AOS Classification Committee – North and Middle America

Proposal Set 2025-C

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Revise the generic limits of Accipiter

Background:

The genus *Accipiter* was until recently the largest genus in Accipitridae, with 46–50 species (Dickinson and Remsen 2013, del Hoyo and Collar 2014, Clements et al. 2023, Gill et al. 2024) that occur on all continents except Antarctica. The genus was considered to typically consist of forest species that had relatively short and broad wings, long tails, and relatively long, thin, unfeathered tarsi. In terms of plumage, there was a fair amount of variation, but many species had superficially similar coloration with grayish upperparts, some amount of reddish or orange vermiculation below, and banded tails. Despite these apparent morphological similarities, molecular phylogenetic research suggests that the genus *Accipiter* was not a monophyletic group (e.g., Griffiths et al. 2007, Hugall and Stuart-Fox 2012, Oatley et al. 2015, Mindell et al. 2018). In 2024, WGAC voted to break *Accipiter* into 5 genera, following the recommendations of Catanach et al. (2024); this was followed by Clements et al. (2024) and the IOC World Bird List (Gill et al. 2025). The AOS Checklist has not yet considered these changes to the genus *Accipiter*, still recognizing the expanded view of the genus.

Morphological convergence across Accipitridae and even Accipitriformes has long confused our understanding of the relationships among hawks, eagles, and other diurnal raptors. Perhaps the best example of this is the finding that the falcons and caracaras (Falconidae) are not actually closely related to the hawks and eagles (Accipitridae), something first suggested by Jollie (1977) but not adopted until large-scale genetic studies found that Falconidae was actually more closely related to the parrots (Psittaciformes) and songbirds (Passeriformes) than to the rest of the diurnal raptors (e.g., Hackett et al. 2008, Jarvis et al. 2014, Prum et al. 2015). In another striking case of convergence within Accipitridae, the "kite" form has apparently evolved multiple times, with for example the Ictinia kites sister to the large radiation of Buteo and Buteo-like hawks, the Swallow-tailed Kite (Elanoides forficatus) being closely related to the honeybuzzards (Pernis, Henicopernis), as well as the Square-tailed Kite (Lophoictinia isura) and Black-breasted Kite (Hamirostra melanosternon), whereas the genera Elanus, Gampsonyx, and Chelictinia are a separate clade that is sister to the rest of Accipitridae (Mindell et al. 2018, Catanach et al. 2024). Although the convergence of these birds has been recognized for some time (historically all kites have been grouped or listed together, e.g., Stresemann and Amadon 1979), it highlights how convergence within Accipitriformes can be confusing.

New Information:

Although studies have shown that the genus *Accipiter* is not monophyletic, it was a long time before any taxonomic authority began to revise generic limits. This was in part due to poor taxonomic sampling of the genus and potential closely related taxa (e.g., Griffiths et al. 2007, Oatley et al. 2015, Mindell et al. 2018), with action not taken out of concern that additionally sampled taxa would affect the topology of the phylogeny and thus require further change and instability to the nomenclature and taxonomy of the group. Catanach et al. (2024) used ultraconserved elements (UCEs) and broad taxon sampling that covered 90% of recognized species in Accipitridae to overcome the shortcomings of other studies, to primarily address the

non-monophyly of *Accipiter*. In the study, Catanach et al. (2024) combined whole genome sequence data, UCE data, as well as sequence data from traditional Sanger sequencing approaches to generate their species tree. The results of the tree largely corroborate what had been found in earlier studies, albeit with much greater support and more importantly, more complete taxon sampling that allows the full scale of the paraphyly of *Accipiter* to be realized.

Across their well-supported phylogeny, where only 5 nodes did not receive 100% bootstrap support, the genus *Accipiter* was found to form 5 distinct clades (see Figure 1, below). Most of the five clades identified by Catanach et al. (2024) are not each other's closest relatives, and instead are successively sister, with other smaller genera (i.e., *Circus*, *Megatriorchis*, *Erythrotriorchis*, *Kaupifalco*, *Melierax*, *Urotriorchis*, and *Micronisus*) interspersed. These revised



Figure 1. Part of Figure 2 of Catanach et al. (2024) that shows the branching pattern among *"Accipiter"* – note here that all former members of *Accipiter* are listed in brackets, while the suggested new generic name is included for the clade.

arrangements call for substantial taxonomic changes to account for the non-monophyly of *Accipiter*, either by lumping many genera into *Accipiter*, including the highly distinctive harriers (*Circus*), or breaking *Accipiter* into at least 4 or 5 different genera. Catanach et al. (2024) provided the following recommendations. I am including recommendations first for all species formerly placed in *Accipiter* for completeness before breaking out the relevant species for NACC in the **Recommendation** section.

- Crested Goshawk (*Accipiter trivirgatus*) was recovered as sister to a large clade that included all of subfamilies Accipitrinae and Buteoninae with strong support. This result was also recovered by Mindell et al. (2018). Catanach et al. (2024) recommended following Sangster et al. (2021) in adopting *Lophospiza* Kaup 1844 for both *trivirgatus* as well as Sulawesi Goshawk (*Accipiter griseiceps*), which was not sampled but is assumed to be closely related (Mayr 1949, Breman et al. 2013). I recommend following Catanach et al. (2024) and Sangster et al. (2021) in adopting *Lophospiza* for these two species.
- 2. Catanach et al. (2024) broke the next group into two genera (*Aerospiza* Roberts 1922 and *Tachyspiza* Kaup 1844), but the two clades are sister. This clade was found to be sister to a group that included the remaining "*Accipiter*" apart from the species already discussed, as well as *Erythrotriorchis*, *Megatriorchis*, and *Circus*. The genus *Aerospiza* would include only two species: *tachiro* (including *toussenelii* when treated as a separate species) and *castanilius*. The genus *Tachyspiza* would be the largest remaining genus of former *Accipiter* hawks, and include the following species: *badius*, *butleri*, *brevipes*, *soloensis*, *francesiae*, *trinotatus*, *hiogaster*, *novaehollandiae*, *fasciatus*, *melanochlamys*, *albogularis*, *haplochrous*, *rufitorques*, *henicogrammus*, *luteoschistaceus*, *imitator*, *poliocephalus*, *princeps*, *erythropus*, *minullus*, *gularis*, *nanus*, *virgatus*, *erythrauchen*, *cirrocephalus*, *brachyurus*, and *rhodogaster*.
- 3. The next clade of "Accipiter" hawks consists of 6 species that are sister to the remaining "Accipiter" plus Megatriorchis and Circus. These 6 species include Eurasian Sparrowhawk (Accipiter nisus), which is the type of the genus Accipiter, so these 6 species would retain the name Accipiter. In addition to nisus, it also includes madagascariensis, ovampensis, rufiventris, striatus, and poliogaster (Catanach et al. 2024). The inclusion of poliogaster in this clade is provisional; although it received some support in Catanach et al. (2024), the only sequence data available for the species was from the COI gene, and Catanach et al. (2024) suggested leaving it in Accipiter until more information is available to clarify its relationship. The inclusion of poliogaster in Accipiter is not without complications: it is not supported by morphology, being larger and bulkier than the other species, with shorter and thicker tarsi and toes, and very different plumage compared to the remaining species, with particularly unique juvenile plumage. Other studies (e.g., Mindell et al. 2018) have not recovered this relationship, finding poliogaster instead sister to Megatriorchis, although this was not well-supported.
- 4. The final clade of "Accipiter" hawks identified by Catanach et al. (2024) was sister to Megatriorchis and Circus. The oldest available genus for this clade is Astur Lacépède 1799, with Astur gentilis designated as the type for the genus. This clade includes 9 species: cooperii, gundlachi, bicolor, chilensis, melanoleucus, henstii, gentilis, atricapillus, and meyerianus.

