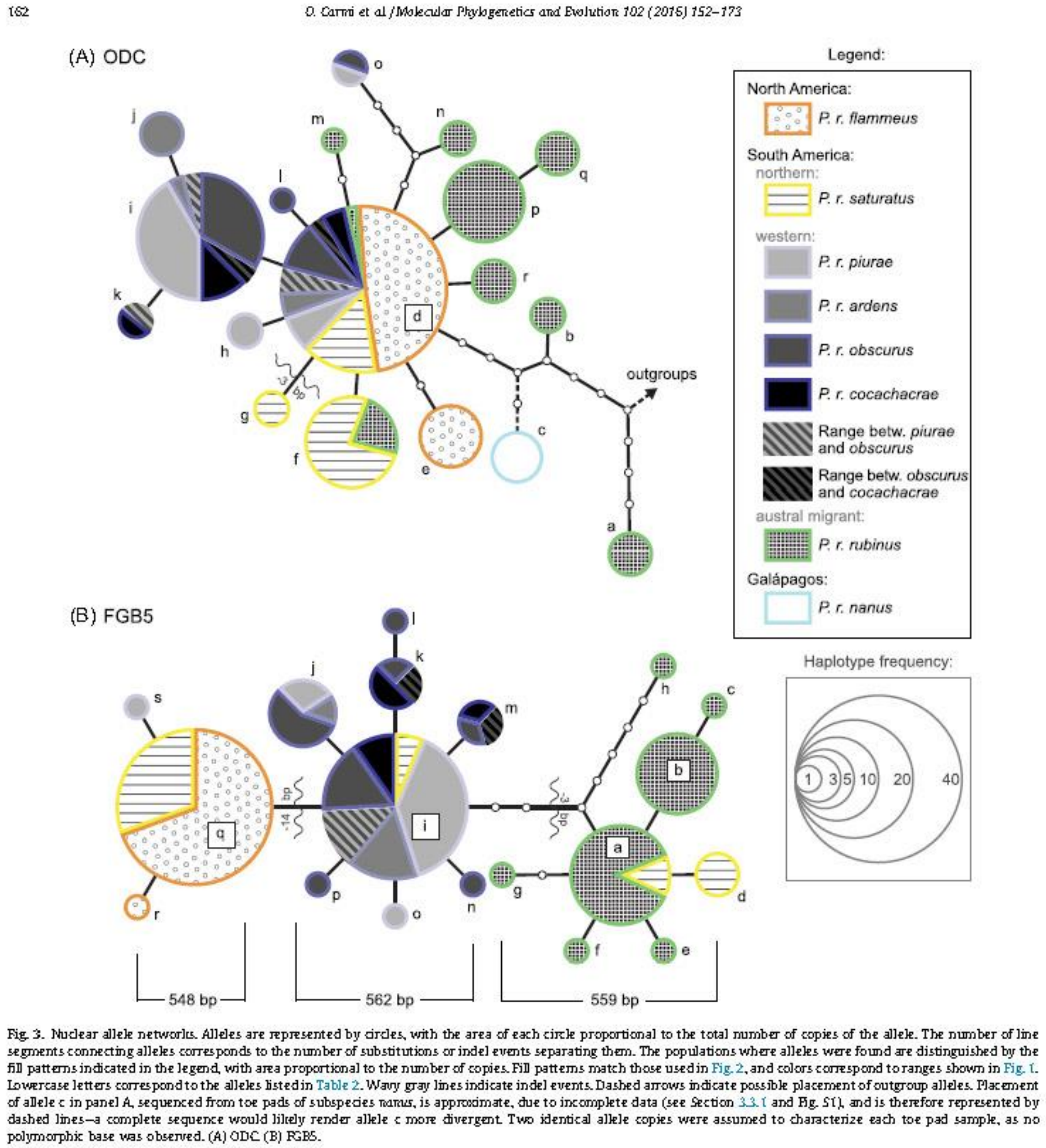


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Fig. 3. Nuclear allele networks. Alleles are represented by circles, with the area of each circle proportional to the total number of copies of the allele. The number of line segments connecting alleles corresponds to the number of substitutions or indel events separating them. The populations where alleles were found are distinguished by the fill patterns indicated in the legend, with area proportional to the number of copies. Fill patterns match those used in Fig. 2, and colors correspond to ranges shown in Fig. 1. Lowercase letters correspond to the alleles listed in Table 2. Wavy gray lines indicate indel events. Dashed arrows indicate possible placement of outgroup alleles. Placement of allele c in panel A, sequenced from toe pads of subspecies *nanus*, is approximate, due to incomplete data (see Section 3.3.1 and Fig. S1), and is therefore represented by dashed lines—a complete sequence would likely render allele c more divergent. Two identical allele copies were assumed to characterize each toe pad sample, as no polymorphic base was observed. (A) ODC (B) FGB5.

American clade, and one of *rubinus* the Austral migratory clade. Structure was evident in this dataset; alleles from *rubinus* were all characterized by a 3-bp deletion, North American birds by a 14-bp deletion. Again, *rubinus* showed the highest allele diversity of any group. No *nanus* data was available for this gene.

Galapagos – The separation between the Galapagos group and the mainland group is estimated to be roughly a million years ago. These birds are smaller than mainland birds, with visibly different female coloration. Males are different as well, with a more restricted red cap than mainland birds. Structurally the Galapagos birds have very short, weak tails, and short, rounded wings. As noted above, *nanus* is vocally quite different from mainland birds. Their preference for open forest and forest edge is a habitat quite different from the more open country taken by the continental populations. Osteological differences have also been noted and used to suggest species status for Galapagos birds (Steadman 1986). In summary, various independent lines of evidence can be used to conclude that there is a different species on Galapagos than the mainland. What is novel is that the genetic data also clarifies the distinctness of the San Cristobal population *dubius*. Unfortunately, no vocal data is available for *dubius*, and it may in fact be extinct now. The branch separating *dubius* from the other Galapagos populations is quite long, suggesting the split is older than any division seen in the mainland clades. The geographic pattern also fits a general one seen in the Galapagos, with the old branch (*dubius*) restricted to the older eastern islands, in this case San Cristobal. More work is needed to understand if more than one species is present in *nanus*, but certainly *dubius* appears to be a good species.

Austral migrant *rubinus* – There are multiple clades within the mainland Vermilion Flycatchers. Perhaps there are multiple species level questions to be resolved although nothing obvious. However, multiple lines of data clarify that the southern migratory *rubinus* deserves species status. What is confusing is that the mtDNA data suggest that it is nested within the mainland group. The nuclear data show a different pattern where the distinctness of *rubinus* is perhaps clearer. There are various reasons why the mtDNA results may be incorrectly showing the relationship of *rubinus,* and on this Carmi et al. (2016) do not elaborate. The mtDNA data show a sister relationship with the northern South American group, where *rubinus* winters. It is not impossible that historical hybridization with that population may be reflected in the current mtDNA results and that this may not be its true history? There is no current evidence for hybridization, and the breeding ranges of *rubinus* and *saturatus* do not come close.

The important point is that the mtDNA do show *rubinus* to be a separate clade within the mainland populations. Nuclear DNA further supports distinctness of this group. But more importantly, the birds themselves show a clear biological difference, vocalizations. This section was taken out of the Carmi et al. (2016) paper by the editors. Although sample sizes were low, playback experiments I have conducted are clear: *rubinus* does not respond to a northern song and vice versa. I have more data currently, all of it unpublished, and the same pattern remains. Furthermore, experiments playing voice of *mexicanus* to *cocachacrae* invoke a response, whereas *rubinus* is ignored by *cocachacrae*. The deleted text in the paper is the following:

"Males from Belize (subspecies *blatteus*) were more likely to respond to song from Arizona males (subspecies *flammeus*) than to song from Uruguay males (subspecies *rubinus*; Wilcoxon signed-rank test W=0, p<0.5, n=10). Males from Uruguay were more likely to respond to song from Uruguay males than to song from Arizona males [Wilcoxon signed-rank test W=0, p<0.5, nr=6 (n=9)]. No male from Belize responded to songs from Uruguay, and similarly no Uruguayan male responded to songs from Arizona."

The general nature and pattern of the song is similar in all mainland Vermilion Flycatchers: a short, rising, and terminally accented trill. The North American, coastal South American, and northern South American birds have similar songs. Compared to *rubinus* they are lower pitched, are delivered more slowly, and the terminal note is clearly lower pitched than the pitch at the crescendo of the trill. Here is a typical example: =

https://www.xeno-canto.org/299099

On the other hand, *rubinus* is higher pitched, rises quickly and the final note is high pitched, similar to the frequency of the end of the crescendo. This gives the voice an upwardly accented nature, quite different from other mainland Vermilion Flycatchers. All can perform bill snaps during the vocal displays. I have not looked at differences in the call notes. As noted above, birds of the different song types (*rubinus* and non-*rubinus*) ignore each other's voice. Given this clear biological response in a suboscine, *rubinus* acts like a good species.

Recommendation:

Based on molecular data, as well as biological (voice) data, we suggest dividing up the Vermilion Flycatcher into four species: *Pyrocephalus rubinus, Pyrocephalus obscurus, Pyrocephalus nanus*, and *Pyrocephalus dubius*. Note that *rubinus*, *nanus* and *dubius* would be monotypic. However, *P. obscurus* would include *obscurus*, *piurae*, *ardens*, *cocachacrae*, *saturatus*, *mexicanus*, *blatteus*, *flammeus*, and *pinicola*.

English names:

This is a tough issue as the Vermilion Flycatcher is one of the most widespread and best known of the Tyrannidae. Although it may be troubling for some to retain this name for *obscurus*, for reasons that have been discussed by this committee elsewhere, in my opinion the argument for keeping the name is persuasive. Essentially every English speaker who watches birds in the Americas knows the Vermilion Flycatcher, changing this name to something else like Northern Vermilion-Flycatcher is adding complexity to an issue that in the end will create very little confusion for most people in English-speaking countries. It really is a non-issue for 99% of the user group of English names to keep Vermilion Flycatcher even though it now refers to a subset of what that name used to mean.

I am not keen on adding a modifier to Vermilion Flycatcher for the various forms and prefer distinct and evocative names. The easiest of which is to call the possibly extinct *Pyrocephalus dubius* the San Cristobal Flycatcher.

For *Pyrocephalus nanus*, the name Galapagos Flycatcher is already taken. In the Galapagos this species is well known, although it is declining at a precipitous rate. It has become a conservation concern, and I think to respect what the locals call it, an evocative name would be Brujo Flycatcher. Locally it is invariably called "pájaro brujo," the witch bird. As so many tyrannids have such forgettable names, why not call the most colorful passerine of the Galapagos by a colorful name?

Finally, *Pyrocephalus rubinus* can be given many names. Perhaps coming up with one that highlights its migratory tendency, being the only firm migrant within *Pyrocephalus* is appealing. But I could not think of any good name that works. I have seen the name "Scarlet Flycatcher" being used, such as on Xeno-canto. I don't know if this is a name they just pulled out of their cloaca or if it has some historical context? In any case, my preference would be Ruby Flycatcher to match with the scientific name. Male *rubinus* are darker than *obscurus*, a darker red below and darker brown above. But I don't think that the color differences are enough that one could make an argument of ruby or scarlet versus what vermilion means; essentially, they all suggest a red coloration.

NACC Recommendation:

SACC voted only to split the Galapagos form *nanus* (including *dubius*) from *P. rubinus*, and I recommend that we do the same. SACC voted to adopt the English name Brujo Flycatcher for *P. nanus* and thus retain the English name Vermilion Flycatcher for the widespread and familiar *P. rubinus*, and I recommend that we follow this as well. More information on SACC's English names proposal and comments can be found online at https://www.museum.lsu.edu/~Remsen/SACCprop911.htm.

Literature Cited:

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Submitted by: Alvaro Jaramillo, NACC recommendation by Terry Chesser

Date of Proposal: April 2019, modified 8 October 2021

Note from Remsen: Voting structure is as follows:

818A. Split Galapagos *nanus* (including *dubius*) from widespread mainland taxa.
818B. Treat *dubius* as a separate species from *nanus.*
818C. Treat all mainland taxa as *P. obscurus*, as a separate species from nominate *rubinus*.

English names (if splits adopted):
818D: Use separate English names for each species rather than compound names, i.e. "Something Vermilion-Flycatcher."
818A-E. Use "Brujo" as the "first name" for *nanus*
818B-E. Use "San Cristobal" as the "first name" for *dubius*
818C-E1. Retain "Vermilion" as the "first name" for widespread *obscurus*
818C-E2. Use "Ruby" as the "first name" for nominate *rubinus*

Comments from SACC:

Comments from Areta:
"818A. YES to recognizing both Galapagos forms as a separate species from mainland taxa. The few vocalizations of *nanus* I´ve heard are clearly different from *rubinus* and *obscurus*, and the females differ notably from those elsewhere.
"818B. NO, until biological data such as vocalizations (if not extinct) or more thorough genetic work provides deeper information on the genetic architecture of *dubius*. The age of the split between *nanus* and *dubius* is not impressive, and given that we do not know what this would mean in terms of reproductive compatibilities, I prefer to recognize *dubius* as a subspecies of *nanus*. Also, note that the difference between the two *nanus* groups is quite deep in comparison to that between *rubinus* and *obscurus*, yet we are not discussing their treatment as different species based only on genetic distance.
"818C. YES. I was skeptical of this given the paraphyly of *obscurus* with respect to *rubinus* (this is something that I would have like explained in the paper itself). However, after checking all available recordings of songs of the different taxa, I agree with Alvaro in that the vocal differences between *rubinus* and *obscurus* (including from *mexicanus* to *cocachacrae*) are constant. The lack of answer between *blatteus* and *rubinus*, while *mexicanus* responds to *cocachacrae* seal the deal for me. There is ample room here to publish these playback experiments together with a thorough vocal analysis of these taxa. It is regrettable that the comments on vocalizations and playbacks were taken out of the Ms."

Comments from Claramunt:
"818A: YES. Very complicated case. I think it is fair to tentatively separate the Galapagos forms as a different species given their plumage, morphological, and song differences, and the fact that they form a separate mitochondrial lineage. So, YES to A.

"818B. NO. Elevating *dubius* to species mainly because of high levels of mtDNA "divergence" is not justified, in my opinion. Despite widespread belief, haplotypes with 2% "divergence" can perfectly coexist within a single species (see Benham & Cheviron 2019 Molecular Ecology 28:1765–1783). I would like to see more evidence regarding this potential split. So, NO to B.

"818C. NO. *P. r. rubinus* is somewhat distinctive in song and in the fact that it is an austral migrant, but male plumage is barely differentiated, and it is not a different lineage genetically: its mtDNA is part of the south American continental genealogy, and it shares nuclear alleles, particularly with *P. r. saturatus*. Regarding reproductive isolation, I don't think that a female of a different subspecies will ignore a male of *rubinus* just because he sounds a little different. She may not react to the song in isolation, but visual cues seem important in this species. Therefore, NO to C."