Recommendation:

The following NACC species are currently classified in the genus Accipiter:

Gray-bellied Hawk (*Accipiter poliogaster*) Chinese Sparrowhawk (*Accipiter soloensis*) Sharp-shinned Hawk (*Accipiter striatus*) Cooper's Hawk (*Accipiter cooperii*) Gundlach's Hawk (*Accipiter gundlachi*) Bicolored Hawk (*Accipiter bicolor*) Eurasian Goshawk (*Accipiter gentilis*) American Goshawk (*Accipiter atricapillus*)

Based on the recommendations of Catanach et al. (2024), I suggest that these species be reclassified as follows (in the following new linear sequence):

Chinese Sparrowhawk (*Tachyspiza soloensis*) Gray-bellied Hawk (*Accipiter poliogaster*) Sharp-shinned Hawk (*Accipiter striatus*) Cooper's Hawk (*Astur cooperii*) Gundlach's Hawk (*Astur gundlachi*) Bicolored Hawk (*Astur bicolor*) Eurasian Goshawk (*Astur gentilis*) American Goshawk (*Astur atricapillus*)

Because the placement of Gray-bellied Hawk in Accipiter sensu stricto is tentative, an argument could be made for placing it in its own monotypic genus. The name Dinospizias Cabanis 1874 is available for *poliogaster*. In the phylogenetic reconstruction in Catanach et al. (2024), poliogaster is sister to the remaining members of Accipter sensu stricto, and its inclusion is based solely on sequence data from a single mitochondrial gene. Given its distinct plumage and morphology relative to the other members of the genus, it may be better to place it in the monotypic genus Dinospizias. However, given the uncertainty in its relationships, I think it creates more instability to place it in a monotypic genus rather than including it in another recognized genus. I think until more information is collected, and its relationships are fully resolved, it is best to treat it tentatively as part of Accipiter sensu stricto. And although it does seem distinctive morphologically, there is clearly extensive convergence in Accipitriformes, and morphology has proven to be an unreliable indicator of relationships for this group. Further work may show it does indeed deserve to be placed in its own monotypic genus, or it may be better placed in one of the other newly recognized genera such as Tachyspiza or Astur. In addition to the need to rearrange the linear sequence of the hawks formerly in the genus Accipter, it is also necessary to move the position of the harriers (Circus) relative to these other hawks. The harriers (Circus) should now follow American Goshawk (Astur atricapillus) in the linear sequence, following Catanach et al. (2024).

Please vote on the following subproposals:

(a) accept the new generic placements as listed above

- (b) accept the new generic placements as listed above, but place the Gray-bellied Hawk in the monotypic genus *Dinospizias*
- (c) accept the new linear sequence for the current and former species of Accipiter
- (d) accept the new linear placement of Circus, following Astur atricapillus

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Submitted by: Shawn M. Billerman, Cornell Lab of Ornithology

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Treat Larus smithsonianus, L. vegae, and L. mongolicus as separate species from Herring Gull L. argentatus

Note: This proposal includes many aspects of Proposal 2024-A-11 with additional information on vocalizations from the Addendum to Proposal 2024-A-11

Background:

The taxonomy and classification of gulls, especially the large white-headed gulls (LWH gulls) of the genus Larus, has been confounding ornithologists, birders, and systematists for centuries. In addition to being generally similar to each other, there is extensive intraspecific plumage variation within and between different age classes, and many species also hybridize with each other, further complicating identification and classification of taxa. Molecular phylogenetic studies have also historically been unable to resolve relationships of this group, not only because of historical and ongoing introgression, but also due to very recent divergence. Different authorities have recognized different numbers of species in the group, and opinions on species limits are constantly changing. The Herring Gull (Larus argentatus) has been a source of much debate for decades and was used by Ernst Mayr as an example of a ring species (Mayr 1942), with European populations of Herring Gull (subspecies argentatus and argenteus) and Lesser Black-backed Gull (Larus fuscus) representing the end-points of the ring that meet but do not interbreed (Liebers et al. 2004, Sternkopf et al. 2010). The Herring Gull complex is comprised of 10+ species, with the Herring Gull (Larus argentatus), as currently recognized by the AOS, comprised of 5 subspecies distributed across the Holarctic. A single subspecies, smithsonianus, breeds across North America, with a second, vegae, breeding in northeastern Siberia and regularly encountered in western Alaska, where it breeds on St. Lawrence Island (Lehman 2019). In addition, birds from Europe (argentatus/argenteus) have occasionally been documented along the east coast of North America (e.g., Newfoundland, Florida). The last subspecies, mongolicus, breeds in south-central Russia, Mongolia, northeastern China, and the Korean Peninsula, and has not been documented in the AOS region.

North American and European populations of Herring Gull have for much of their history been considered conspecific, including by the AOS (formerly AOU). North American *smithsonianus* was originally described by Coues in 1862 as a separate species, but he later considered it conspecific with European populations (1873), a stance followed by all versions of the AOU/AOS Check-List (e.g., 1886, 1998). However, there has been a growing call to recognize North American and European populations of Herring Gull as separate species, largely following the publication of genetic studies that showed that these populations might not even be sister groups (Liebers et al. 2004, Pons et al. 2005). On the basis of these earlier genetic studies, as well as consistent morphological differences and behavioral differences, Yésou (2002) and Olson and Banks (2007) recommended recognizing North American and European populations of Herring Gull as distinct species, *L. smithsonianus* and *L. argentatus*, respectively. Dickinson and Remsen (2013) also followed this treatment. The placement of the two Asian subspecies of Herring Gull is not entirely settled, but many place both subspecies with *smithsonianus* (e.g., Dickinson and Remsen 2013, del Hoyo and Collar 2014, Clements et al. 2022). Although vegae and *mongolicus* have both been treated as separate species (e.g., Clements et al. 2024, Gill et

al. 2025), *mongolicus* has also been treated as a subspecies of Caspian Gull (*L. cachinnans*; Olsen and Larsson 2003). In their treatment of the complex, Olsen and Larsson (2003) recognized a monotypic *Larus smithsonianus* and *Larus vegae*, and placed *mongolicus* with Caspian Gull. Harrison et al. (2021) presented a final treatment, splitting Herring Gull into three species, with a monotypic *smithsonianus*, and placing both Asian taxa together under Vega Gull (*L. vegae*, with subspecies *vegae* and *mongolicus*, and also including an indeterminate taxon from the north-central Siberian-breeding *L. vegae "birulai*," widely known as "Taimyr Gull").

New Information:

Genetic Data and Hybridization

In their discussion of the Herring Gull complex, Yésou (2002) noted that argentatus/argenteus are sympatric with Lesser Black-backed Gull (L. fuscus) and Yellow-legged Gull (L. michahellis), and only occasionally interbreed, suggesting that hybridization is limited enough to warrant recognition as species (an approach followed by all current global authorities). Although argentatus/argenteus shows evidence of only limited interbreeding with fuscus and michahellis, it appears that it hybridizes more frequently with Caspian Gull (L. cachinnans) where the two now come into contact in eastern Europe (Neubauer et al. 2009). Neubauer et al. (2009) documented extensive hybridization and introgression in genetic markers and multiple phenotypic characters, except for bare parts color. Notably, they found some evidence for assortative mating on the basis of orbital-ring color and divergent breeding phenology; these differences, however, were found to be incomplete, and so hybridization was still widespread (Neubauer et al. 2009). These examples only serve to highlight the fact that we have no way of knowing how argentatus/argenteus would interact with smithsonianus in sympatry; both fuscus and cachinnans are part of the same mtDNA clade that smithsonianus is part of, and the degree of reproductive isolation from argentatus/argenteus seems quite different between the two taxa. On the contrary, cachinnans does not interbreed with michahellis where their ranges approach each other, with the two showing different long-call displays (Yésou 2002). Unfortunately, nothing has been noted of the long-call displays of smithsonianus versus argentatus/argenteus.

Liebers et al. (2004) undertook a study that tested Mayr's (1942) hypothesis that the Herring Gull complex represented a ring species, with Lesser Black-backed Gull (L. fuscus) and European Herring Gull (L. argentatus argentatus/argenteus) representing the ends of the ring that meet in Europe and that are reproductively isolated. Using mtDNA sequence data, they found that this complex did not represent a ring species, and instead represented a much more complicated pattern of colonization, isolation, and gene flow. Important to consideration of North American and European Herring Gull populations (smithsonianus and argentatus/argenteus, respectively), Liebers et al. (2004) found that these two groups were not each other's closest relatives, and had different evolutionary histories, with *smithsonianus* the result of a colonization event from eastern Asia (vegae-type), which was derived from an ancestral refugium in central Asia, whereas argentatus/argenteus was instead derived from an ancestral refugium in the northeastern Atlantic. In addition, mongolicus appears to represent a separate colonization of interior east-central Asia from a vegae-type ancestor. Importantly, they found no evidence that smithsonianus is the result of colonization of an argentatus/argenteus ancestor from Europe (Liebers et al. 2004). Further, the authors found that argentatus/argenteus and Glaucous Gulls (L. hyperboreus) contained mitochondrial haplotypes of both ancestral refugia, likely the result

of ancient hybridization. In Europe, the overlap of *argentatus/argenteus* and Lesser Blackbacked Gull (*L. fuscus*) represents sympatry of the two ancestral haplotypes with limited current hybridization, suggesting reproductive isolation; similarly, in North America, overlap between *smithsonianus* and Great Black-backed Gull (*L. marinus*) also represents sympatry between the two ancestral haplotypes with limited current hybridization, again suggesting reproductive isolation.

Sonsthagen et al. (2016) studied hybridization and its impacts on phylogenetic signal across *Larus* using multilocus data (mtDNA, nuDNA, microsatellites). In their study, they found evidence that *argentatus/argenteus* was not sister to *smithsonianus*. Instead, in their combined dataset, which included mtDNA and six nuclear introns, *smithsonianus* appeared to be sister to California Gull (*L. californicus*), whereas nominate *argentatus* formed a clade with Glaucous Gulls from Europe (North American Glaucous Gulls occurred in a different part of the phylogeny, more on that later; Fig. 1). In addition, *vegae* was found to be more closely related to Lesser Black-backed Gull (*L. fuscus*) and Caspian Gull (*L. cachinnans*), although this study included *mongolicus* with Caspian Gull, so that close relationship may in part be due to the grouping of *mongolicus* with *vegae* (samples of *cachinnans* samples in the study are closest to *vegae*).



Figure 1. From Sonsthagen et al. (2016), showing the phylogeny of gulls based on sequence of mtDNA control-region and six nuclear introns constructed using BEAST.

Sternkopf et al. (2010) studied patterns of hybridization and introgression in the Herring Gull complex, focusing specifically on those species that exhibited paraphyly in their mitochondrial

DNA (European Herring Gull *argentatus/argenteus*, Great Black-backed Gull *marinus*, and Glaucous Gull *hyperboreus*) identified in Leibers et al. (2004). They also included samples of other members of the Herring Gull complex, including North American *smithsonianus*, but *vegae* and *mongolicus* were not included. This study again found that North American *smithsonianus* was not closely related to European *argentatus/argenteus*, but that the paraphyly exhibited within *argentatus/argenteus* appears to be the result of ancient hybridization and complex demographic events.



Figure 2. Mitochondrial haplotype network showing *smithsonianus* (dark blue, cluster "I") and *argentatus/argenteus* (light blue, clusters "B" and "F").

Linklater (2021) studied population genetics and hybridization between Glaucous Gulls (*L. hyperboreus*), North American Herring Gulls (*smithsonianus*), European Herring Gulls (*argentatus/argenteus*), and Glaucous-winged Gulls (*L. glaucoides*). Using a ddRAD approach, she sequenced 2,145 loci across the four species. In her study, Glaucous-winged Gull was consistently distinct and separate from the other three species, and will not be further discussed here. They also found that *smithsonianus* and *hyperboreus* were consistently recovered as distinct from each other, whereas *hyperboreus* and *argentatus/argenteus* were not (Fig. 3). Further, *smithsonianus* and *argentatus/argenteus* were weakly separated, although the program

NewHybrids was not able to diagnose any of the taxa species (including Glaucous-winged Gull) as separate species, as the models failed to converge. In STRUCTURE analyses, a model with 2 clusters was identified as the top model (when Glaucous-winged Gull was excluded), with *smithsonianus* separating out from *hyperboreus* and *argentatus/argenteus*, which together formed a single cluster. Migration rates from *smithsonianus* into *hyperboreus* were significantly greater than 0, and this was the only pairwise comparison in the study that was significantly greater than 0; the author also noted that this migration rate is higher than that documented between highly structured populations of some species, reflecting limited reproductive barriers across *Larus*. In addition, Linklater (2021) also identified some hybrids between *smithsonianus* and *hyperboreus*, but none between *hyperboreus* and *argentatus/argenteus*; the author speculated that the lack of strong genetic divergence, itself likely a result of ongoing gene flow between *hyperboreus* and *argentatus/argenteus*, prevented the identification of definitive hybrids, as studies based on morphology have identified many hybrids from some colonies in Iceland (e.g., Ingólfsson 1970). One hybrid between *smithsonianus* and *argentatus/argenteus*.



Figure 3. From Linklater (2021). STRUCTURE plots using ddRAD loci, where (a) shows the admixture model, (b) shows the admixture model and species as prior population information, and (c) shows only species as the prior population information. Notably, *smithsonianus* is distinct from *argentatus/argenteus* and *hyperboreus* together.

Vocal Data

There has been little formal study of the vocal differences between the different taxa of Herring Gull. In one study, Frings et al. (1958) noted that *argentatus/argenteus* did not respond to recordings of *smithsonianus*, suggesting some degree of isolation. Birds in Europe did not respond either to the feeding call or to the alarm call, even when broadcast at short distances. However, these experiments only involved playback of feeding and alarm calls of North American birds to winter populations in Europe. The reciprocal playback experiment was not done with recordings of European birds in North America, nor were calls used during breeding tested.

Despite the lack of formal study, many calls of all taxa are archived in both Macaulay Library and Xeno-canto and available for comparison. Below is a discussion of vocal differences among the various taxa of Herring Gull based on these archived recordings. Downloaded recordings were categorized as to whether they contained the three main note types summarized in Weseloh et al. (2020): 1) Kek Kek notes, which are short calls also termed Alarm Calls in Weseloh et al. (2020); 2) Long Calls, which are series starting with a variable number and type of long notes, usually plaintive and somewhat muffled, followed by a series of shorter Keow notes forming a recognizable strophe; see description in Weseloh et al. (2020); and/or 3) Keow calls, called Long-call Notes in Weseloh et al. (2020), which are rather short (but variable-length) downslurred calls, not part of a Long Call. Poorer-quality recordings were not used, nor were those which appeared to be of chick-begging or other rarer vocalization types. *Larus a. argentatus/argenteus* were not distinguished from each other. Recordings from the Asian wintering grounds were not used in case misidentifications might be involved.

First, we could not find any obvious differences between any of these taxa (including *cachinnans*) in the Kek Kek notes, which are given in variable series and have closely packed harmonics (see below for Kek Kek notes of *argentatus*, *smithsonianus*, *vegae*, and *mongolicus*, in that order). If consistent differences exist in the Kek Kek notes they must be subtle, so this call type will not be considered further here.