Comments from Stiles: "The genetic data seem quite clear in mandating splitting up *Pyrocephalus rubinus* into SIX species. To begin with, the name "Vermilion Flycatcher" is solidly entrenched and applicable to the complex as a whole, as a hyphenated group name - trying to find separate names that do not include Vermilion seems a bit silly, as any birder anywhere will recognize a Vermilion Flycatcher! Henceforth, I will go through the phylogeny as it stands, suggesting E-names en route. 1) the oldest split is between the Galápagos group and the continental group, so at the least, one species must be split for the Galápagos, and the internal split between *nanus* and *dubius* is about the same age as the oldest continental splits, so clearly two species are justified here. Because *dubius* apparently is extinct, San Cristobal V-F is appropriate. I see no great problem with staying with Galápagos V-F for *nanus*, as it is now the only extant V-F there but if one must find another name for *nanus*, Least V-F at least goes with the Latin name. 2) The next oldest split is between the North-Middle American and the South American groups, hence at least both must be recognized as separate species. The former group could be called Northern V-F (I think *mexicanus* has priority as the Latin epithet). 3) The South American group splits into three well-defined clades of virtually identical ages. If considered as only one species, Southern V-F would do for all, but if one splits *rubinus* from the others, then three species is the only way to go. 4) Very slightly older is the split between saturatus and the other two.. genetic data are from Guyana and W Venezuela, but *saturatus* also occurs in NE Colombia, so that its distribution is centered on Venezuela, hence Venezuelan V-F at least does no violence to its distribution relative to the other two! Carib V-F could be an alternative. 5) From northwestern Colombia to SW Peru occurs *obscurus* (originally named for the localized melanistic form from C Peru, so forget "Dark V-F" as a useful option!) Hellmayr's name of Pacific V-F fits pretty well. 6) Finally, nominate *rubinus*, as the southernmost taxon and an austral migrant, could be called Austral V-F. As a final comment, I can see no sense in including the northern group under *obscurus*, producing a flagrant paraphyly. The song of the southernmost member of the *obscurus* group, *cacachorea*, may show some resemblance to that of the northern group, but must have been derived independently; I regard any resemblance as coincidental, or perhaps the resurfacing of an ancestral character (seems less likely)."

Comments from Robbins: "At a minimum, at least two species should be recognized, Galapagos and mainland based on the differences in vocalizations and genetics. Genetic data support a mainland split into at least two species, North and South America. Based on genetic data and the time axis, if one recognizes North and South America as different species, then one should also recognize Galapagos *dubius* as a species. Given the three options we have been presented, for now, I vote as follows:
"818A. YES.
"818B. YES, based on comments above.
"818C. NO, for now. I do support recognizing North/Central American birds from South America, but recognize that is beyond the scope of our committee. However, depending on member's viewpoint, that element may be important for being consistent on how SACC members vote on the proposals at hand."

Comments from Pacheco: "The multiple data available are compelling to separate the Galapagos taxa from those on the Continent. However, for the reasons listed by Nacho and Santiago, I also prefer to maintain *nanus* associated subspecifically with *dubius*. Agreeing with Nacho, I am particularly impressed by the constant vocal distinctions between the northern taxa and that southern (nominate) migratory taxon in the continental bloc. Therefore, my votes are: 818A – YES; 818B – NO; 818C – YES."

Comments from Remsen: "A. YES. All lines of evidence point to species rank, as summarized in the proposal."

<u>Comments from Bonaccorso</u>:
"818A. YES. All available evidence (molecular, song, plumage, osteology) point towards a distinct species.
"818B. NO. Agree with Santiago. Genetic distance and structure should not be the only criteria for species status.
"818C. Abstain. Neither tree topology nor nuclear networks show a different enough clade. Also, based on tree topology only, it will seem odd to call *P. rubinus* a species and lump all other subspecies into *P. obscurus* (then *P. obscurus* will be paraphyletic). On the other hand, migratory species are different in the way they speciate (they may cause paraphyly on the tree). So, it would be important to publish those song and playback records and do proper analyses, in order to make a better-informed decision."

<u>Comments from Stotz</u>:
"A. "YES to splitting Galapagos populations from mainland populations. They separate out genetically, vocally, and morphologically.
"B. NO to splitting *Pyrocephalus dubius*. This taxon is part of a clade with the rest of the Galapagos birds. Without some sort of data to suggest species status, I think this is best treated as a part of a Galapagos endemic species.
"C. NO to splitting *obscurus* from *rubinus*. The vocal information is very suggestive, but is not published and conflicts with the published genetic information. I think I need to see either more information or a clearer statement of the argument accounting for the distributional and genetic inconsistencies.
"D. "NO. I think I am with Gary on this. While I generally prefer not to create new compound names, the fact that Vermilion Flycatcher is a very distinctive flycatcher with a distinctive and good descriptive name, I would like to hang on to Vermilion Flycatcher for the whole group. Brujo Flycatcher seems like a mistake. There is no geographic or descriptive information in it, and Brujo is not an English word. Ruby Flycatcher is not too bad, but feels like we are forcing it. One problem with using Galapagos Vermilion-Flycatcher, given the way the voting is going, is that then we need a name for the entire mainland group. Only thoughts I have for that are Mainland Vermilion-Flycatcher or Common Vermilion-Flycatcher, neither of which are great names (although HBW uses Common Vermilion-Flycatcher). My guess is that this is a short-term problem because I expect that we will eventually have sufficient data to split up the mainland forms into multiple species."

<u>Comments from Zimmer</u>:
"A. YES. I agree with Mark that this is the minimum that we should do, based upon concordant vocal, morphological, and genetic data that appear unambiguous in supporting a split of all Galapagos populations from all mainland populations.
"B. NO. Without more data, I'm inclined to treat this taxon as a subspecies and part of a single clade of Galapagos birds specifically distinct from mainland birds, particularly given that there is geographic structure to the genetic data even within *nana* populations.
"C. YES. I'm more than a little confused as how to proceed on this, given the limitations of how 818C is worded. I agree with those who see a clear North/Middle American versus South American split, so I don't feel that lumping all mainland forms into a paraphyletic *obscurus*, separate from nominate *rubinus* is the way to go. And I definitely don't support keeping all mainland populations (from North America to South America) together in *rubinus*. In looking at the clades supported by the data, and with biogeographical considerations in mind, my gut tells

me that Gary's approach is probably the correct one with respect to mainland populations: 1) North & Middle American birds (*flammeus, blatteus, mexicanus, pinicola*) as one species; 2) Pacific Coast of South America populations (*piurae, ardens, obscurus, cocachacrae*) as another; 3) Northern South America populations (*saturatus*) as a third; and 4) migratory Austral populations (*rubinus*) as a 4th, with Galapagos populations (*nanus & dubius*) representing a 5th species. This approach does not fit within 818C as currently constructed, unless one views the separation of a paraphyletic *obscurus* from *rubinus*, as a necessary first step to further splitting. With that in mind, I'll vote YES, based on the vocal distinctions of *rubinus* from everything else (including the results of reciprocal playback trials, which, unfortunately, were edited out of the paper), just to get the ball rolling, and to pave the way toward further splitting. I agree with both Gary and Doug that using "Vermilion-Flycatcher" as an English group name (to be paired with a species-specific modifier) is the way to go, in what is a demonstrably monophyletic group. But that would be putting the cart before the horse, since we don't yet know which way the committee will go with respect to the number of splits. If I am understanding Van's instructions correctly, we will vote on English names once/if the splits are adopted, but not until then."

Additional comments from Stiles: "Taking a closer look at the topology of the genetic results, I note that the branch separating *saturatus* from *rubinus* + *obscurus* is extremely short and not all that well supported, such that the relationships of these three taxa almost constitute a polytomy (calling into question whether the supposed polyphyly of *obscurus* if including *saturatus* really exists). Hence, I think that the most reasonable course for now is to include all three under *rubinus*, and await more conclusive evidence for their relationships. It therefore means that "Southern V-F" will do for the E-name, at least for now."

Change the scientific name of *Anthus lutescens* (Yellowish Pipit) to *Anthus chii*

Note: This proposal is a slightly modified version of SACC Proposal 910, which was accepted unanimously.

Effect on NACC:

Acceptance of this proposal would replace the name *Anthus lutescens* with the senior synonym *Anthus chii*.

Background:

The current note on the SACC website reads: "*Anthus lutescens* was formerly (e.g., Zimmer 1953c) know as *A. chii*, but see Hellmayr (1934) and Meyer de Schauensee (1966)."

New information:

Smith and Clay (2021) revisited the issue of the priority of *chii* and *lutescens* and indicate that *chii* has priority and therefore must be used.

John T. Zimmer was outstanding when dealing with pipits. Indeed, he is to be commended for describing *Anthus chii chacoensis* (Zimmer 1952). In another paper, Zimmer (1953: 19) realized that *chacoensis* was better afforded species status and elaborated on his usage of *chii* as a replacement for *lutescens*:

"Although I gave no reasons in the paper cited for adopting the specific name *chii* in preference to *lutescens*, I believe the course was justifiable. A careful reading of Azara's description of his Alondra chií (no. 146), the basis for *Anthus chii* Vieillot, shows no such uncertainty of application as Hellmayr (1921, El Hornero, vol. 2, p. 183, footnote) thought to exist. Even were the details of coloration less precise than they are, the short tail and tarsi recorded by Azara indicate the present species or *chacoensis* while the long hind claw (noted as 6 lines) and the pattern of the tail (with a longitudinal white stripe on the subexternal rectrix) narrow the application still further. Neither of these features belongs to *chacoensis*. "

The situation is put in perspective by Smith & Clay (2021: 119):

"Azara's No. 146 "Alondra Chií" (Azara [1805] Volume 2: p. 6–11)
Azara stated that the name of his "Chií" is derived from the clear call note given by the bird when it descends, with the last "letter" greatly extended. He gave a series of measurements (Table 1), which clearly place it amongst the "small" pipits, and provided a detailed description of the bird in which he described a "faint golden tinge" to the underparts of what he believed to be the male, streaking on the flanks, and uniform dark upperparts with pale fringes."

After discussing some other nuances and misunderstandings, Smith and Clay (2021: 120) concluded that "*Anthus chii* Vieillot, 1818 predates *Anthus lutescens* Pucheran, 1855 and there

are multiple usages of it in the 20th and 21st Century literature (e.g., Bertoni 1939; Zimmer 1952, 1953; Schade & Masi Pallarés 1971; Contreras *et al*. 1990; Narosky & Yzurieta 1993). Thus it is available for application under Article 23.9 of the Code (ICZN 1999), and the correct name for the Yellowish Pipit under the Principle of Priority (Article 23 of the ICZN) is *Anthus chii* Vieillot, 1818. As this is simply a replacement of a younger name for an older name in a well-known species, there is no requirement for neotype designation.
Another name entirely based on Azara's No. 146 Alondra Chií is *Anthus turdinus* Merrem, 1820, and is thus a junior objective synonym of *A. chii* Vieillot, 1818."

I want to stress here that at present, the diagnostic song of *lutescens* is exactly as that described by Azara for his Alondra Chií, thereby leaving no doubt at all that *lutescens* and *chii* pertain to the same species. Azara´s original description reads "Así lo llamo, por no hallar otro nombre mejor; y porque quando se eleva como la anterior, canta claramente **chií**, alargando mucho la última letra." It is conceivable that neither Hellmayr nor Zimmer were acquainted with the song of "*lutescens*/*chii*", but there is no question as to which pipit Azara was describing. It is a great example of the usage of vocalizations in taxonomy in 1805!

Recommendation:

I recommend an emphatic YES, in full support of Zimmer (1952, 1953) and Smith & Clay (2021). *Anthus chii* has priority, it has been used recently in relevant publications, the situation was lucidly clarified by Zimmer (and inexplicably put aside in the modern literature) and as a plus, the description of Azara is wonderful, accurate and refers to the highly diagnostic song of this pipit. Finally, the usage of *Anthus lutescens* bypasses the priority of two names.

Literature Cited:

Azara, F. de (1805) *Apuntamientos para la Historia Natural de los Páxaros del Paraguay y Rio de la Plata. Tomo 2*. Imprenta de la Viuda Ibarra, Madrid, 562 pp.

Smith, P., and R.P. Clay (2021) The identity of Félix de Azara's "Alondras" and implications for Neotropical pipit nomenclature (Aves, Motacillidae: *Anthus*). *Zootaxa* 4942: 118–126.

Zimmer, J.T. (1952) A new subspecies of pipit from Argentina and Paraguay. *Proceedings of the Biological Society of Washington* 6: 31–34.

Zimmer, J.T. (1953) Studies of Peruvian Birds. No. 65. The jays (Corvidae) and pipits (Motacillidae). *American Museum of Natural History Novitates* 1649: 1–28.

Submitted by: Nacho Areta

Date of Proposal: 17 March 2021, submitted to NACC 21 September 2021

Revise the linear sequence of genera in Troglodytidae, especially *Ferminia*

Note: This is just a book-keeping proposal that I should have done long ago and was reminded about it when doing the recent proposal on species limits in *Thryothorus*.

Our current linear sequence is as follows:

Salpinctes
Microcerculus
Catherpes
Hylorchilus
Ferminia
Troglodytes
Thryorchilus
Cistothorus
Thryothorus
Campylorhynchus
Pheugopedius
Thryophilus
Cantorchilus
Uropsila
Henicorhina
Cyphorhinus

I haven't researched the origin of our sequence but was likely revised when we split *Thryothorus* into several genera. Regardless, that was made obsolete by Barker (2017), who used DNA sequence data (8000+ bp from 6 genes) to generate a new phylogeny for the family (see Figs. 4 and 6 below).

Note that our current *Troglodytes* might not be monophyletic, but we can avoid that for now based on what Barker wrote:

> "In the current study, both *Cistothorus* and the genus *Ferminia* (never before included in a molecular phylogeny) separate *Nannus* from *Troglodytes*, though neither relationship showed substantial support (figs. 4, 6). Bayes factor comparison of these results to an analysis with *Troglodytes* monophyly constrained strongly favored the former (table 4). However, the marginal likelihood of an analysis with *Nannus*, *Thryorchilus*, and *Troglodytes* constrained as monophyletic was indistinguishable from the unconstrained analysis (table 4), indicating that the strongest signal is for monophyly of *Troglodytes*+*Thryorchilus*. Thus, these data would not contradict a classification that subsumed all three genera (*Nannus*, *Thryorchilus*, and *Troglodytes*) within *Troglodytes*, as previously done by its describer (Bangs, 1902), and some subsequent taxonomies (e.g., Paynter and Vaurie, 1960). Unless subsequent data strongly separate *Nannus* from *Troglodytes*+*Thryorchilus*, this would seem appropriate, despite the distinctiveness of *Thryorchilus*."

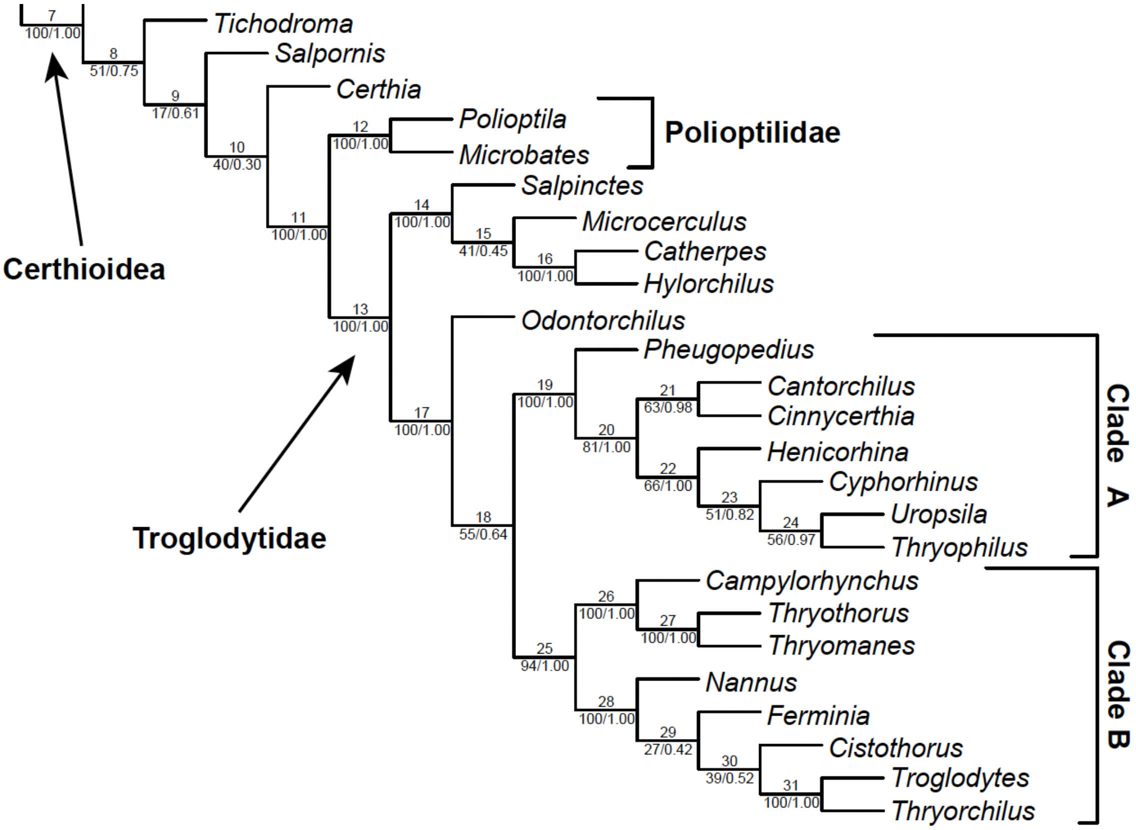


FIGURE 4. Best estimate of certhioid phylogeny, based on concatenated analysis of 8517 bases from five gene regions (cytb, FGB-I4, FGB-I7, RAG1, RAG2, and ZEB1). Shown is the maximum-likelihood tree from a partitioned RAxML analysis, with nonstationary partitions AGY-recoded (see text). Bootstrap support values (from 1000 fast bootstrap replicates; left) and estimated posterior probabilities from partitioned, concatenated Bayesian analysis (right) are shown below each branch. Node numbers correspond to barplots in figure 5.