- 2. Long Calls tend to be the most structured call type in the complex, but nevertheless there is extensive variation. Usually the Long Call is readily recognized as such unless the beginning is cut off, but in *mongolicus* it is not as distinct from the Keow calls as in the other taxa, and there are few obvious examples of Long Calls for this taxon despite the large number of recordings available.
 - a. Long Calls of *argentatus/argenteus* are typically fairly clear, with even-pitched and even-length notes that are round-topped in sonograms, e.g.:



There are exceptions, however. For example, the recording below is the only one of 18 *argentatus/argenteus* Long Calls sampled for this proposal that shows these short non-rounded yelping notes, but its location (St. Petersburg, Russia) makes it unlikely that it has been misidentified.



b. Long Calls of *smithsonianus* are more varied in note shape and quality, hoarser and more yelping, with broken notes, some of which sound upturned earlier in the series and then downturned later in the series. Most notes are sharp-topped rather than round-topped in sonograms (although some *smithsonianus* Long Calls are more similar to the St. Petersburg recording of *argentatus*):



c. Long Calls of *vegae* are more similar to those of *argentatus/argenteus* than to *smithsonianus*, in being more even-pitched, even-noted, and clearer. This similarity is mentioned by Weseloh et al. (2020), although without explicitly stating that *vegae* is more similar to *argentatus* than to *smithsonianus*.



d. Finally, Long Calls of *mongolicus* seem infrequent and are a less distinctive call type compared to the other taxa; they are much hoarser and with many more harmonics than the others:



To summarize, here is a sample of one typical Long Call for each taxon (from left to right, *argentatus, smithsonianus, vegae*, and *mongolicus*) in color, making the relative power of each harmonic more readily visualized):



3. Keow calls vary considerably in length and seem indistinguishable between the first three taxa groups (argentatus/argenteus, smithsonianus, and vegae). Much of the overlap in these calls is because of the variability of smithsonianus and vegae, but argentatus/argenteus does give mostly consistent mid-length, clearly downslurred notes. However, Keow calls of mongolicus are normally hoarser and include more harmonics and white noise, thus forming noticeably dark broadband profiles on a sonogram compared to the others. In fact, Weseloh et al. (2020) stated that the voice of mongolicus is apparently more similar to that of *L. cachinnans* (for those comparisons, see farther below).

a. Representative Keow calls of *argentatus/argenteus*:



b. Representative Keow calls of *smithsonianus*:



c. Representative Keow calls of *vegae*:



d. Representative Keow calls of *mongolicus*:



In summary, of the three main call types sampled, *mongolicus* clearly differs from the other three in two call types: the Long Call and the Keow call. In addition, *smithsonianus* differs but less obviously so from *argentatus/argenteus* and apparently also from *vegae* in the Long Call.

Comparison of mongolicus with cachinnans

Because *mongolicus* has been considered conspecific with *L. cachinnans* (including in the influential Olsen and Larsson 2003), vocal comparisons are required here as well. To be sure, the overall quality of *mongolicus* calls does sound more like that of *cachinnans* than any of the other Herring Gull-complex taxa considered here. However, *cachinnans* sounds generally lower pitched, and other differences have been said to exist, as pointed out by Yésou (2001), though this was based on his discussion with others. These putative differences require further clarification.

The most obvious difference between the Long Calls of *mongolicus* and *cachinnans* is that the Long Call of *cachinnans* consists primarily of very short notes, much like Kek Kek notes rather than the more prolonged Keow notes given in the Long Call by *mongolicus* and other taxa. This striking difference surely argues strongly against conspecificity of *mongolicus* and *cachinnans*.



Larus cachinnans Long Calls:

In addition to these vocal differences, the limited information we have from genetic studies shows that *mongolicus* and *cachinnans* do not appear to be particularly closely related to each other (e.g., Liebers et a. 2003, Collinson et al. 2008, Černý and Natale 2022) or to *vegae* (Černý and Natale 2022, *contra* Collinson et al. 2008), although clearly relationships in this complex have yet to be well-resolved. However, *cachinnans* and *mongolicus* were lumped together in the genetic analyses of Sonsthagen et al. (2016), in which they were very close to *vegae*; however, judging from the Ukraine locality of some of the samples, these would be nominate *cachinnans* rather than *mongolicus* (the Russian samples could be either, but their similarity to the Ukraine samples also suggests nominate *cachinnans*).



Part of the time-calibrated phylogeny from Černý and Natale (2022) showing the positions of the four main taxa of the Herring Gull under consideration in this proposal, as well as *L. cachinnans*.

<u>Moores (2017)</u> provided a useful and up-to-date summary regarding the differences between *mongolicus* and *vegae* (the page also discusses differences with *taimyrensis*, which is often recognized as a subspecies of *L. fuscus*, and is a separate issue). Yésou (2001) also provided information on identification of *mongolicus*.

Ecological and Life History Data

Moores (2017) reported that *vegae* and *mongolicus* occupy quite different niches and have very different migration strategies and timing of molt. Whereas *vegae* breeds near the coast in far north-central and northeastern Russia, *mongolicus* breeds on islands in lakes from Mongolia and the Baikal region of southern Siberia east at least locally through islands in the Yellow Sea off the Korean Peninsula. Both winter in eastern Asia, but generally *vegae* is the common species wintering on rocky coasts, whereas *mongolicus* mostly occurs on mudflats and sandflats. Moores (2017) also observed that kleptoparasitic behavior is common among *mongolicus*, but not *vegae*.

The only other case among large gulls in which such ecologically distinct taxa are still generally treated as subspecies is in the also highly contentious *Larus fuscus* complex, when it is considered to include the steppe-breeding *barabensis*. However, both European Herring Gull and American Herring Gull have both coastal and inland-breeding populations, and even *mongolicus* breeds coastally to a limited extent in the Yellow Sea islands of Korea.

Phenotypic Data

Adults of all taxa under consideration here are quite similar, but then so are all of the taxa of the broader Herring Gull complex that also includes Yellow-legged Gull (*Larus michahellis*), Caspian Gull (*Larus cachinnans*), Armenian Gull (*Larus armenicus*), and others. The descriptions below come from Olsen and Larsson (2003) and examination of photos in Macaulay Library, unless otherwise noted. Adult *smithsonianus* and *argentatus/argenteus* are extremely similar and in many cases seem impossible to separate, with differences being subtle and not diagnostic; *smithsonianus* tends to have paler gray upperparts, solid black markings on p5-6, pink legs (some populations of *argentatus* show yellowish legs), a yellow to orange orbital ring (*argentatus* variable, some yellow, some orange, some grayish pink, others even red). Adult *vegae* is the most distinctive taxon, especially compared to *smithsonianus* and *argentatus/argenteus*, having darker upperparts, deeper pink to almost purple legs, a broader white tertial crescent when perched, and distinctive white subterminal spots on p5-6; nonbreeding adults also tend to have a more heavily marked head with brown streaking and spotting; the orbital ring is also red.

Adult *vegae* and *mongolicus* also differ, most notably in leg color, with *vegae* showing bright, deep pinkish legs and *mongolicus* showing dull pink to yellowish legs; bill color can also differ, with *vegae* showing a pale yellow-based bill versus a rich yellow bill (including the base) in *mongolicus*. In plumage, the two differ during the nonbreeding period, with *mongolicus* tending to have very limited head streaking, usually restricted to just the nape, whereas *vegae* tends to show a very heavily marked head. Harrison et al. (2021) also mentioned the (usually) more extensive black on the wingtip of *mongolicus*, and the larger size and bulkier appearance of *mongolicus*. However, to the best of our knowledge the usual extent of head streaking early in the non-breeding season in *mongolicus* remains to be clarified, and some adults (e.g. in November) may not be identifiable from *vegae* on present knowledge.

Although adult *smithsonianus* and *argentatus/argenteus* are extremely similar and not reliably separated, the two are readily separable in juvenile plumage and some other younger ages. Most notably, juvenile *argentatus/argenteus* are paler with bolder edging and spotting on the upperwing coverts and mantle; the underparts are paler, and appear more mottled than in *smithsonianus*, which, although quite variable, is more solidly dark chocolate brown below. Another key to the separation of *smithsonianus* and *argentatus/argenteus* is rump color; in *smithsonianus* the rump is white and brown but shows very little contrast with the mantle and lower back, whereas in *argentatus/argenteus*, the rump is much more boldly white, contrasting strikingly from the mantle and lower back.

Juvenile *vegae* is perhaps most similar to *argentatus/argenteus*, being overall paler than *smithsonianus* with a contrasting whitish rump. However, juvenile *vegae* is very different from juvenile *mongolicus*, with *mongolicus* having evenly pale-scaled upperparts, a pale belly (also

strikingly different from the more uniform chocolate brown of juvenile *smithsonianus*), and often a pale base to the dark bill, compared to *vegae* which is less scaly above, has a dark belly, and typically has an entirely dark bill.

Recommendation

Despite considerable recent work and intense interest, gull taxonomy, especially in the Herring Gull complex, remains extremely confused and contentious, and still lacks a clear resolution. However, based on available evidence, it seems clear that what the AOS classifies as the Herring Gull, Larus argentatus, represents multiple taxa for which species status seems as welljustified as for some others long recognized as such. Based on the earlier genetic work of Liebers et al. (2004) and Sternkopf et al. (2010), North American Herring Gull populations (*smithsonianus*) and European Herring Gull populations (*argentatus/argenteus*) have distinctly different evolutionary histories and appear to have evolved from separate refugia, with argentatus/argenteus originating from a refugium in the northeastern Atlantic, and smithsonianus originating from a refugium in central Asia (with North America likely having been colonized from northeastern Asia). The genetic distinctness of *smithsonianus* and argentatus/argenteus was further shown by Sonsthagen et al. (2016) and Linklater (2021), who both used multilocus datasets that continued to show that smithsonianus and argentatus/argenteus were not particularly closely related, with smithsonianus possibly more closely related to California Gull (L. californicus), and argentatus/argenteus possibly more closely related to Glaucous Gull (L. hyperboreus). Linklater (2021) focused only on North American Herring Gulls, European Herring Gulls, Glaucous Gulls, and Glaucous-winged Gulls in their study, but again found that smithsonianus was genetically more distinct from argentatus/argenteus than argentatus/argenteus was from hyperboreus. Although no systematic study has been done, there is also behavioral evidence for the recognition of smithsonianus as a separate species from argentatus/argenteus: as mentioned above, Frings et al. (1958) found that argentatus/argenteus did not respond to the feeding calls or alarm calls of smithsonianus. Unfortunately, courtship vocalizations were not included in the study, nor were the reciprocal comparisons made in North America. As a practical matter, a complicating factor to the recommendation of splitting *smithsonianus* from *argentatus/argenteus* is that birds in adult plumage are nearly identical and not reliably identifiable. This contrasts to the plumages of young birds, which are distinctive (Yésou 2002, Olsen and Larsson 2003).

Although recognizing *smithsonianus* as distinct from *argentatus/argenteus* is well-supported by the available evidence, less clear is the status of the two Asian taxa of Herring Gull (*vegae* and *mongolicus*). Both the HBW/BirdLife International Checklist (del Hoyo and Collar 2014) and the Howard and Moore Checklist (Dickinson and Remsen 2013) placed *vegae* and *mongolicus* together with *smithsonianus* (Arctic Herring Gull and American Herring Gull, respectively). The IOC World Bird List 13.1 (Gill et al. 2023 and earlier versions) and Harrison et al. (2021) further split the group, recognizing a monotypic *smithsonianus* (American Herring Gull) and Vega Herring Gull (with nominate *vegae* and *mongolicus*). Finally, AviList (2025), the IOC World Bird list 15.1 (Gill et al. 2025), and Clements et al. (2024) all recognized four species in this complex, with Vega Gull (*L. vegae*) and Mongolian Gull (*L. mongolicus*) as separate monotypic species. There appears to be evidence for all treatments. The earlier work of Liebers et al. (2004), using only mitochondrial DNA, found that *smithsonianus*, *vegae*, and *mongolicus* grouped together, and they hypothesized that both *smithsonianus* and *mongolicus* were both derived from

colonization events from northeastern Asia. In their study of the Herring Gull complex, Sonsthagen et al. (2016), who also included nuclear intron and microsatellite data, found that *vegae* instead grouped with Caspian Gull (*L. cachinnans*), whereas *smithsonianus* grouped with California Gull (*L. californicus*). Although this may seem like an extremely different result from the others, it must be noted that Sonsthagen et al. (2016) included *mongolicus* in their definition of *L. cachinnans*, and did not separate the two in their analyses, so it does not rule out that their study indeed shows a close relationship between *vegae* and *mongolicus*. Although Olsen and Larsson (2003) placed *mongolicus* with *L. cachinnans*, they noted that it was more closely related to *vegae* (citing Yésou 2002). And, as detailed above, there is also strong evidence for recognizing *vegae* and *mongolicus* as separate monotypic species from both *smithsonianus* and *argentatus/argenteus* on the basis of vocal differences (with *mongolicus* being the most vocally distinct of all the Herring Gull taxa considered here), ecological differences, phenotypic differences, and genetic differences seen in the analyses of Černy and Natale (2022).

Although the status of *vegae/mongolicus* is perhaps less clear than *smithsonianus* relative to *argentatus/argenteus*, given the available evidence, we recommend splitting Herring Gull into 4 species: a monotypic *L. smithsonianus*, a monotypic *L. vegae*, a monotypic *L. mongolicus*, and *L. argentatus* (with subspecies *argentatus* and *argenteus*). Although this is our recommendation, we present five voting options for this proposal:

- A) A 4-way split that is the recommendation of this proposal, with the recognition of *L. smithsonianus*, *L. vegae*, *L. argentatus*, and *L. mongolicus* (as adopted by Gill et al. 2025, Clements et al. 2024, and AviList).
- B) A 3-way split that would recognize *L. smithsonianus*, *L. vegae* (with subspecies mongolicus), and *L. argentatus* (with subspecies argenteus), as adopted by Harrison et al. (2021).
- C) A 3-way split that would recognize a monotypic *L. smithsonianus*, a monotypic *L. vegae*, and *L. argentatus* (with subspecies *argenteus*), but would not deal with whether *mongolicus* should be considered a separate species, or if it should be included as part of *cachinnans* (as an Old World issue). (However, it seems likely that this taxon will eventually turn up in the NACC area as well)
- D) A 2-way split that would recognize *L. smithsonianus* (with subspecies *smithsonianus*, vegae, and mongolicus) and *L. argentatus* (with subspecies argentatus and argenteus), as adopted by del Hoyo and Collar (2014) and Dickinson and Remsen (2013).
- E) No change, retaining *smithsonianus*, *vegae*, and *mongolicus* as subspecies of *L. argentatus*.

If either options A, B, C, or D pass, a separate proposal for English names will be required. Recommendation of English names will vary depending on the option chosen.

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Submitted by: Shawn M. Billerman and Pamela C. Rasmussen, Cornell Lab of Ornithology

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2025-C-3 N&MA Classification Committee p. 436

Treat Warbling Vireo Vireo gilvus as two species

Background:

The Warbling Vireo (*Vireo gilvus*) is recognized currently as a single polytypic species with five subspecies classified into two groups: the Eastern (*gilvus*) Group and the Western (*swainsoni*) Group (AOU 1998, Clements et al. 2024; Table 1).

Group	Subspecies	Breeding Distribution
Eastern Group	V. g. gilvus	southwestern Canada to east-central USA
Western Group	V. g. swainsoni**	southeastern Alaska to northern Montana, along
		Pacific coast to northern Baja California
Western Group	V. g. brewsteri	southwestern Montana and southern Idaho to western
		South Dakota, south to western Texas and south-
		central Mexico
Western Group	V. g. victoriae	Cape Region, Baja California Sur
Western Group	V. g. sympatricus	South-central Mexico

Table 1. Currently recognized groups and subspecies of Warbling Vireo.

** Originally described as *V. g. swainsonii* but that spelling was changed to *swainsoni* following David et al. (2009) and Chesser et al. (2010).

A sixth subspecies, *V. g. leucopolius* from the Great Basin, is variably recognized as a separate taxon (Hayward et al. 1976, Browning 2019) or as part of *V. g. swainsoni* (Phillips 1991, Gardali and Ballard 2020, Clements et al. 2024, Gill et al. 2024). In addition, *V. g. victoriae* has been elevated to species by some (Sibley 1996) but is generally retained as a subspecies in current treatments. Finally, the Brown-capped Vireo (*Vireo leucophrys*) has sometimes been lumped with the Warbling Vireo (e.g., Mayr and Short 1980, Barlow 1981) but is treated currently as a separate species (AOU 1983).