Meanwhile, I suggest that this general topology reflects phylogenetic relationships better than our existing one, especially with respect to the oddball Cuban endemic *Ferminia*, which was the focus of the paper and the relationships of which have always been mysterious. In addition to the genetic data, here are other points made by Barker:

> "The species exhibits some interesting parallels with *Cistothorus*, including living in a marsh habitat, construction of woven domed nests on grasses or emergent vegetation (Martínez and Martínez, 1991; Llanes Sosa and Mancina, 2002; Forneris and Martínez, 2003), and vocal similarities."
>
> "At least some *Ferminia* songs include a series of repeated low-frequency syllables most closely matched among wrens, based on my extensive listening to wren vocalizations both in the field and in recordings, by songs of the Marsh Wren *C. palustris* (e.g., fig. 9)."

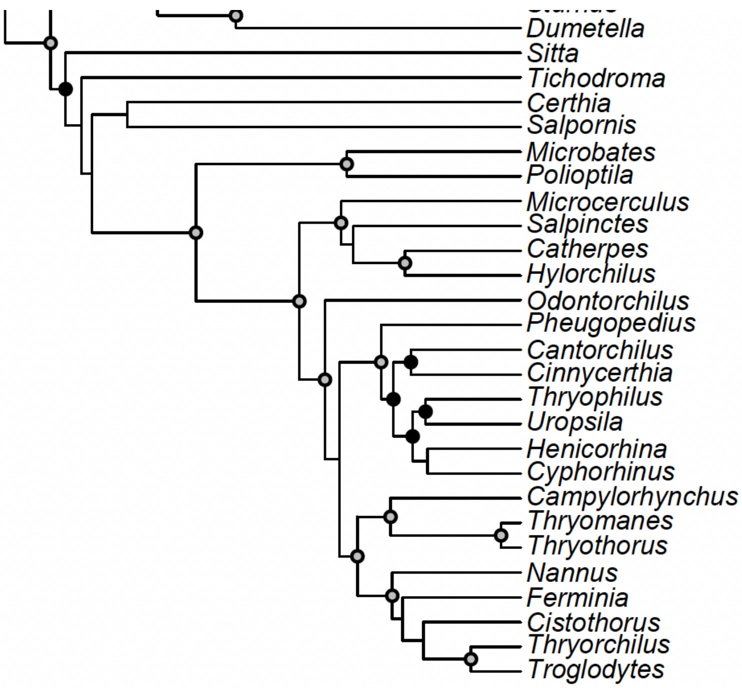


FIGURE 6. Best estimate of certhioid phylogeny, based on species tree analysis of five gene regions (cytb, FGB-I4, FGB-I7, RAG1, RAG2, and ZEB1). Shown is the maximum clade credibility tree from analysis with *BEAST v1.8.3, coding the data as four "genes" based on close linkage of several gene regions. Nodes with estimated posterior probabilities ≥0.95 from partitioned, concatenated Bayesian analysis are indicated by black circles, and those also receiving support at the same level in species tree analyses are indicated by gray circles with black outline.

Converting Keith's Fig. 4 tree to a linear sequence using sequencing conventions produces the following (using indentations to try to help visualize the tree structure):

- *Salpinctes*
  - *Microcerculus*
    - *Catherpes*
    - *Hylorchilus*

- *Odontorchilus* (extralimital)

  - *Pheugopedius*
    - *Cinnycerthia* (extralimital)
    - *Cantorchilus*

    - *Henicorhina*
      - *Cyphorhinus*
        - *Uropsila*
        - *Thryophilus*

- *Campylorhynchus*
  - *Thryomanes*
  - *Thryothorus*

Troglodytes
    Ferminia
    Cistothorus
    Thryorchilus

Notes: (1) There are some minor conflicts between the analyses in Fig. 4 and Fig. 6, but the topology in Fig. 4 causes the least perturbation to the current sequence, so we might as well use that one for now. (2) The lack of resolution in the *Troglodytes* group makes any sequence somewhat arbitrary. (3) *Thryomanes* should precede *Thryothorus* using the convention of northwesternmost taxon first for sisters with equivalent diversity; ditto *Uropsila* and *Thryophilus*; *Cinnycerthia* should precede *Cantorchilus* because of it has fewer species. Please check my work and let me know if there are problems.

I recommend a YES on this because it reflects the best phylogenetic data we have and especially in that it reflects the best hypothesis for the relationships of *Ferminia*.

Literature Cited:

Barker et al. 2017

Submitted by: Van Remsen

Date of Proposal: 9 October 2021

Split *Leucolia wagneri* from *L. viridifrons* (Green-fronted Hummingbird)

Effect on NACC:

Approval of this proposal would treat the currently recognized species *Leucolia viridifrons* (Green-fronted Hummingbird) as two species, both in the NACC area: (1) *Leucolia viridifrons* (Elliot 1871) from Guerrero and western Oaxaca (western population) and eastern Oaxaca and Chiapas (eastern population); and (2) *Leucolia wagneri* (Phillips 1964) from central and southern Oaxaca.

Background:

Leucolia viridifrons wagneri was described as a subspecies in 1964 by Phillips, but Howell (1993) suggested that *wagneri* should be considered a species distinct from *viridifrons*. HBW-BL elevated it to species following the Tobias et al. method ("Until recently treated as conspecific with *A. viridifrons*, but bill slightly longer (effect size 1.14; score 1) (Peterson & Navarro-Sigüenza 2000); both sexes with bright cinnamon vs metallic green cheek to neck side (3); male with dull rufous wingpanel (2); female with rufous outer rectrices (2) (Howell & Webb 1995); purported subspecies *rowleyi* of *A. viridifrons* from C Oaxaca probably indicates intergradation of *viridifrons* and present species in zone of supposed secondary contact (score at least 1).") and IOC split it based on Howell and Webb (1995 – see below).

The taxonomic history of *Leucolia viridifrons* is very complex because it is linked to the taxonomic history of *Leucolia violiceps*, the only other species in this genus. A brief summary of the taxonomic history of *Leucolia viridifrons*:

- The species *Cyanomyia viridifrons* was discovered in western Oaxaca, near Putla. The species was described by Elliot (1871).

- Salvin and Godman (1896) reviewed a specimen from the type locality near Putla, Oaxaca, in addition to another specimen from southern Oaxaca (Tehuantepec), and two from Chiapas (Tonalá). The authors noted that they all appeared to belong to the same species.

- Ridgway (1911) listed the Mexican states of Guerrero, Oaxaca, and Chiapas as the geographic range of *Cyanomyia viridifrons*, which he placed in *Amizilis*. Ridgway did not mention intraspecific variation, with the exception of one specimen from Guerrero with a deep blue crown, but he was convinced that it was a conspecific because both green-crowned and blue-crowned birds had been collected at the same locality (Acahuitzotla).

- Peters (1945) considered *Cyanomyia viridifrons* as synonymous with *Cyanomyia violiceps*, and listed both forms as *Amazilia violiceps violiceps*.

- Wetmore (1947) also considered *viridifrons* a subspecies within *Amazilia violiceps*.

- Eisenmann (1955) treated *viridifrons* as a different species from *violiceps*. Eisenmann added a note saying that Peters regarded *viridifrons* as the immature plumage of *violiceps*.

- AOU (1957) treated *viridifrons* and *violiceps* as a single species, *Amazilia verticalis* (Deppe). The geographic range of this species included from Sonora and Chihuahua to Chiapas, and casual in Arizona.

- Phillips (1964) described the subspecies *wagneri*. Phillips treated *viridifrons* and *wagneri* as subspecies of *Amazilia violiceps* (currently *Leucolia violiceps*) since there was no evidence of the two forms breeding in sympatry. Phillips noted that *viridifrons* and *violiceps* might represent distinct species and found evidence that their plumage coloration differences were not correlated with age.

  Phillips (1964) noted that the diagnostic traits of *wagneri* when compared to *viridifrons* are the rufous bases of the secondaries and under wing covers, the rufous sides and flanks, sides of crissum and a line bordering the white up to the face and extending to the bill; *wagneri* also has more rufous in the tail and upper tail covers.

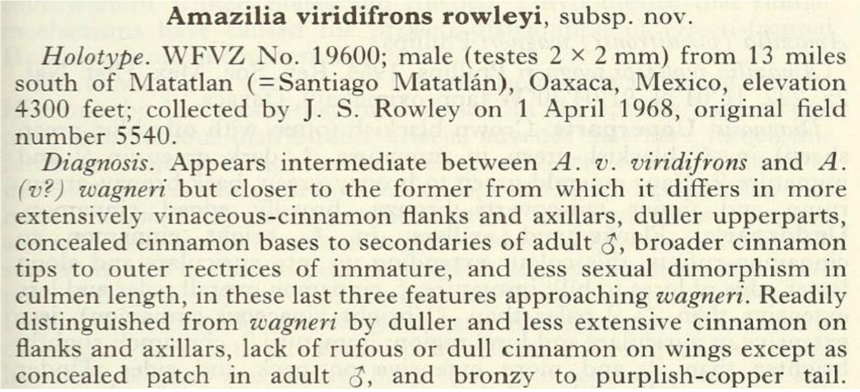
- Davis (1972) listed *violiceps* and *viridifrons* as a single species, *Cyanomia verticalis*, with a geographic range as described in AOU (1957).

- AOU (1983) treated *viridifrons* as a different species from *violiceps* and included the following note: "*A. violiceps* and *A. viridifrons* are sometimes considered conspecific, but sympatry in Guerrero and Oaxaca without intergradations seem to support their status as full species."

- Howell (1993) considered *viridifrons* to be a different species from *violiceps*. He noted that the two forms are visually distinct; their call notes are distinguishable; when the two forms co-occur seasonally in Guerrero, they favor different habitats; and there are no hybrids known.

  He (1993) examined 113 specimens of *Amazilia viridifrons*. When he arranged the specimens by geography, sex, and age, he discovered four groups: (1) Guerrero and western Oaxaca (*Amazilia viridifrons viridifrons*); (2) central Oaxaca (*A. v. rowleyi* subsp. nov. – see description below); (3) southern Oaxaca and western Isthmus of Tehuantepec (*A. v. wagneri*); and (4) eastern Oaxaca and Chiapas (*A. v. viridifrons*). The specimens from group (1) and group (4) are very similar and some specimens from both groups are indistinguishable; Howell mentioned that they do not warrant subspecific recognition.

  Below is Howell's (1993) description of new subspecies *A. viridifrons rowleyi*:



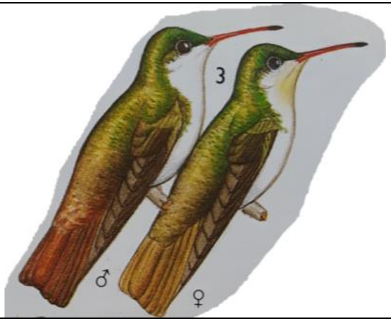
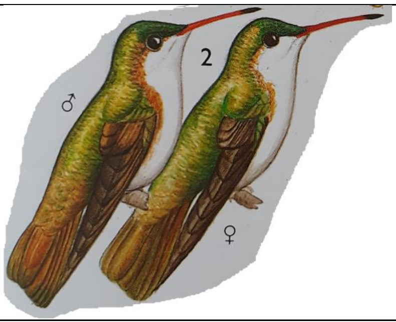
Amazilia viridifrons rowleyi, subsp. nov.

Holotype. WFVZ No. 19600; male (testes 2 × 2 mm) from 13 miles south of Matatlan (=Santiago Matatlán), Oaxaca, Mexico, elevation 4300 feet; collected by J. S. Rowley on 1 April 1968, original field number 5540.

Diagnosis. Appears intermediate between *A. v. viridifrons* and *A. (v?) wagneri* but closer to the former from which it differs in more extensively vinaceous-cinnamon flanks and axillars, duller upperparts, concealed cinnamon bases to secondaries of adult ♂, broader cinnamon tips to outer rectrices of immature, and less sexual dimorphism in culmen length, in these last three features approaching *wagneri*. Readily distinguished from *wagneri* by duller and less extensive cinnamon on flanks and axillars, lack of rufous or dull cinnamon on wings except as concealed patch in adult ♂, and bronzy to purplish-copper tail.

About *wagneri*, Howell noted that it might be specifically distinct from *A. viridifrons* because it is a distinguishable form when all characters are considered, especially the wing and tail patterns and the striking cinnamon sides. In eastern Oaxaca, *wagneri* appears to be sympatric with *A. v. viridifrons*. In the upper Río Grande drainage, *wagneri* is sympatric with *rowleyi*, where 94.6% of specimens are clearly one form or the other. Two specimens from the Río Grande drainage appear to be intergrades. Howell recommends further studies about the degree of sympatry and interbreeding. If *wagneri* is considered a distinct species, Howell suggests the English name “Cinnamon-sided Hummingbird”.

- Howell and Webb (1995) split *wagneri* from *viridifrons*. In addition to diagnostic characteristics in plumage (already mentioned above), the voice and habitats are described.

	viridifrons	***wagneri***
Voice	Dry chattering, reminiscent of Broad-billed Hummingbird but slightly harder; softer than calls of Violet-crowned Hummingbird (*A. violiceps*).	Dry chattering, much like Green-fronted Hummingbird (*A. viridifrons*); also a quiet, hard crackling *zzzzrr´k chiuk*, repeated from perch.
Habitat	Arid to semiarid scrub, thorn forest, riparian woodland, semiopen areas with hedges and scattered trees. Feeds and perches low to high, usually at mid- to upper levels. Nesting: Dec-Feb, Apr-Jun.	Arid to semihumid scrub, thorn forest, riparian woodland. Feed and perches low to high, usually at mid- to upper levels. Nesting: Jan-Feb, May, Aug-Oct.
		

- AOU (1998) continued treating *viridifrons* as a different species from *violiceps* but this time added a note in *viridifrons* about the groups within the species: "*A. viridifrons* [Green-fronted Hummingbird] and *A. wagneri* Phillips, 1965 [Cinnamon-sided Hummingbird]. The form *wagneri* may represent a distinct species (Howell 1993, Howell and Webb 1995)."