The taxonomy of the Warbling Vireo complex has been of interest for a long time. Baird (1858: 336) noted morphological differences between Warbling Vireos from the Eastern states and those from the Pacific Coast and stated, "Should the western specimens really prove distinct, they may appropriately bear the name of *Vireo swainsonii*." Since then, numerous authors have considered the Eastern and Western groups to be separate species (e.g., Sibley and Monroe 1990, Phillips 1991, Voelker and Rohwer 1998, Browning 2019, Lovell et al. 2021). Although Phillips (1991) split them, he stated: "*V. swainsonii* is dubiously distinct at the species level. But recent studies by J. C. Barlow indicate reproductive isolation where they meet in Alberta...There does seem to be some hybridization or intergradation...And no single morphological character holds for all *gilva* vs. all *swainsonii*...But tentatively I maintain *swainsonii* (with its races) as a distinct species...I find the differences in bill swelling and darkness the most consistent distinction between the 2 'species' (except, of course, when young)." In addition to morphology and plumage, other differences that have been cited to support species-level treatment include

genetics, molt and migration strategies, voice, ecology, and response to cowbird parasitism (Browning 2019, 2021). These differences are summarized here:

Morphology and plumage

Eastern and Western groups differ subtly in morphology and plumage coloration (Gardali and Ballard 2020). Compared to eastern birds, western birds:

- are smaller
- have a more slender bill (smaller average depth and width) with a more extensively dark upper mandible
- tend to be more tinged olive-green in the dorsal plumage, with greater contrast with the crown
- show less yellow in the ventral plumage

Lovell (2010) examined morphological differences between *V. g. gilvus* and *V. g. swainsoni* in and near a contact zone in Alberta, Canada. He measured 176 males and found that the two taxa differed significantly in all 9 characters measured, with mass showing the greatest difference (*gilvus* ~30% heavier than *swainsoni*). While Gardali and Ballard (2020) reported that *swainsonii* has a longer tail relative to *gilvus*, Lovell (2010) found the opposite result. Lovell (2010) also quantified plumage variation (mantle, crown) in his study area and found that *gilvus* had higher percent reflectance (brighter plumage) in the crown and mantle patches compared to *swainsoni*. Both morphology and crown patch color showed a sharp cline in the transition between subspecies (Figure 1), with cline widths approximately 67 km and 40 km, respectively.



Figure 1. Best-fit clines for morphological and crown data across a transect from north (*V. g. swainsoni*) to south (*V. g. gilvus*) in Alberta.

Genetics

Johnson et al. (1988) published the first genetic study of the Vireonidae using allozyme electrophoresis. They analyzed variation at 29 loci in 32 taxa (20 species, 4 genera), including five western *V. gilvus* from California (1 *V. g. swainsoni,* 4 *V. g. leucopolius*) and one eastern *V. gilvus* from Louisiana. In their analyses, Eastern *gilvus* grouped with the Brown-capped Vireo *V. leucophrys* rather than with Western *gilvus*.

Murry (1994) sequenced 273 bp of the mitochondrial cytochrome *b* gene for 32 samples that included 9 *Vireo* species plus *Vireolanius* and *Cyclarhis*. Their sampling included representatives of both *V. g. gilvus* (Canada: Saskatchewan, Alberta) and *V. g. swainsoni* (Canada: Alberta), which showed divergence between these groups at 7-9 base pairs (2.9% uncorrected difference). They did not include *V. leucophrys* in their sampling.

A more comprehensive, multilocus phylogeny was published by Slager et al. (2014), who sequenced 221 individuals of 46 vireonid species representing all four genera in the family (*Vireo, Vireolanius, Cychlaris, Hylophilus*). Their data set included the complete ND2 gene for all individuals plus three Z-linked nuclear introns for a subset (n = 34) of specimens. For *Vireo gilvus*, they sampled 9 individuals representing both Western (n = 7) and Eastern (n = 2) groups. They also included 15 *V. leucophrys*. Their Bayesian tree (Figure 2) shows monophyly of *V. gilvus* contrary to the results of Johnson et al. (1988) and strong support for a relatively deep split between the two *V. gilvus* groups. Relationships between *V. gilvus, V. leucophrys*, and *V. philadelphicus* vary depending on the loci (ND2: *V. gilvus* is sister to *V. philadelphicus* + *V. leucophrys*; Z-linked: *V. gilvus* is sister to *V. philadelphicus*, with *V. philadelphicus* sister to that pair of taxa).





Lovell (2010) conducted the first intraspecific molecular study of variation in *V. gilvus*. He sequenced 1078 bp of the cytochrome b gene for 191 birds collected along a north-south transect in Alberta as well as from southeastern British Columbia, western Saskatchewan, and northern Montana. Samples fell into two distinct clusters that match the taxonomic groups (Figure 3). Average raw sequence divergence was 4.0%, with an estimated divergence time dated to the late Pliocene or early Pleistocene. The average raw sequence divergence between samples within each group was low (0.30% within *V. g. gilvus* and 0.40% within *V. g. swainsoni*). As with the morphological and plumage data, mtDNA showed a sharp cline along the north-south transect in Alberta (Figure 4).



Figure 3. Minimum-spanning haplotype network of unique haplotypes for *V. g. swainsoni* and *V. g. gilvus.*





Molt and Migration

Voelker and Rohwer (1998) examined 1,228 museum specimens of Eastern and Western Warbling Vireos to assess patterns and timing of molt. They found that adult *gilvus* quickly replace their primaries (38 days) and complete their prebasic molt after breeding but while still on the breeding grounds. In contrast, adult *swainsoni* take longer to replace their primaries (55 days) and begin their prebasic molt on the breeding grounds but continue molting during migration (i.e., undergo molt-migration). Voelker and Rohwer (1988) also noted that adult *swainsoni* replace their body feathers during migration and that adults migrate well in advance of hatch year birds (hatch year birds finish molting on the breeding grounds). They argued that

these differences in timing of molt and migration may be a strong selective force against hybridization because "hybrids between species that molt before the fall migration and species that molt after the fall migration might end up molting twice in a single fall or, perhaps, not at all."

The two taxa also use different routes during migration to their winter ranges (Voelker and Rohwer 1998, Lovell et al. 2021). Individuals of *gilvus* have a land-based migration from the midwestern and eastern United States around the Gulf of Mexico to their wintering grounds from southern Mexico to Nicaragua. In contrast, *swainsoni* individuals migrate through the western United States to northwestern Mexico where they complete their prebasic molt (flight feather replacement), then continue to their wintering grounds from southern Mexico south to El Salvador.

Song

Spencer (2012) summarized differences in the song of Eastern and Western Warbling Vireo and noted that song is the best way to identify these taxa if they were to be split. However, he acknowledged that some birds are harder to classify (especially where they contact) and that more study is needed, particularly to determine whether there is a cline in song types and how birds respond to heterotypical songs. He described their songs as follows:

- Eastern Warbling Vireos have a song made up of rich, slightly modulated whistles, with most of the initial notes being of the same pitch and often ending in higher notes ("series of low caroling notes").
 <u>https://xeno-canto.org/100053</u> (Massachusetts)
 <u>https://xeno-canto.org/66261</u> (Wisconsin)
 <u>https://xeno-canto.org/738209</u> (Iowa)
- Western Warbling Vireos tend to have more high-pitched notes that are placed evenly throughout the song ("jumbled and less structured feel, with an overall higher pitch"). <u>https://xeno-canto.org/22036</u> (Wyoming) <u>https://xeno-canto.org/80751</u> (Arizona) <u>https://xeno-canto.org/408016</u> (California)

Lovell (2010) studied song variation in *V. g. gilvus* and *V. g. swainsoni* throughout Alberta, Canada, including the contact zone. He recorded songs of 199 territorial males (3,290 songs) and analyzed seven variables per song: duration, syllable delivery rate, maximum frequency, minimum frequency, frequency range, frequency of maximum amplitude, and number of syllables. Songs were found to be significantly different (p < 0.001) between taxa in six of the seven variables; there was no difference between songs in minimum frequency.