- Peterson and Navarro-Sigüenza (2000) examined and measured 134 specimens and concluded that:

    - *Amazilia wagneri* should be recognized as a different species from *A. viridifrons*.
    - The subspecies *rowleyi* is not valid and it should be merged with *wagneri*.
    - The eastern population of *A. viridifrons* should be split from the nominal western population *A. v. viridifrons* and recognized as *A. v. villadai*.
      A. v. villadai has marked sexual dimorphism in size, which is not detectable in *A. v. viridifrons*. Additionally, in *villadai* the green flecking on the flanks and sides is less frequent and its underparts appear whiter.
    - Potential sympatry exists between *A. wagneri* and *A. v. villadai* but no evidence of intergradation, suggesting reproductive isolation.

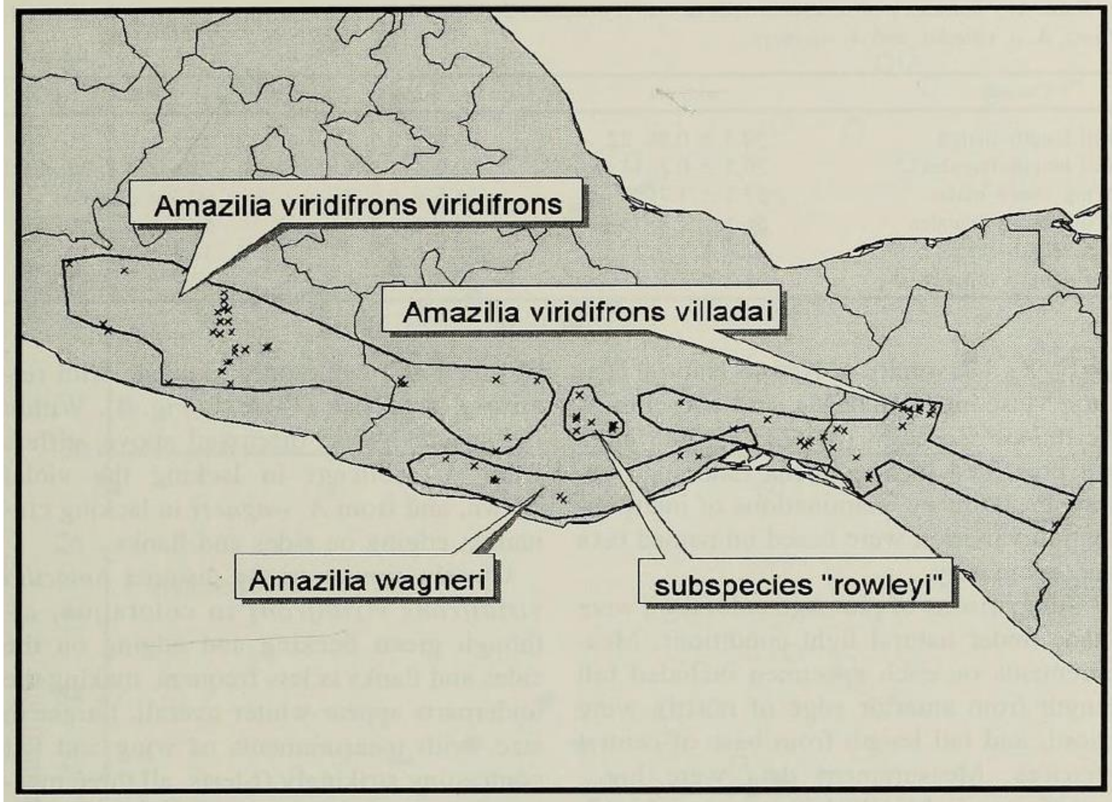


Fig. 1. Map showing geographic distributions of the *Amazilia viridifrons* complex in southern Mexico.

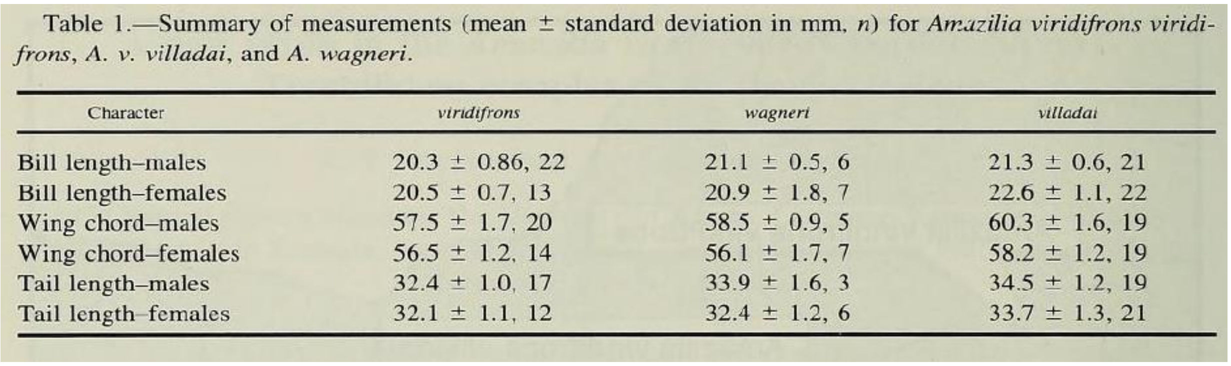


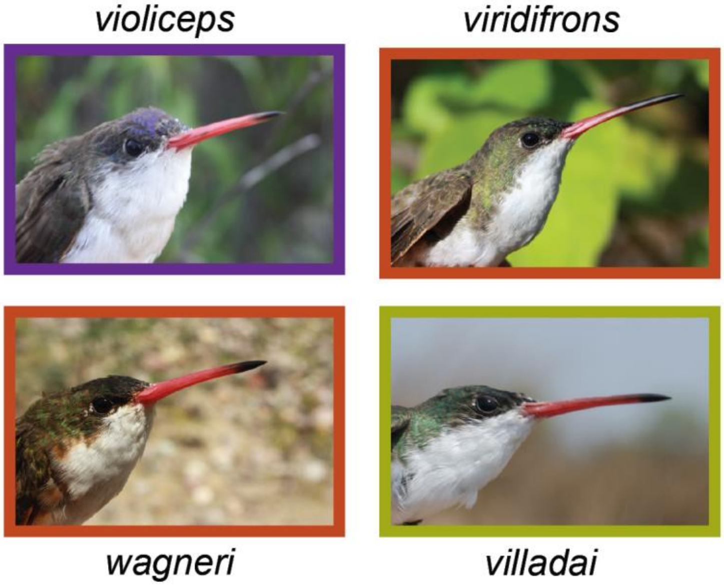
Table 1.—Summary of measurements (mean ± standard deviation in mm, *n*) for *Amazilia viridifrons viridifrons*, *A. v. villadai*, and *A. wagneri*.

Character	*viridifrons*	*wagneri*	*villadai*
Bill length–males	20.3 ± 0.86, 22	21.1 ± 0.5, 6	21.3 ± 0.6, 21
Bill length–females	20.5 ± 0.7, 13	20.9 ± 1.8, 7	22.6 ± 1.1, 22
Wing chord–males	57.5 ± 1.7, 20	58.5 ± 0.9, 5	60.3 ± 1.6, 19
Wing chord–females	56.5 ± 1.2, 14	56.1 ± 1.7, 7	58.2 ± 1.2, 19
Tail length–males	32.4 ± 1.0, 17	33.9 ± 1.6, 3	34.5 ± 1.2, 19
Tail length–females	32.1 ± 1.1, 12	32.4 ± 1.2, 6	33.7 ± 1.3, 21

- Dickinson and Remsen (2013) treated *A. viridifrons* as a separate species from *A. violiceps*. Within *A. viridifrons*, they listed the subspecies *A. v. viridifrons*, *A. v. wagneri*, and *A. v. villadai*.

- To date, sympatric breeding of *viridifrons* (*villadai*) and *wagneri* has not been documented (Arizmendi et al. 2021).

- Photos of the taxa are shown in Figure S3 from Rodríguez-Gómez and Ornelas (2015):

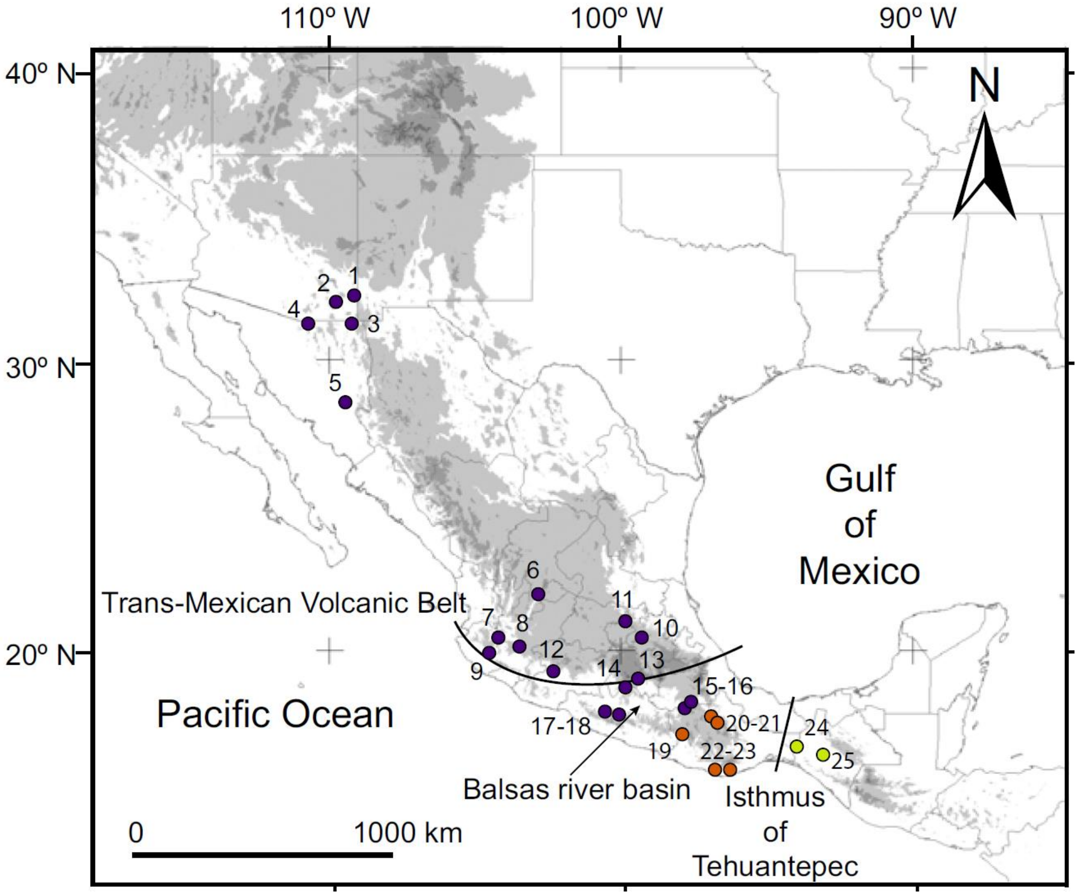


New information:

There are two recent publications by Rodríguez-Gómez and Ornelas (2015, 2018) in which *Amazilia violiceps* and *Amazilia viridifrons* are examined genetically. In summary, shallow divergence and incomplete lineage sorting are important in the evolution of the species complex. Historic and contemporary gene flow was inferred between the two species, *violiceps* and *viridifrons*, as well as between subspecies within *viridifrons*, highlighting the role of divergence with gene flow in the species complex.

Rodríguez-Gómez and Ornelas (2015) examined four mitochondrial regions and one nuclear locus of 56 *violiceps* and 21 *viridifrons* (see their sampling map below). The sampling of *viridifrons* included the four subspecies described to date:

- *viridifrons*, n = 3, Oaxaca, Putla de Guerrero, [sampling locality 19]
- *rowleyi*, n = 4, Oaxaca, San Baltazar [20] and Totolapan [21]
- *wagneri*, n = 4, Oaxaca, Pochutla [22] and Miahutlán [23]
- *villadai*, n = 10, Oaxaca, Cerro Baúl [24] and Chiapas, Ocozocuautla [25]



Map from figure 1 in Rodríguez-Gómez and Ornelas (2015). The colored circles represent the localities of the samples included in the study: *Amazilia violiceps (*purple); *Amazilia viridifrons*, including *A. v. viridifrons*, *A. v. rowleyi*, and *A. v. wagneri* (orange); *Amazilia viridifrons villadai* (light green). The lines drawn in the map represent the geographic barriers mentioned in the paper as limits between genetic groups: Trans-Mexican Volcanic Belt in central Mexico, and the Isthmus of Tehuantepec in southern Mexico.

The Bayesian phylogenetic reconstruction from Rodríguez-Gómez and Ornelas (2015 – see Figure 2a on the next page) recovered two main clades:

- Clade 1: including the localities north of the Trans-Mexican Volcanic Belt. This clade was mainly integrated by *violiceps* but also included two *viridifrons* samples, one *A. v. viridifrons* from Putla [19], and one *A. v. rowleyi* from Totolapan [21].

- Clade 2: including the localities south of the Trans-Mexican Volcanic Belt. This clade included *A. violiceps*, and the majority of individuals assigned as *A. viridifrons*: *A. v. rowleyi*, *A. v. wagneri*, and *A. v. villadai*.

Species delimitation analyses suggested the existence of three species within the *violiceps* – *viridifrons* species complex (see Figure 2b below):

1) *violiceps* (including populations north of the Trans-Mexican Volcanic Belt – TMVB)
2) *viridifrons* (including *violiceps* from south of the TMVB, and *viridifrons*)
3) *villadai*

The authors suggested that *A. violiceps* and *A. viridifrons* may qualify as a single phylogenetic species, and acknowledged that understanding the phylogenetic relationships within *A. viridifrons* would require a greater sampling effort.

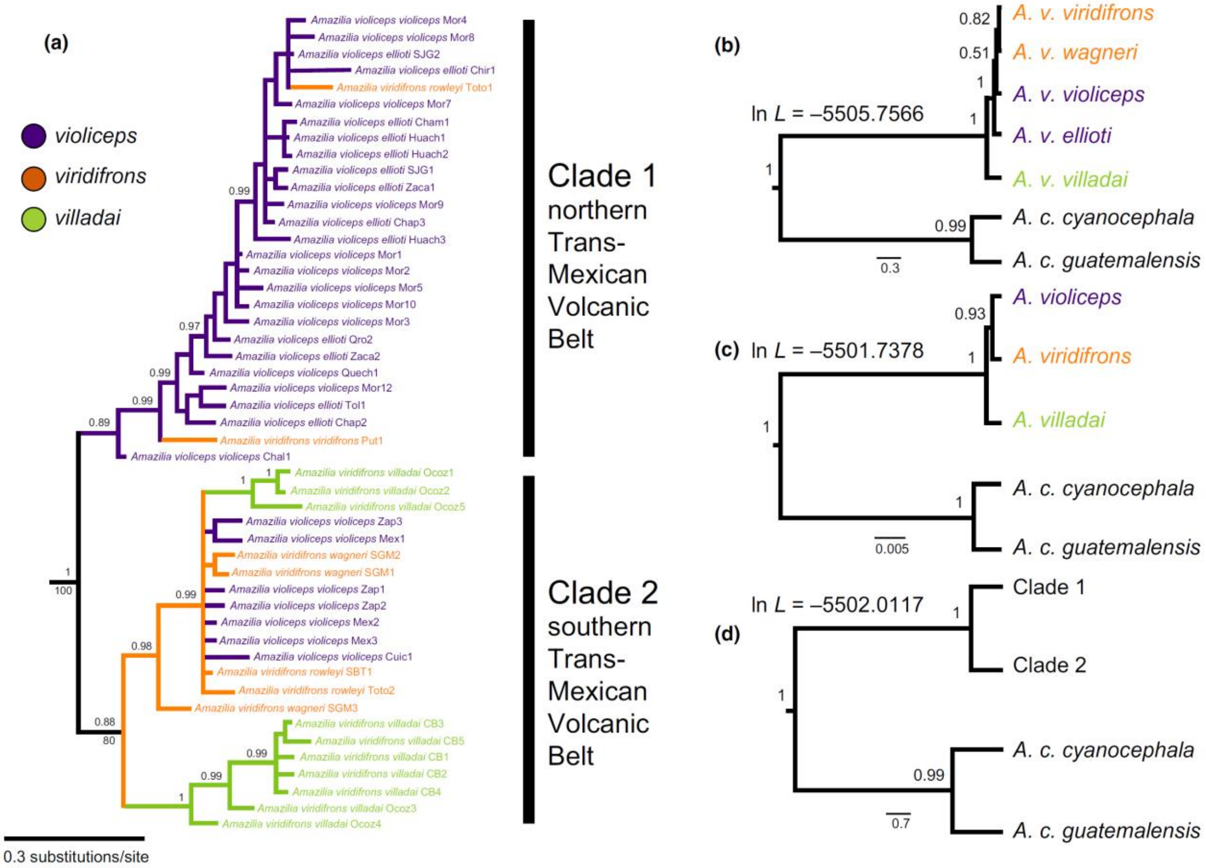


Figure 2 Illustration of tree topology based on multilocus DNA sequence data of *Amazilia violiceps* and *A. viridifrons*. (a) Bayesian posterior probabilities (PP) are shown above the branches and below are bootstrap values for the MrBayes analysis with data partitioned (see Appendix S1 for more details). Nodes were considered as highly supported when PP values of the Bayesian inference (BI) were ≥ 0.95 and bootstrap values of the maximum-likelihood (ML) analyses were ≥ 70. Results for the *BEAST analyses with individuals assigned by (b) subspecies of *A. violiceps* (*A. violiceps violiceps* and *A. violiceps ellioti*) and *A. viridifrons* (*A. viridifrons viridifrons*, *A. viridifrons wagneri* and *A. viridifrons villadai*), (c) three species (*A. violiceps*, *A. viridifrons* and *A. villadai*) or (d) by two species according to the BI and ML phylogenies (clade 1 and clade 2). Marginal-likelihood scores are indicated for *BEAST analyses (b–d). The likelihood scores under the three species delimitation hypotheses are compared with ln Bayes factors (BF) tests. The three-species hypothesis produced a higher likelihood score than those for the alternative hypotheses (2 × ln BF; five-species hypothesis versus three-species hypothesis = 8.037, five-species hypothesis versus two-species hypothesis = 7.488, two-species hypothesis versus three-species hypothesis = 0.547). ln L = marginal likelihood in natural log units.