- *V. g. gilvus* songs: longer duration, more syllables, higher syllable delivery rates.
- *V. g. swainsoni* songs: greater frequency range, higher maximum frequencies, higher frequencies of maximum amplitude.

Discriminant Function Analysis (Figure 5 left) classified 89% of the individuals correctly (36 of 44 *V. g. gilvus* and 88 of 96 *V. g. swainsoni*). Recordings from a transect across the contact zone showed significant differences between songs from pure *swainsoni* versus pure *gilvus*

populations, with birds from the contact zone demonstrating a transition in song characteristics from northwest to southeast (Figure 5 right). The best-fitting cline model was bimodal with no introgression, with a narrow cline (Figure 6) centered in approximately the same area as the equally narrow clines in morphology, crown plumage, and mtDNA.

Floyd (2014) reported on Warbling Vireo songs from the lowlands of eastern Boulder County, Colorado, that he identified as Eastern *gilvus*, thus documenting the presence of that taxon further west than previously known. Western *swainsoni* songs were observed in the foothills of the Rocky Mountains immediately to the west. These observations support a sharp demarcation between the breeding ranges of *swainsonii* and *gilvus* in that region.



Figure 5. Discriminant Function Analysis (left) and Principal Components Analysis (right) of seven song variables for *V. g. swainsoni* and *V. g. gilvus.*



Figure 6. Cline for mtDNA (cytochrome b) data across a transect from north (*V. g. swainsoni*) to south (*V. g. gilvus*) in Alberta. Cline width ~42 km.

Cowbird Parasitism

Behavioral studies have shown that nesting *V. g. swainsoni* accept introduced *Molothrus ater* (Brown-headed Cowbird) eggs while nesting *V. g. gilvus* generally reject them (Sealy 1996, Sealy et al. 2000). Differences in the rejection or acceptance of cowbird eggs have been attributed to genetic differences and host-brood parasite coevolution rather than phenotypic plasticity (Peer et al. 2011, Kuehn et al. 2014), and have been used as further evidence to suggest species status in Warbling Vireos (Sealy et al. 2000, Browning 2019).

New Information:

Lovell et al. (2021) analyzed mitochondrial and nuclear DNA variation in *V. g.* gilvus and *V. g. swainsoni* with a focus on determining levels of genetic differentiation and hybridization where they contact in central Alberta (Figure 7). Cytochrome b was sequenced from 191 individuals and AFLP genotyping was performed on 145 individuals (data set reduced to 67 informative loci). Results were similar to those presented by Lovell (2010) in that the two taxa fell out into distinct mitochondrial groups separated by 35 diagnostic substitutions (Figure 8 left). Likewise, samples clustered separately by Principal Components Analysis on AFLP scores (Figure 8 right). Q values indicated that 136 of 145 individuals were either pure *swainsoni* ($Q \le 0.1$) or pure *gilvus* ($Q \ge 0.9$), nine individuals had Q values suggesting mixed ancestry (0.1 > Q < 0.9), and four birds demonstrated a mismatch between Q value assignment and mtDNA haplotype (two had *swainsoni* Q values but *gilvus* mtDNA, and two had *gilvus* Q values but *swainsoni* mtDNA). Two of the mis-matched birds are from the contact zone whereas the other two are from northwestern Alberta, possibly as a result of females from the contact zone dispersing into populations with only *swainsoni* males.



Figure 7. Sampling localities in and near the contact zone between *V. g. gilvus* and *V. g. swainsoni* (n = 213; Lovell et al. 2021).



Figure 8. Minimum-spanning network of mtDNA haplotypes (left) and Principal Components Analysis of AFLP scores (right). In the AFLP plot, green squares are classified as hybrids and yellow triangles are individuals where mtDNA and AFLP are mis-matched.

Lovell et al. (2021) estimated the expected cline width to be ~4,192 km. However, the observed width was 69 km for mitochondrial DNA, 84 km for a "hybrid index" (probability that an individual was assigned to the *gilvus* cluster by STRUCTURE), and ~220 km for the mean of all individual AFLP clines. They suggest that the narrowness of these clines is a result of selection maintaining (limiting the extent of?) the hybrid zone and that this zone is a hybrid sink.

Finally, Lovell et al. (2021) noted that the location of the contact zone occurs at an ecological transition in south-central Alberta (Figure 9): pure *swainsoni* prefer mixed deciduous-coniferous forests and are found primarily in the foothills, mountains, boreal forests, and coniferous forests of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) interspersed with trembling aspens (*Populus tremuloides*); pure *gilvus* are found primarily in aspen parklands and along grassland river systems. The contact zone (Barrhead County, Alberta) is in the boreal transitional zone between aspen parkland to the south and east and mixed boreal forest to the north and west. There does not appear to be ecological segregation within the contact zone, where **males of the two taxa may occupy adjacent territories**. According to Lovell et al. (2021), differences in spring arrival dates (*swainsoni* arrives on their breeding grounds in central Alberta about two weeks before *gilvus*), molt schedules (see above), and migration routes (see above) indicate that a migratory divide may play an important role in reproductive isolation.

Carpenter et al. (2022a) examined genetic variation in three subspecies of Warbling Vireo (*V. g. gilvus, V. g. swainsoni, V. g. brewsteri;* n = 378) using mtDNA and microsatellites, and incorporated bioacoustic, morphometric and ecological niche modelling analyses to further examine differences. Their results were similar to those of Lovell et al. (2021), with two strongly divergent mtDNA lineages corresponding to Eastern and Western groups. The microsatellite data identified greater population structuring that divided the Warbling Vireo into four groups (Figure 10): Eastern, Black Hills, Northwestern, Southwestern; the two western lineages do not correspond to current subspecies boundaries.



Figure 9. Maps showing genetic frequencies (A-mtDNA; B-Q values from STRUCTURE analysis of AFLP data) relative to ecological zones for sampled populations of *V. g. swainsoni* (blue) and *V. g. gilvus* (red); green indicates hybrids by AFLP Q-scores (0.1> Q <0.9).



Figure 10. Map showing the distribution of four genetic groups of Warbling Vireo, genotyped at 14 microsatellite loci. Current subspecies distributions are in gray.

Three genetic groups (Black Hills excluded) also differed morphologically at five of six measurements (mass, wing chord, bill depth, bill width, tarsus), with Eastern birds being heavier with longer wings and deeper bills than Western birds; for Western birds, Northwestern birds were found to have smaller tarsi and narrower bills compared to Southwestern and Eastern birds (Carpenter et al. 2022a). Ecological niche models based on 19 bioclimatic variables clearly

separated Eastern and Western groups, whereas bioclimatic boundaries between the two western groups were less clear (more niche overlap, Carpenter et al. 2022a).

Bioacoustic analyses for the three genetic groups showed significant differences, with eastern birds singing longer songs with a higher syllable delivery rate than birds from the two western genetic groups (P < 0.001; Carpenter et al. 2022a). Carpenter et al. (2022a) also found that *swainsoni* songs were shorter and slower paced than *brewsteri* songs, although this difference was not significant (P = 0.06).

Carpenter et al. (2022b) investigated the role that habitat and elevation play in the distribution of three genetically distinct groups (Carpenter et al. 2022a) of Warbling Vireos. They focused on two contact zones (Great Plains - Eastern versus Western; Rocky Mountains - Northwestern versus Southwestern) and examined mtDNA, microsatellites, and morphology across two transects within each zone (n = 544). Both elevation and habitat had a strong association with the frequency of Eastern genetic ancestry, which declined sharply above 1000 m and in areas of more mixed or coniferous forest (Figure 11A-D). While Lovell et al. (2021) focused on a narrow contact zone in Alberta, Carpenter et al. (2022b) found that hybridization between Eastern and Western Warbling Vireos occurs across a much broader transitional area (Figure 12). In the Great Plains contact zone, 27 of 294 individuals (9.2%) were identified as hybrids with a mix of advanced and possible first-generation hybrids. When Carpenter et al. (2022b) compared individuals with both mtDNA and microsatellite data from the Great Plains contact zone, a small proportion (2.6%) of individuals showed cytonuclear discordance. Carpenter et al. (2022b) concluded that Western and Eastern Warbling Vireos likely diversified as the result of isolation in multiple refugia during Pleistocene glaciations, and that habitat and elevation play an important role in promoting and maintaining reproductive isolation.