Rodríguez-Gómez and Ornelas (2018) examined 95 samples from the species complex *A. violiceps* and *A. viridifrons*, using 10 microsatellites. Additionally, they analyzed four morphological measurements from 293 samples. The authors confirmed the differentiation of *A. v. villadai* from *A. violiceps* – A*. viridifrons* from the western side of the Isthmus of Tehuantepec (see their Figure 2 on the next page). Additionally, they found evidence of genetic admixture in most of the samples within the *viridifrons* group and some of the samples of the *violiceps* group. The morphological data showed that individuals of *villadai* have larger bills and longer wing chords, and that those of *violiceps* and *viridifrons* have longer tails.

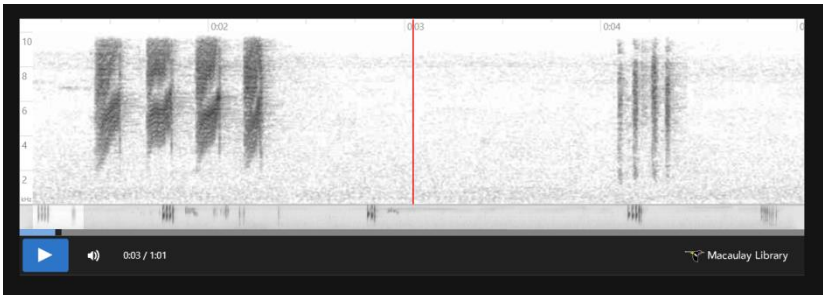
The authors grouped the sampling localities in three groups: *A. violiceps*, *A. viridifrons*, and *A. villadai*. However, following on previous publications, and the geographic ranges of the different subspecies within *A. viridifrons*, the subspecies included are as follows:

- *viridifrons*, n = 5, Oaxaca, Putla de Guerrero
- *rowleyi*, n = 10, Oaxaca, Santiago Matatlán and Totolapan
- *wagneri*, n = 7, Oaxaca, Pochutla and Miahutlán
- *villadai*, n = 10, Oaxaca, Cerro Baúl and Chiapas, Ocozocuautla

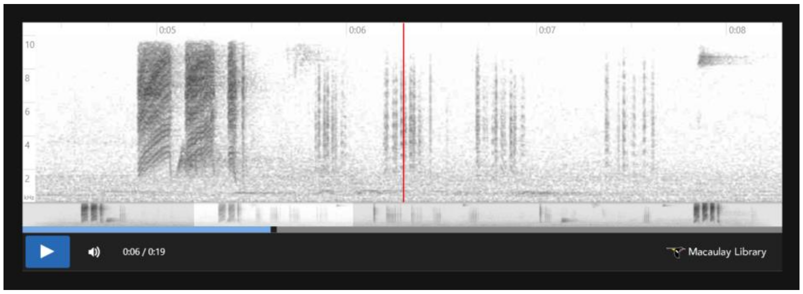
The subspecies *viridifrons*, *rowleyi*, and *wagneri* were grouped as *A. viridifrons*, and *villadai* was treated as a different group (Rodríguez-Gómez and Ornelas 2018). No genetic structure was found within *A. viridifrons.* Therefore, the results based on 10 microsatellites leave *wagneri* as genetically undistinguishable from *viridifrons* and *rowleyi*.

Sonograms from Macaulay Library:

Song recordings of *Leucolia viridifrons* are scarce. There are five recordings in the Macaulay Library (https://ebird.org/media/catalog?taxonCode=grfhum1&regionCode=&mediaType=a), one of them representing the only recording archived in xeno-canto. One of the recordings is from Chiapas and by geography it would correspond to *L. v. villadai*. Two of the recordings are assigned to *L. v. wagneri*, and the two additional recordings do not include subspecies and are listed as *L. viridifrons*. Below, I include one sonogram from *L. v. wagneri* and one sonogram from *L. viridifrons*, which was assigned to *L. v. viridifrons* in the Birds of the World webpage (https://birdsoftheworld.org/bow/species/grfhum1/cur/introduction). As noted by Howell and Webb (1995), the song and calls from both subspecies are very similar to the ear, although qualitative and quantitative analyses do not yet exist.



Leucolia viridifrons wagneri. Juquila, Oaxaca, Mexico. ML47719331. https://macaulaylibrary.org/asset/47719331



Leucolia viridifrons. Tlacolula, Oaxaca, Mexico. ML47719061.
https://macaulaylibrary.org/asset/47719061

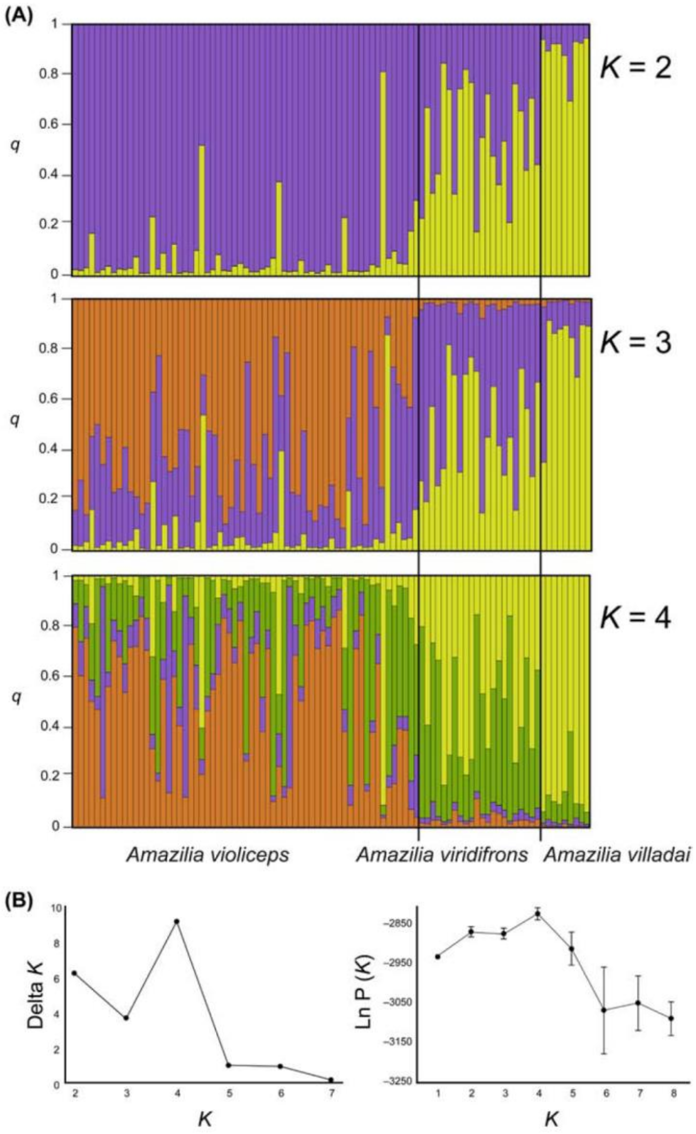


Figure 2. (A) Assignment probabilities of white-chested *Amazilia* species complex individuals to putative population clusters at K = 2, K = 3 and K = 4 using STRUCTURE. Each individual is represented by a vertical line that is partitioned into K coloured sections, with the length of each section proportional to the estimated membership coefficient. (B) Log-likelihood value of data, *Ln* P(*K*), as a function of *K* for 8 replicates and mean posterior probability values (Δ*K*) plotted against *K* (number of clusters) according to Evanno et al. (2005) suggesting K = 4.

Recommendation:

It appears that *wagneri* is distinguishable from *viridifrons* (*viridifrons* and *villadai*) by the striking cinnamon flanks and sides, and more subtly by other plumage traits (more rufous on wings, and tail). The genetic differences of *wagneri* from other subspecies and species in the *A. violiceps* – *A. viridifrons* species complex are not clear. Ten microsatellite loci do not allow for distinguishing *wagneri* from *viridifrons* and *rowleyi*. Additional research with more exhaustive sampling has been recommended. So far, I have not read anything about the importance of flank and side color for mate recognition, but with the extensive signature of genetic admixture it seems to be of low relevance. There is no evidence of sympatric breeding where *wagneri* overlaps *villadai*. The voice is very similar between *wagneri* and *viridifrons*, as described by Howell and Webb (1995). Therefore, my recommendation would be to NOT split *wagneri* from *viridifrons*.

English names:

If *wagneri* is split from *viridifrons*, *Leucolia viridifrons* can continue with the name “Green-fronted Hummingbird”. For *Leucolia wagneri*, the name “Cinnamon-sided Hummingbird” is already being used by checklists that consider it a separate species.

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Submitted by: Rosa Alicia Jiménez**,** Museum of Vertebrate Zoology – UC Berkeley and Escuela de Biología – Universidad de San Carlos de Guatemala

Date of Proposal: 11 October 2021

External comment on Proposal 2022-A-18

Green-fronted Hummingbird. Another case of genetics and morphology not aligning. I recall Chris Wood asking me about the Peterson and Navarro-Sigüenza (2000) paper, as he also has experience of these taxa in Mexico and found their paper rather at odds with the facts; P & N-S were completely confused about *rowleyi* and their map and range descriptions (e.g., for *rowleyi* and *villadai*) reveal their fundamental ignorance of biogeography in Oaxaca, admittedly a complex state, as well as sophistry vs fact in other statements, such as tail coloration. That said, they did seemingly ID the Chiapas birds as a valid taxon, distinct from populations west of the Isthmus, "clearly" a PSC species, presumably… And as to *wagneri*, still a flip-a-coin issue; I recall asking Phillips why *wagneri* was described as ssp but *Eupherusa cyanophrys* as a species, and he admitted it was rather arbitrary. For the new Mexico guide we treat both with equal uncertainty, as with Wedge-tailed Sabrewing, along with Amethyst-throated Mountain-gem and Berylline Hummer. Hence, provisionally (I have yet to critically investigate *villadai*):

***Green-fronted Hummingbird** *Leucolia (Amazilia) viridifrons* 10–11.5cm. Fairly large, white-bodied hummer of arid scrub, riparian woodland, subtropical forest edge, semi-open areas with hedgerows, scattered flowering trees. Feeds low to high, often at mid–upper levels in trees. Distinctive in most of range, with black-tipped red bill, bright white underparts, dark greenish crown; cf. possible overlap with Violet-crowned Hummingbird in sw. interior. Comprises 2 groups that may represent species: **Green-fronted Hummingbird** *L. [v.] viridifrons* in sw. interior and disjunctly e. of Isthmus; **Cinnamon-sided Hummingbird** *L. [v.] wagneri* of Sierra Madre del Sur in Oax. Typical Green-fronted has clean white underparts (some have buff wash to sides and flanks in interior Oax); tail purplish copper (male) to coppery green (female). Cinnamon-sided has distinct cinnamon mottling on sides of neck and breast; tail rusty chestnut (male) to bronzy gold (female). Imm. (all populations) has dingier underparts, extensively blackish maxilla.

Submitted by: Steve Howell

Date of comment: 23 November 2021

Split Black-billed Streamertail *Trochilus scitulus* from (Red-billed) Streamertail *T. polytmus*

Background

Endemic to Jamaica, the genus *Trochilus* as currently recognized on the *Check-list of North American Birds* (Chesser et al. 2020) consists of a single monotypic species, Streamertail (*Trochilus polytmus*). Two taxa, however, are recognized by most other global checklists, either as two subspecies as in the Clements Checklist (Clements et al. 2021), or as two distinct species, as in several other checklists (e.g., Dickinson and Remsen 2013, Collar and del Hoyo 2016, Gill et al. 2021). The two taxa are very similar and differ mostly in the color of the bill (Fig. 1), which is red in nominate *polytmus* (Red-billed Streamertail) and black in *scitulus* (Black-billed Streamertail). *Trochilus (polytmus) scitulus* appears to have been overlooked until described in 1901 from a series of *Trochilus* collected between 1890 and 1891 (Brewster and Bangs 1901). In describing the new species, Brewster and Bangs (1901), compared it to *polytmus*, noting its shorter, slenderer, and entirely black bill, shorter wings, and dark grass-green plumage on the rump, uppertail coverts, and wing coverts, where it lacked the coppery tones of *polytmus*. On the island of Jamaica, *polytmus* appears to be widespread across most of the island, whereas *scitulus* is only found on the extreme eastern end of the island, where it is mostly restricted to the John Crow Mountains. The two taxa come into contact in a very narrow area that is centered on the Rio Grande Valley, where they hybridize (Gill et al. 1973, Graves 2015, Judy 2018).

New Information

Graves (2015) and Judy (2018) studied hybridization between the two streamertail taxa. Graves (2015) developed a hybrid index based on bill color, and also used a series of morphological measurements to assess the prevalence of hybrids in Jamaica, and the respective ranges of the two taxa. Judy (2018), using some of the same specimens from Graves (2015), collected additional specimens from the area of contact, used the same hybrid index system and measured the same set of morphological characters, and also used microsatellite and GBS data to understand the genetics of the hybrid zone.

Using microsatellite markers, Judy (2018) found no significant levels of divergence between the two taxa and was unable to detect any genetic structure associated with the phenotypic differences. Analyses based on over 6,000 SNPs generated using genotyping by sequencing found similar results, with no clear genetic structure, although a discriminant analysis of principle components was able to resolve some structure between *scitulus*, *polytmus*, and their hybrids. Although no fixed differences were found in the sample of 6,000 SNPs, 23 SNPs did show significant allele frequency differences; using these loci, distinct genetic clusters that corresponded to the two taxa were found (Judy 2018).

Although the genetic differences were very slight between the two taxa, both studies found very narrow clines for bill color and bill width (Graves 2015), with the cline for bill color ranging from 2.2–3.74 km, and the cline for bill width ranging from 13.9–16.0 km (Fig. 2a; Judy 2018). The cline was narrower in males than in females. The width of the cline using data on genetic admixture was similarly narrow and was estimated to be 6.75 km wide (Fig 2b; Judy 2018). The clines for bill color, bill width, and genetic admixture were all coincident, and had the same cline center (Judy 2018). Dispersal distance is not known for *Trochilus* hummingbirds, but using a conservative dispersal distance of 1 km, Judy (2018) estimated that given the extremely narrow width of the hybrid zone, if there was no selection, then the hybrid zone should have formed less than five years ago. However, the hybrid zone appears to be stable, as hybrids were first documented nearly 70 years ago, and Gill et al. (1973) estimated the hybrid zone to be in approximately the same location it is currently in. Using an even more conservative dispersal distance of 180 m (the maximum distance pollen was moved in a study of pollen dispersal in Purple-throated Carib *Eulampis jugularis*; Gowda 2009), and the narrow width of the hybrid zone, if selection were not acting on these two *Trochilus* taxa, then the hybrid zone should have formed only 24 years ago (using a dispersal model developed by Barton and Gale (1993), where the width of the hybrid zone equals 2.5 * dispersal distance * √ time). Given the extremely narrow cline widths for genetic admixture and bill color and width, selection, whether due to some aspect of natural selection or sexual selection, must be very strong in this system. Indeed, the displays of males appear to emphasize their bill color (Gill 1973), suggesting that the differences in bill color between the two taxa are important in mate choice.

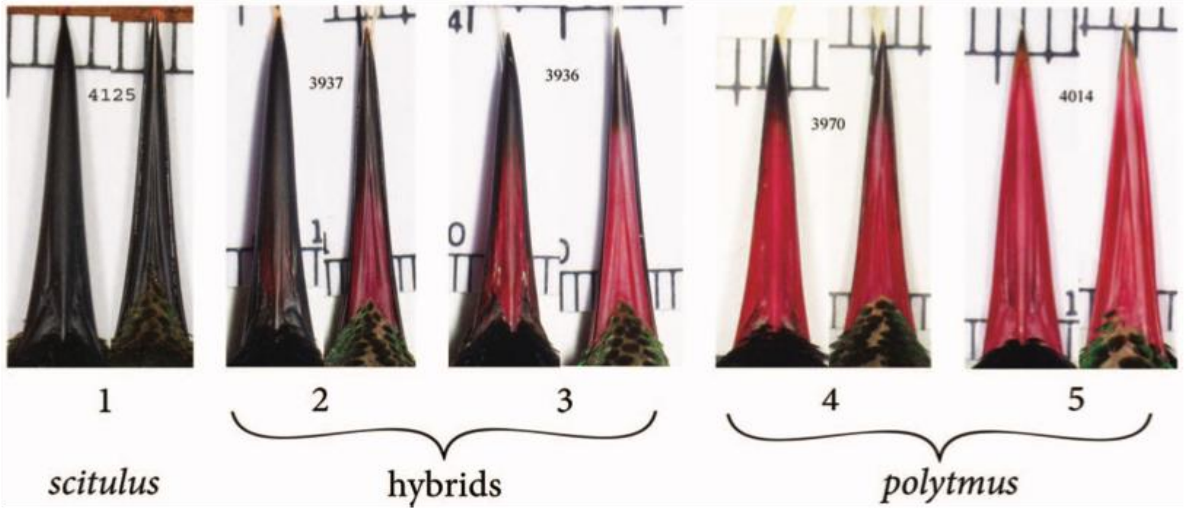

Figure 1. From Figure 1 of Graves (2015), showing bill color and widths of streamertails, categorized by their hybrid index based on bill color, with 1 representing *scitulus* and 4-5 representing *polytmus*.

Recommendation

Despite very low levels of genetic divergence, which is not even detectable in some analyses, hybridization between *scitulus* and *polytmus* appears limited. Given the stability of the hybrid zone over nearly 70 years, and the narrowness of the morphological and genetic clines, selection is clearly acting on these two taxa, and they do not form a freely and randomly breeding population. Given these data and analysis, I recommend voting to split Streamertail (*Trochilus polytmus*), into two species: Red-billed Streamertail (*Trochilus polytmus*) and Black-billed Streamertail (*Trochilus scitulus*). These English common names already have a long history of usage, and are currently the names used by the Howard and Moore Checklist (Dickinson and Remsen 2013) and the IOC Checklist (Gill et al. 2021).

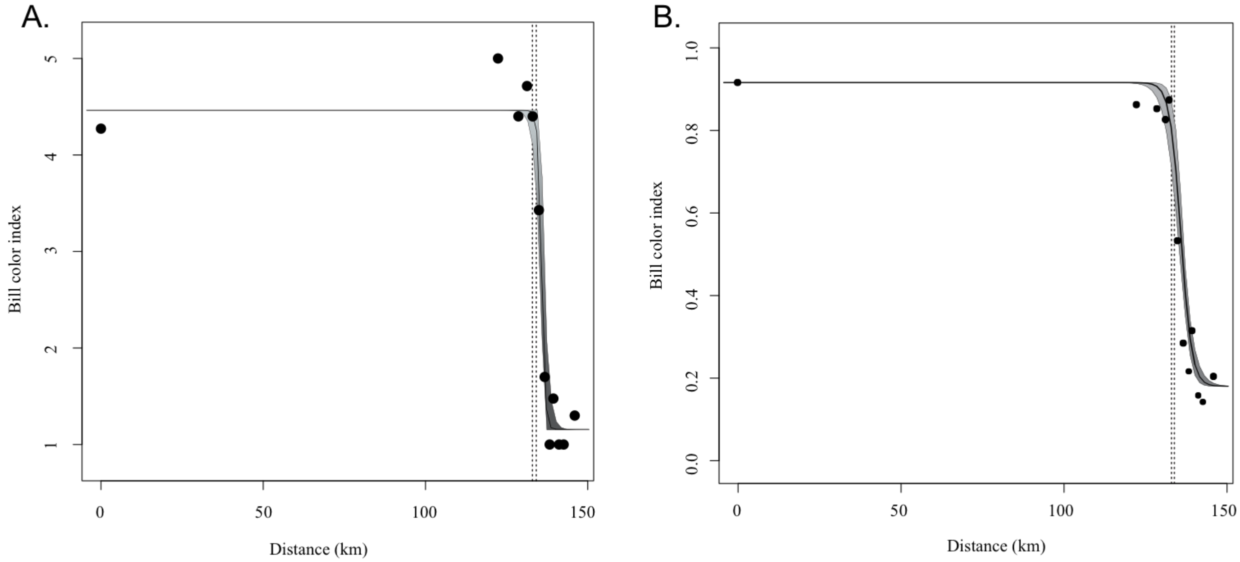

Figure 2. From Figure 3 of Judy (2018). A) Cline of bill color for male streamertails, with values of 4 and 5 representing *polytmus* and 1 representing *scitulus*. The cline for male bill color was 2.2 km, the gray shading represents the 95% confidence intervals, and the vertical dotted line represents the east and west boundaries of the Rio Grande River. B) Cline of genetic admixture for all individuals sampled, with 1 representing *polytmus* and 0 representing *scitulus*. The cline for genetic admixture was 6.75 km, the gray shading represents the 95% confidence intervals, and the vertical dotted line represents the east and west boundaries of the Rio Grande River.

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Submitted by: Shawn M. Billerman

Date of Proposal: 11 October 2021

Split *Cynanthus latirostris* (Broad-billed Hummingbird) into three species

Effect on NACC:

Acceptance of this proposal would split *Cynanthus latirostris*, with *C. latirostris*, *C. lawrencei,* and *C. doubledayi* as separate species. This would add two species to the NACC area.

Background:

Cynanthus latirostris is a member of a subclade of Mesoamerican emerald hummingbirds (Aves: Trochilidae: Trochilini), restricted to the west coast of Mexico and the Tres Marías Islands. The emeralds comprise about 30% of all hummingbird species and are one of the groups in which reconciling phylogeny with taxonomy has proved challenging (Bleiweiss et al. 1997; Bleiweiss 1998a, b; Schuchmann 1999; McGuire et al. 2007, 2009, 2014). A multilocus molecular study distinguished two large groups within the emeralds (McGuire et al 2014); one of them is composed of *Cynanthus*, *Cyanophaia*, and *Chlorostilbon*, three genera showing relatively limited phenotypic variation.

C. latirostris, C. doubledayi, and *C. lawrencei* were considered separate species by Ridgway (1911) and Cory (1918), but all were lumped with *latirostris* by Peters (1945) without comment. More recent authors have recognized *C. latirostris doubledayi* as a separate species (Schuchmann 1999; García-Deras et al. 2008; Gill & Donsker 2019, Hernández-Baños et al. 2020).

García-Deras et al. (2008) used partial sequences of the mitochondrial gene ND2 and three phylogenetic approaches (maximum parsimony, maximum likelihood, and Bayesian inference) and provided support for the validity of *C. doubledayi* as a species.

McGuire et al. (2014) using multilocus data, found that *Cynanthus sordidus* is sister to a clade comprising three genera (*Cynanthus*, *Chlorostilbon*, and *Cyanophaia*), that the species from the West Indies are monophyletic, that the South America species (except *Chlorostilbon. assimilis*) are closely related to the two Mesoamerican species (*Cynanthus latirostris* and *Chlorostilbon canivetii*), and that *Cynanthus latirostris doubledayi* is the sister of *Chlorostilbon canivetii*.

Description of the taxa:

Cynanthus l. latirostris is widespread throughout most of mainland Mexico, excluding the Balsas River drainage and coastal southwest Mexico where it is replaced by *C. sordidus* and *doubledayi*, respectively. It ranges into the southwestern USA. *C. latirostris* contains three subspecies (aside from *lawrencei* and *doubledayi*). *C. l. magicus* of western Mexico south to Colima is relatively small with a paler vent and intermediate extent of blue on the throat. The majority of interior Mexico is divided between nominate *latirostris* in the northern half and *propinquus* in the southern half (Powers & Wethington 2021). *C. l. propinquus* is darker with more extensive blue below.

Cynanthus l. lawrencei is endemic to the Tres Marias Islands off the coast of northwestern Mexico. In comparison to *latirostris* it has a green throat (rather than blue) and is smaller. Ridgway (1911) provided this description of its morphological distinction from *latirostris*: "Similar to *C. latirostris* but smaller, with shorter bill; adult male with chin and throat slightly bluish green (never blue), back and rump more bronzy, and under tail-coverts dusky centrally; adult female with basal half (more or less) of lateral rectrices brownish gray instead of bronze-green and middle rectrices darker and much duller bronze-green."

Cynanthus l. doubledayi is endemic to the coastal plain of southwestern Mexico from western Guerrero, Oaxaca, and, probably, to the western part of Chiapas (Howell & Webb 1995; Navarro & Peterson 1999; Schuchmann 1999, Dickinson 2003). *C. l. doubledayi* is similar overall to *C. l. latirostris* but the forehead of the male is iridescent turquoise blue, the throat is deeper violet-blue, the under parts are generally bluer and the undertail coverts are black (Montes de Oca 1875; Ridgway 1911; Berlioz 1937; Moore1939; Howell & Webb 1995; Navarro & Peterson 1999; Schuchmann 1999).

Ridgway (1911) first placed *doubledayi* in the genus *Cynanthus* and later authors included it as a subspecies of *C. latirostris* (Peters 1945; Friedmann et al. 1950; Schuchmann 1999; Dickinson 2003), although Howell & Webb (1995) and Navarro & Peterson (1999) suggested that *C. doubledayi* is a separate species.

The next three photos on the following pages show the four subspecies of *latirostris* (*sensu stricto*), *doubledayi*, and *auriceps* (the sister taxon of *doubledayi*) in the following order left-to-right: 2 *magicus*, 2 *latirostris*, 1 *propinquus*, 1 "*toroi*" (= *propinquus*), 2 *doubledayi*, 1 *auriceps*.


LOUISIANA STATE UNIVERSITY 228158 MUSEUM OF ZOOLOGY
ARIZONA: Santa Cruz Co.: Santa Rita Mountains, Forest Service Road 143, 7.5 mi ENE Tubac. 31.651°N, 110.927°W, 4410 ft.
23 July 2019
Matthew L. Brady 900
♂
3960
♂
1950
LA. STATE UNIV. 16844 MUSEUM OF ZOOLOGY
MEXICO
1951
LA. STATE UNIV. 16848 MUSEUM OF ZOOLOGY
Mexico; S.L.P., Bledos
18 May 1951 J. Graber
R.R.G. 1242
♂
COL. NO.
11018
Mexico: Guanajuato; 3 mi NE Irapuato, 5600 ft.
COLLECTION OF W. J. SHEFFLER
Gift from William J. Sheffler
406 W. George
Michoacan, Mexico
15 June, 1957
LA. STATE UNIV. 33088 MUSEUM OF ZOOLOGY
MEXICO; Oaxaca: 9 mi WNW Estancia Grande, 300'
18 February 1964 L.C. Binford # 895
♂
LA. STATE UNIV. 33087 MUSEUM OF ZOOLOGY
MEXICO; Oaxaca: 4 mi SE Puerto Escondido
4 March 1964 L.C. Binford # 951
♂
COL. NO.
10203
Mexico: Jalisco; La Cumbre, 9 mi SSW Autlan
COLLECTION OF W. J. SHEFFLER


This photo of two *latirostris* and to two *doubledayi* shows the iridescent crown of the latter:

The following four photos show specimens of *lawrencei* from the UNAM collections (Museo de Zoología, Facultad de Ciencias):

Females

Males


ITM 212
ITM 221
19204
MZFC Colección
Cynanthus la
México, Nayarit
Campamento
21° 37'
319
ITM 158
ITM 227
19194

The photos and specimens show that *doubledayi* is a notably small bird in comparison with *latirostris* and strikingly bluer below and to a lesser degree on the crown. Taxon *lawrencei* does appear to show less blue on the underparts than does *latirostris*. It would be good to check this on specimens. Searching for other differences, the eye spot may also be reduced in *lawrencei*.

New information:

Hernández-Baños et al. (2020) provided new evidence with a multilocus study of a clade of emeralds. They found that this group originated in Mesoamerica about 12 million years ago and comprises four geographically congruent clades (see tree on next page). One of these is a widespread Mexican clade that includes a subclade restricted to the west coast of Mexico and the Tres Marías Island, composed of *C. latirostris* and *C. lawrencei*. On the other hand, *C. doubledayi* and *C. auriceps,* both from the western coast of Mexico, are in fact sister species included in a Mesoamerican clade.

Methods of Hernández-Baños et al. (2020):
A concatenated dataset of 4,612 base pairs was obtained for 96 individual including outgroups, the best-fit models for each molecular marker were: GTR+G+I (ND2, ND4); TPM2uf (MUSK); TPM1uf+G (AK1); TVM+G (Bfib); and HKY+G (ODC). They found a significant genetic differentiation between *Riccordia bicolor* and *Cynanthus* and *Chlorostilbon* (values between 0.076 and 0.103), but in contrast observed lower values between *C. lawrencei* and *C. latirostris* (0.004), and between *C. canivetii* and *C. forficatus* (0.005), as expected.

Summary and contextualization of new findings:
Hernández-Baños et al. (2020) identified two sub-groups within the Mesoamerican clade. The first group includes two species inhabiting arid and semiarid regions associated with dry forests: *Cynanthus latirostris* is found in central and north-western Mexico up to a small area in southwestern USA, whereas the closely related *C. lawrencei* is restricted to the Tres Marías Islands (García-Deras et al. 2008) and likely originated from mainland *C. latirostris* individuals that colonized the islands. The second subgroup contains two branches, one including two species distributed in the west coast of Mexico*, C. auriceps* and *C. doubledayi*, and the second containing *C. canivetii* and *C. forficatus*.

The subclade of emerald hummingbirds shows that the diversification of the group is the product of several factors. First, the complex geological history of the region, with its numerous geographic barriers, likely contributed to the isolation and differentiation of populations during the evolutionary history of the group. Second, their ability to colonize islands has resulted in a number of single-island endemics, such as those of the West Indies, *C. lawrencei* in the Tres Marías Islands and *C. forficatus* in Cozumel Island. Finally, their ability to occupy new ecological niches allowed some populations to invade environments that differed from the original lowland dry forest of the ancestral *Phaeoptila*, giving rise to the Central and South American group that today inhabits higher-elevation humid forests. Despite this complex evolutionary history,

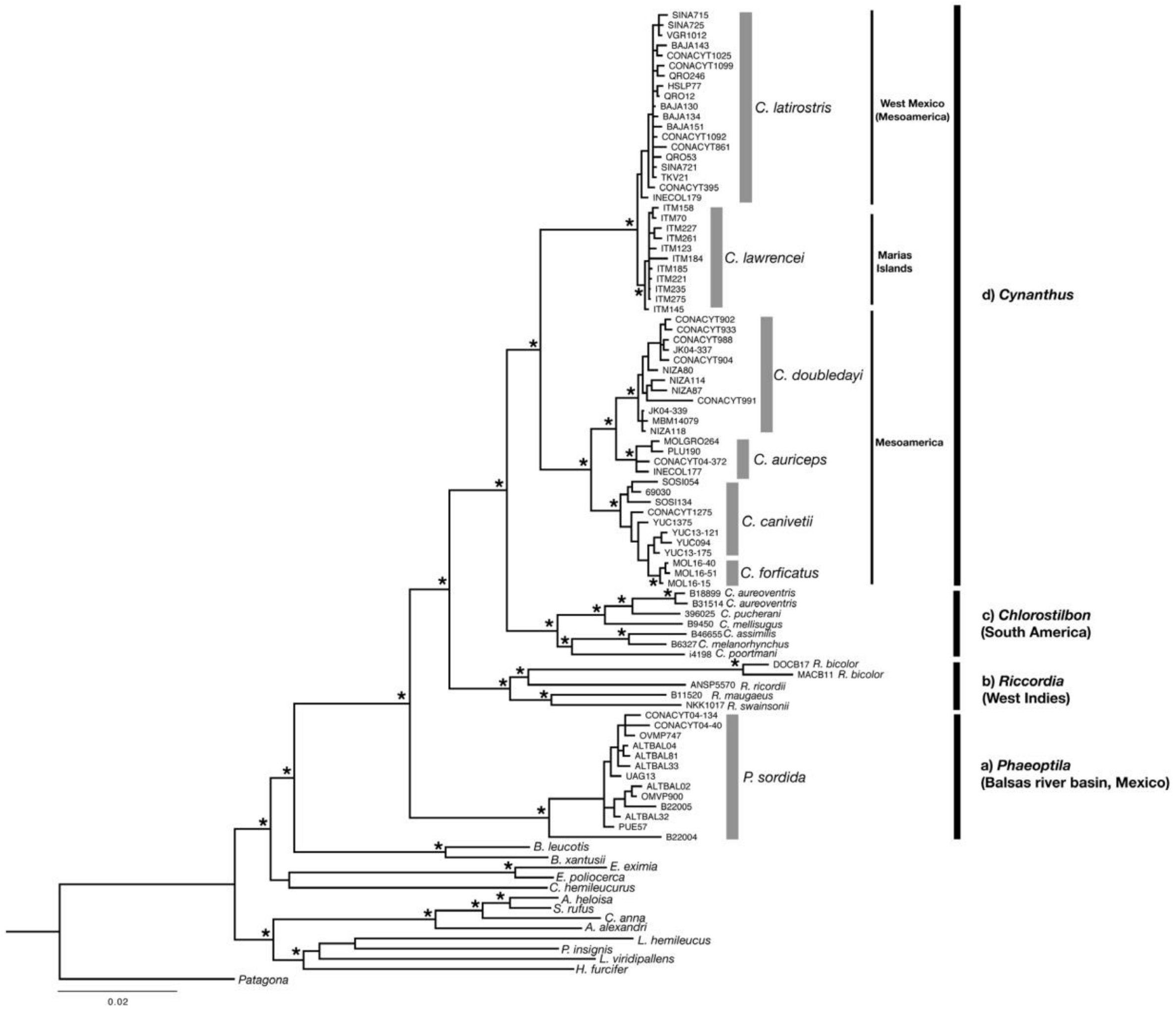

Figure 1: Phylogenetic Bayesian Inference reconstruction of *Cynanthus*, *Chlorostilbon* and *Cyanophaia* species using mitochondrial and nuclear markers (ND2, ND4, Bfib, ODC and MUSK). Asterisks indicate posterior probabilities of node support > 0.95

phenotypic differences among species in emeralds have remained relatively small. This, combined with likely cases of convergence and rapid divergence in plumage coloration and shape, have often misled earlier inferences of evolutionary relationships and caused considerable taxonomic confusion.

Because *doubledayi* is sister to *Cynanthus auriceps* and unrelated to *latirostris*, the split of *doubledayi* is fairly straightforward. The only confounding factor would be rampant gene flow between *auriceps* and *doubledayi*, which would affect the phylogenetic branching pattern, but this seems unlikely given that the two species are broadly sympatric, and males at least are consistently distinct morphologically. This split was recognized by Clements et al. (2021).

The split of *lawrencei* from *latirostris* is more of a borderline case, given that *lawrencei* is a recently diverged island form clearly allied with *latirostris*. However, the NACC treats a similar borderline case, *Cynanthus forficatus*, as a species. The divergence time of *lawrencei* and *latirostris,* 2.15 Mya (1.32–3.03), is a bit older than that of *forficatus* from the most closely related populations of *canivetii*, 1.19 Mya (0.53–1.94).

Please vote on the following two proposals:
(a) split *doubledayi* from *latirostris*
(b) split *lawrencei* from *latirostris*

Recommendation:

We recommend splitting *Cynanthus latirostris* into three species: *C. latirostris*, *C. lawrencei* and *C. doubledayi*. This is based on phylogenetic evidence and some differences in plumage color.

English names:

Broad-billed Hummingbird has long been used for *Cynanthus latirostris* and *doubledayi* and *lawrencei* are peripheral range isolates, so this well-established name should stay with *latirostris*.

Turquoise-crowned Hummingbird has been used for *Cynanthus doubledayi* in recent treatments (e.g. Clements et al. 2021).

Tres Marías Hummingbird has been used for *Cynanthus lawrencei* of the Tres Marías Islands, Sinaloa (Clements et al. 2021), and highlights the restricted distribution of this taxon.

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Submitted by: Blanca E. Hernández-Baños, Universidad Nacional Autónoma de México, and Oscar Johnson, Louisiana State University

Date of proposal: 11 October 2021

2022-A-21 N&MA Classification Committee pp. 304-305

Split *Lampornis cinereicauda* from White-throated Mountain-gem *L. castaneoventris*

Effect on NACC:

Acceptance of this proposal would split *Lampornis castaneoventris* to recognize *Lampornis cinereicauda* as a separate species, which would add one species to the NACC area.

Background:

Species limits among mountain-gems in the genus *Lampornis* have been contentious for decades. Specifically, the species status of three taxa that comprise the "Variable Mountain-gem" species complex have eluded consensus: Purple-throated Mountain-gem (*L. calolaemus*), "Blue-tailed" Mountain-gem (*L. castaneoventris castaneoventris*), and "Gray-tailed" Mountain-gem (*L. castaneoventris cinereicauda*) (Fig. 1). These taxa are distributed from southern Nicaragua to central Panama (NW to SE: *pectoralis, calolaemus*, *cinereicauda*, *castaneoventris*, *homogenes*.

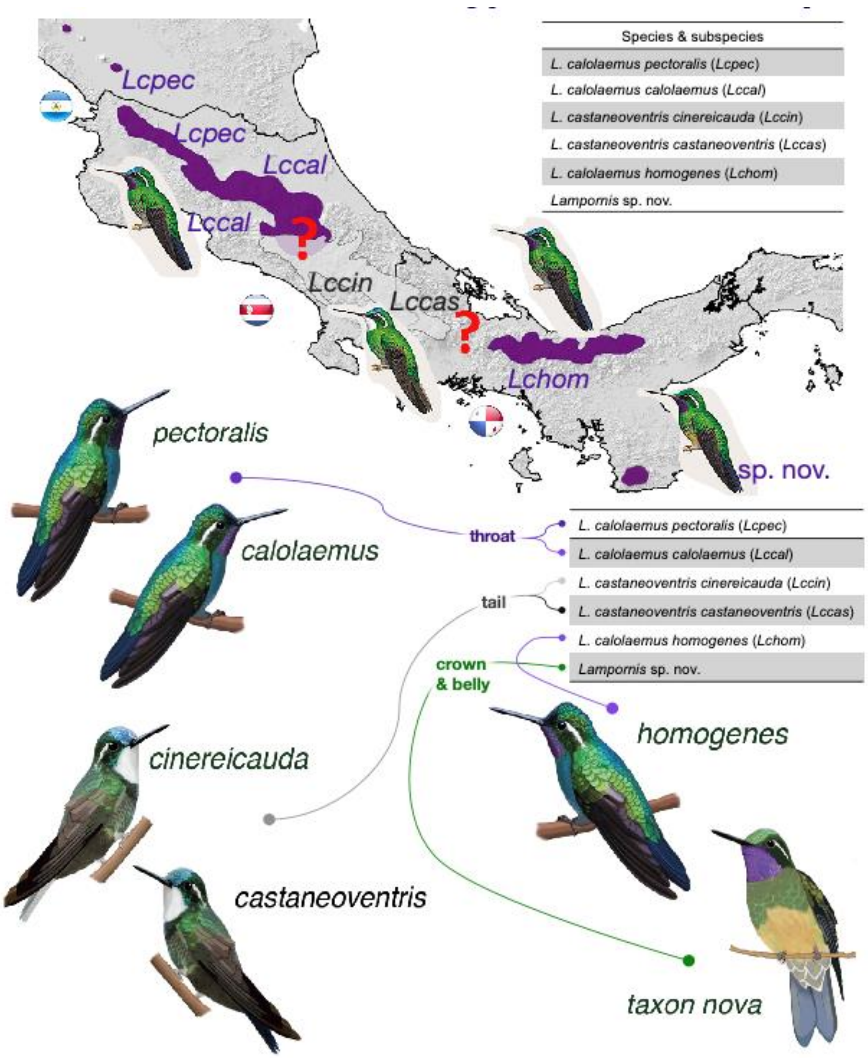


Figure 1: Distribution and phenotypic variation within the "Variable Mountain-gem" species complex. Note that *L. castaneoventris* is geographically located in between the different subspecies of *L. calolaemus*. This also includes a separate population *Lampornis sp. nov.* not discussed in this proposal. Taken from Rosas and Miller (unpublished).

<u>calolaemus vs castaneoventris/cinereicauda</u>

The NACC recognized *L. calolaemus* as a separate species from *L. castaneoventris castaneoventris* and *L. castaneoventris cinereicauda* (but maintained the latter two as conspecific) in the 6th edition of the AOU Checklist (American Ornithologists Union 1983). The AOU's (1983) rationale for this split is as follows…

> some introgression occurs in areas where both [*L. calolaemus* and *L. castaneoventris*] are found, although they tend to maintain their distinctness. Until the matter is resolved, it seems best to treat the forms as separate species with limited hybridization in the areas of sympatry.

<u>castaneoventris vs cinereicauda</u>

Recently, the IOC decided to split *L. castaneoventris cinereicauda* and *L. castaneoventris castaneoventris* citing Stiles and Skutch (1989) as rationale. Stiles and Skutch (1989) stated:

> We believe [*L. calolaemus*, *L. castaneoventris cinereicauda*, and *L. castaneoventris castaneoventris*] should be given the same taxonomic treatment, whether as allospecies of a superspecies or as subspecies of a single species. Without further data (difficult to obtain because of extensive deforestation in most of the critical contact zones), choice between these alternative treatments is arbitrary.

The Handbook of Birds of the World and Birdlife International also recognized three species within the Variable Mountain-gem complex based on phenotypic and distribution differences in line with the "seven-point system" (Tobias et al. 2010). Specifically, they stated:

> Classification unstable; [*cinereicauda*] is commonly treated as conspecific with *L. calolaemus* and *L. castaneoventris*, but, while females of all taxa are very similar, combination of highly distinctive male plumages and parapatric distributions, along with observations that where white-throated and purple-throated forms occur on the same slopes they tend to segregate altitudinally (white-throated higher), suggests species status more appropriate; hybridization is very limited, and many previous reports of hybrids may refer to young birds. Thus, *cinereicauda* achieves species status, distinct from *castaneoventris* by its blue vs green forecrown (3), grey vs dark blue tail (3) and parapatry (3), and from *calolaemus* by its white vs purple throat (3), grey vs dark blue tail (3) and parapatry (3).

Although there are phenotypically differentiated parapatric assemblages in this group, little is known about hybridization and introgression at contact zones. Below, I summarize some new, unpublished information on this complex that may help in reaching a decision. Note that much of this new information is derived from a student presentation that has not been subject to peer review.

New information:

This proposal is in response to the reconciliation of major global checklists rather than the publication of new information on the subject. That said, various more recent papers on the Variable Mountain-gem complex, published since Skutch and Stiles (1989), are worth reviewing. García-Moreno et al. (2006) published a phylogeny of the genus *Lampornis* that included mtDNA (cyt *b* and ND5) and two nuclear genes (AK-5 intron and c-mos). García-Moreno et al. (2006) found that *calolaemus*, *castaneoventris*, and *cinereicauda* all form a clade, but were unable to resolve relationships among them (Fig. 2).

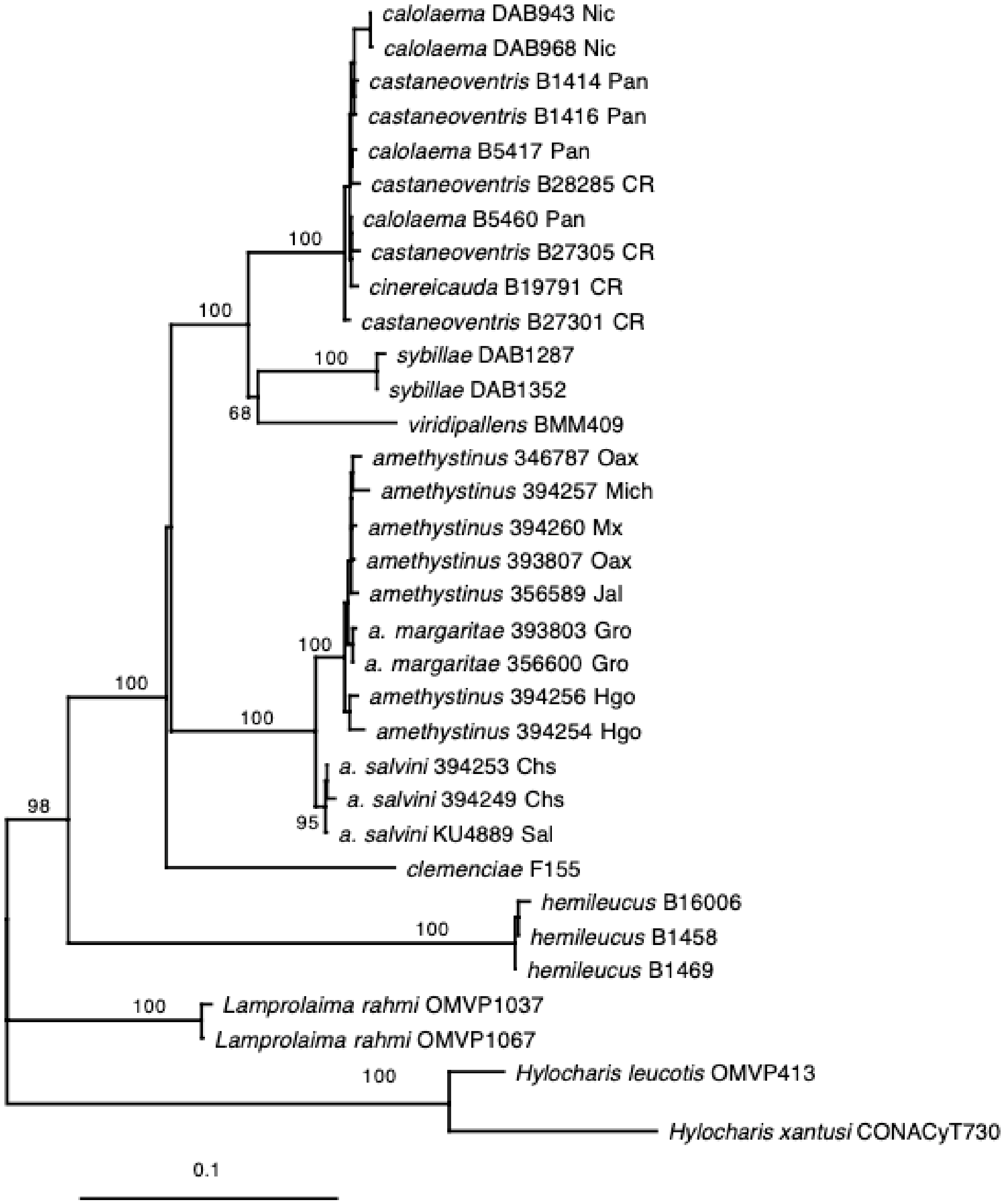


Figure 2: Phylogeny from García-Moreno et al. (2006) showing lack of support for monophyletic groups corresponding to taxa within the Variable Mountain-gem complex.

This result was recapitulated in the family-level phylogeny of hummingbirds by McGuire et al. (2014; Fig. 3):

Figure 3. Phylogeny from McGuire et al. (2014) showing polytomy and unresolved relationships corresponding to the Variable Mountain-gem complex.

Rosas and Miller (unpublished) conducted a set of analyses to further investigate genetic and phenotypic differentiation within the complex. They found no morphometric differentiation among currently recognized subspecies (Fig. 4). Rosas and Miller (unpublished) also uncovered similarity in ecological niche models (Fig. 5). They also conducted a species-tree analysis and found that *calolaemus* is paraphyletic as currently described (Fig. 6).

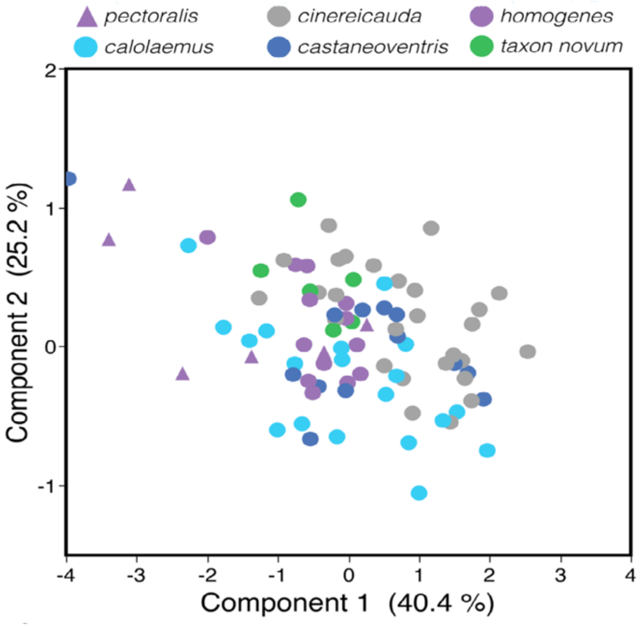


Figure 4: PCA on morphometric characters of taxa within the Variable Mountain-gem Complex. Taken from Rosas and Miller (unpublished).

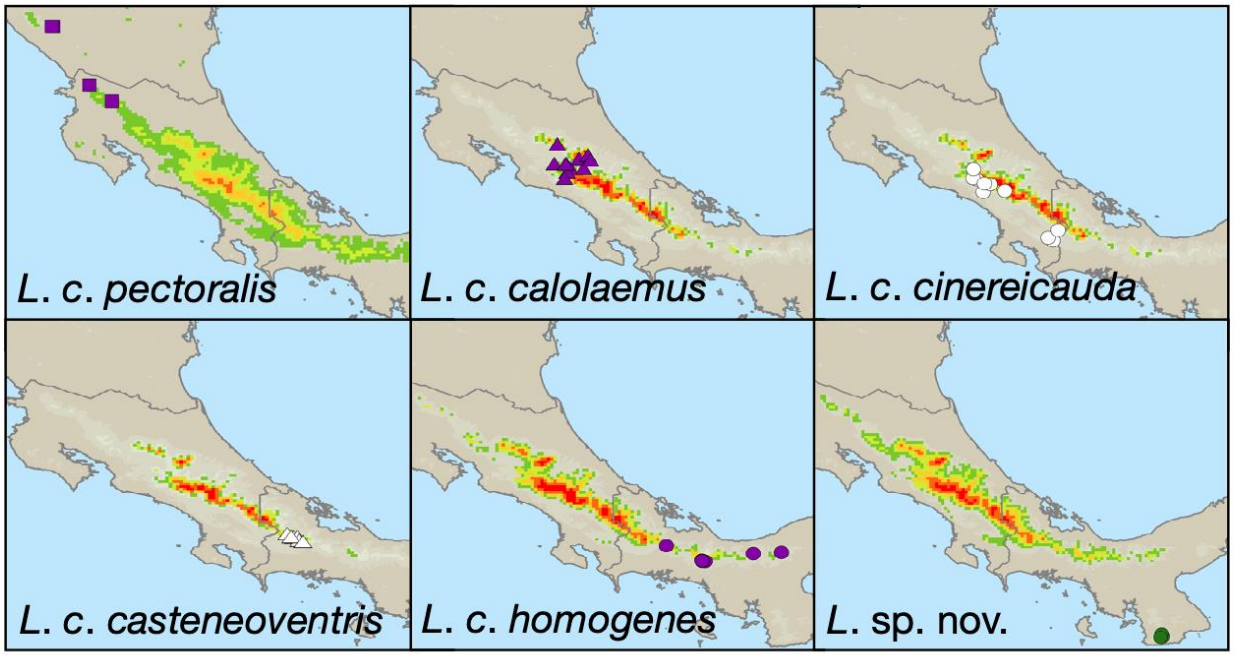


Figure 5: Ecological niche models generated for taxa within the Variable Mountain-gem complex showing what appears to be considerable overlap in abiotic conditions among ecological niche models. Taken from Rosas and Miller (unpublished).

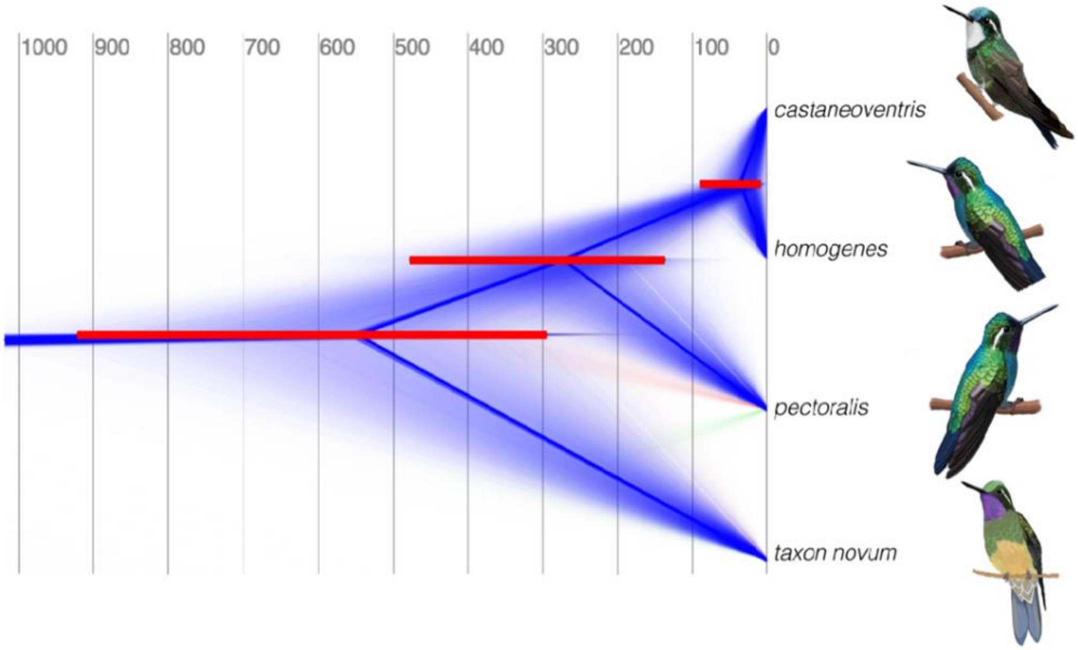
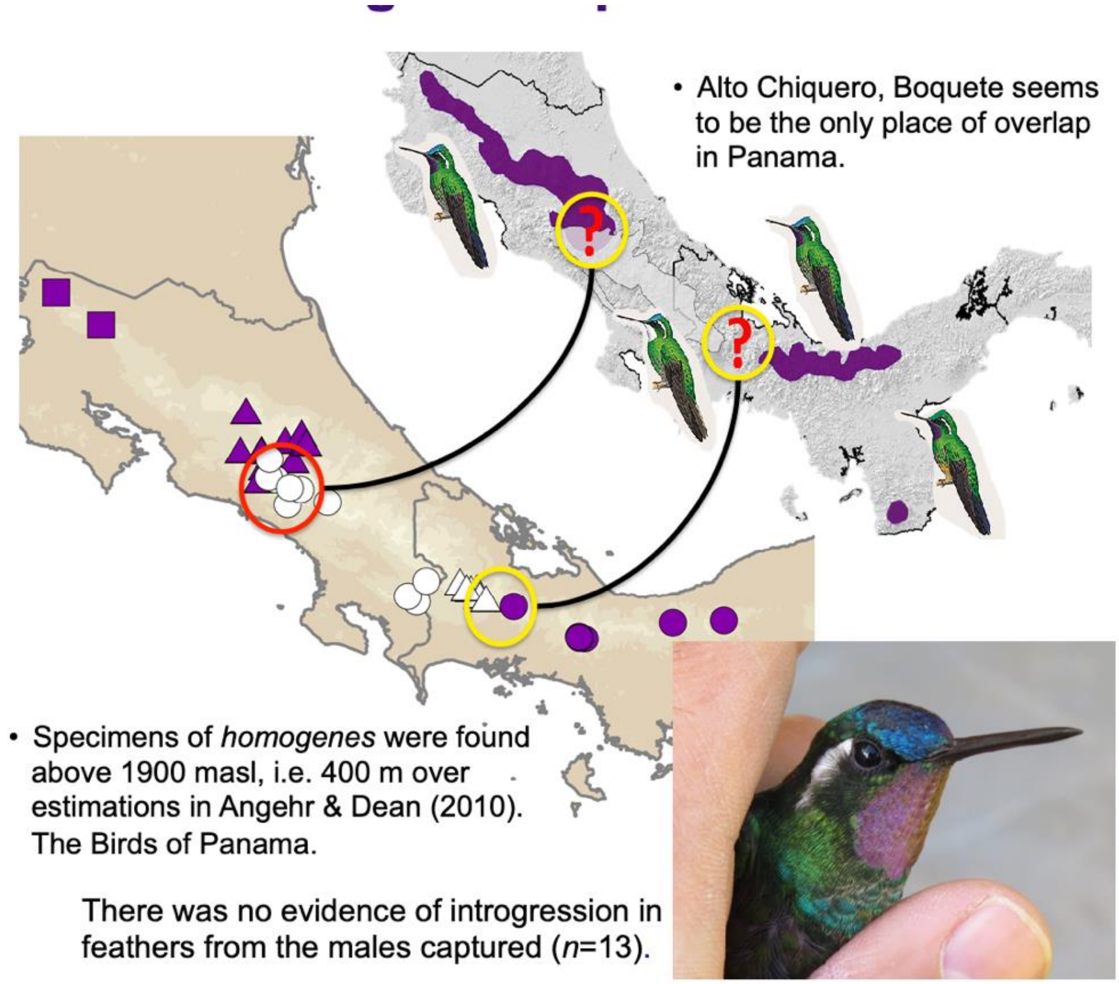


Figure 6: Species tree analysis of taxa in the Variable Mountain-gem group (*castaneoventris*, *calolaemus homogenes*, *calolaemus pectoralis*, and *taxon novum*) based on one mitochondrial and two nuclear markers. Taken from Rosas and Miller (unpublished).

Although hybridization among these taxa has been reported, the level of hybridization remains unknown and has not yet been examined with rigorous genomic methods. However, there is some anecdotal evidence of ecological displacement between purple and white-throated forms (Fig. 7):



- Alto Chiquero, Boquete seems to be the only place of overlap in Panama.

- Specimens of *homogenes* were found above 1900 masl, i.e. 400 m over estimations in Angehr & Dean (2010). The Birds of Panama.

There was no evidence of introgression in feathers from the males captured (*n*=13).

Figure 7: Evidence of ecological character displacement between purple and white-throated taxa within the Variable Mountain-gem complex. Taken from Rosas and Miller (unpublished).

Recommendation:

We still lack rigorous analyses of potential admixture and introgression from contact zones among taxa within this complex. Although phenotypic differences are pronounced among males, it is still not clear whether these influence gene flow and patterns of reproductive isolation. Given the data at hand, I see three possible solutions:

1. Split *L. cinereicauda* from *L. castaneoventris*.

This split would be based entirely on differences in male coloration that are roughly parapatric, but we have no data on patterns of gene flow or admixture where these taxa overlap.

2. Lump *cinereicauda*, *castaneoventris*, and *calolaemus* into a single polytypic species (*L. castaneoventris*)

   This is a viable alternative given the data at hand and the lack of genetic differentiation in the small number of mtDNA and nuDNA markers examined thus far.

3. Split *L. homogenes* from *L. calolaemus* in addition to splitting *L. cinereicauda* from *L. castaneoventris*.

   This would be the most "fine-scale" taxonomic of the species complex, reflecting the topology recovered by Rosas and Miller (unpublished) and may make sense in light of the geographic proximity and relatedness of *L. homogenes* to *L. castaneoventris*.

Until more data are collected, choosing among these alternatives is arbitrary and, in my opinion, premature. I therefore recommend a NO vote on splitting *L. cinereicauda* from *L. castaneoventris*. I personally favor lumping all of these into a broadly defined, polytypic species until a detailed study is conducted.

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Submitted by: Nicholas A. Mason

Date of proposal: 20 October 2021

External comment on Proposal 2022-A-21

Variable Mountain-gem, what a mess, a bit like Green-fronted Hummingbird with 2 similar (in this case Purple-throated) populations separated by something different. Our Costa Rica guide appendix is suitably vague:

Gray-tailed (White-throated) [Variable] Mountain-gem *Lampornis [castaneoventris] cinereicauda* and **Purple-throated [Variable] Mountain-gem** *Lampornis [castaneoventris] calolaemus* (p. XXX). Taxonomy of the appropriately named Variable Mountain-gem *Lampornis castaneoventris* complex remains unresolved, with 6 taxa involved, one of them formally undescribed (Miller & Rosas, unpubl. data). The main differences are in male gorget and tail color. One option is to lump all taxa into a single variable species; another is to treat various taxa as distinct, which we do here for the 2 main types occurring in Costa Rica, as also done provisionally by Stiles & Skutch (1989).

Submitted by: Steve Howell

Date of comment: 23 November 2021