Figure 11. Proportion of individuals assigned to Eastern or Western genetic groups based on mtDNA or nuclear data across the Great Plains (A–D) and Rocky Mountain (E, F) contact zones as a function of elevation and habitat.



Figure 12. Distribution of hybrids in the Great Plains contact zone across (A) elevational and (B) habitat gradients.

Browning (2021) studied museum specimens, Vertnet specimen data, and identifications provided for song recordings to clarify the distributions of Eastern and Western Warbling Vireos (treated as species *V. gilvus* and *V. swainsoni*) in Wyoming where both taxa occur. Of 18 specimens examined from the U.S. National Museum, Browning (2021) identified 15 as *swainsoni* and three as *gilvus*. Identifications were based on crown color, back color, and wing and bill measurements. One locality in north-central Wyoming (Greybull, Big Horn County) had five specimens collected between 8-10 June 1910, of which three were identified as *swainsoni* and two as *gilvus*. Unfortunately, it is unclear whether these birds were breeding or migrants.

Recommendation:

Multiple studies and lines of evidence suggest that Eastern and Western Warbling Vireos have separate evolutionary histories and should be elevated to full species. These include differences in genetics, morphology, song, molt, migration, ecology, and response to brood parasitism. Furthermore, separate studies of contact zones have shown relatively low levels of hybridization and cytonuclear discordance across a large area, even where males of the two taxa occupy adjacent territories. On the basis of concordance in different suites of traits, I recommend that we recognize Eastern and Western Warbling Vireos as separate species.

English Names:

English names in the literature have been presented either as Eastern Warbling Vireo and Western Warbling Vireo (Phillips 1991) or as Eastern Warbling-Vireo and Western Warbling-Vireo (Voelker and Rohwer 1998, Browning 2019) – *V. gilvus* and *V. swainsoni*, respectively.

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Submitted by: Carla Cicero

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2025-C-4 N&MA Classification Committee pp. 460-461

Treat Riparia diluta as a separate species from Bank Swallow R. riparia

Effect on NACC:

Approval of this proposal would split *Riparia riparia* into two species: *R. riparia* and *R. diluta*. Since *R. diluta* is extralimital, the split would not add a species to the checklist. However, a change in the Notes and geographic distribution of *R. riparia* would be necessary.

Background:

The Bank Swallow *Riparia riparia* and the Pale Martin *R. diluta* are currently considered conspecific by the NACC (AOU 1998). Species status for *R. diluta* has been accepted by some sources since the 1990s (Schweizer and Ayé 2007, Pavlova et al. 2008). Moreover, *riparia* and *diluta* are already considered separate species by the four main global avian checklists (Howard & Moore 2021, eBird/Clements 2024, HBW-BirdLife 2024, IOC 2024). The absence of conflict between global checklists before the formation of WGAC excluded this split from WGAC discussions.

Riparia riparia breeds throughout Europe, northwestern Africa, Asia, and North America; *R. diluta* breeds from southern Siberia and western Mongolia south to eastern Iran, Afghanistan, northern India, and southeastern China (Pavlova et al. 2008). The two species can be found in separate breeding colonies in a wide area of sympatry in central Asia (Sangster et al. 2011, Turner 2020) or in colonies with both species but no mixed pairs (Sangster et al. 2011); which would undoubtedly support species status for *riparia* and *diluta* under the Biological Species Concept. *R. riparia* and *R. diluta* have different habitat preferences in the area of overlap; *R. riparia* nests closest to rivers, other freshwater habitats, and the ocean, whereas *R. diluta* shows a preference to nest in arid steppes (Sangster et al. 2011).

Morphology

Bank Swallows and Pale Martins differ in the coloration of the upperparts, throat, and breastband (Sangster et al. 2011). The Bank Swallow has a grayish brown mantle, rump, and wing coverts, contrasting with darker brown remiges and rectrices; the throat is white, and the breastband is brown (Garrison and Turner 2020). The Pale Martin is paler and grayer than the Bank Swallow, especially on the crown and back, the throat is washed-buff, and the breast-band is faded and indistinct (Schweizer and Ayé 2007, Garrison and Turner 2020). Both species differ in the depth of the tail fork, which is slight in the medium-length tail in the Bank Swallow and shallower in the Pale Martin (Schweizer and Ayé 2007, Sangster et al. 2011, Garrison and Turner 2020).

Vocalizations

There is no formal analysis of vocalizations. Some authors consider that there are differences in the alarm call (Sangster et al. 2011). The voice of the Pale Martin is described as soft and burbling compared to the vocal calls of the Bank Swallow; however, much variation exists, and whether all calls can be positively identified remains questionable (Schweizer and Ayé 2007).

Genetics

Pavlova and collaborators (2008) examined mitochondrial DNA (ND2) of 88 *R. riparia* from 15 Eurasian and four North American breeding localities and of 33 *R. diluta* from four breeding localities. The authors also sequenced a nuclear intron (MUSK I3) from nine individuals representing unique mitochondrial haplotypes. Maximum likelihood phylogenies, one based on mtDNA and the other based on the intron, showed reciprocal monophyly for *R. riparia* and *R. diluta* from Mongolia and *R. diluta* from Central Siberia. Estimates of time to the most recent common ancestor between *R. riparia* and *R. diluta* suggested that the two species diverged between the late Pliocene and the middle Pleistocene.

New information:

Recent studies have increased our understanding of the species pair *R. riparia* - *R. diluta*, including detailed studies in contact zones.

Morphology

Gryaznova and Savchenko (2017) measured wing length, tail length, tail split, tarsometatarsus length, and beak length. They found significant differences in morphometry. However, the measurements of both species overlap (Table 1 from Gryaznova and Savchenko 2017).

collection specin	iens)				
Parameter n		R. riparia	n	R. diluta	Р
Mass, g	79	14.7 ± 0.12 (11.9–17.9)	298	12.5 ± 0.06 (10.0–15.7)	< 0.001
LW, mm	113	110.8 ± 0.23 (105.0-116.0)	319	104.2 ± 0.13 (97.0-111.0)	< 0.001
	25	$110.2 \pm 0.44 \ (105.0 - 114.0)^*$	47	103.5 ± 0.39 (98.0–110.0)*	< 0.001
LT, mm	34	54.3 ± 0.39 (49.8–59.5)	39	49.3 ± 0.27 (45.8–52.8)	< 0.001
	25	53.5 ± 0.42 (47.3–57.1)*	43	48.9 ± 0.26 (45.5–53.8)*	< 0.001
TS, mm	106	9.2 ± 0.15 (5.0–13.0)	193	7.2 ± 0.09 (3.0–10.0)	< 0.001
	25	9.7 ± 0.28 (7.0-12.5)*	42	7.7 ± 0.22 (5.0–10.5)*	< 0.001
TM, mm	34	$10.6 \pm 0.06 (10.0 - 11.5)$	37	$10.3 \pm 0.04 \ (9.8 - 10.9)$	< 0.001
	25	$10.2 \pm 0.04 \ (9.9 - 10.6)^*$	46	9.9 ± 0.07 (7.0-10.3)*	< 0.001
LB, mm	35	7.0 ± 0.04 (6.5–7.5)	37	6.7 ± 0.04 (6.1–7.0)	< 0.001
	19	6.94 ± 0.03 (6.5–7.2)*	45	6.58 ± 0.06 (4.6–7.8)*	<0.010
LMN, mm	108	4.76 ± 0.03 (4.0–5.6)	108	$4.39 \pm 0.02 \ (3.7 - 5.1)$	< 0.001
	19	4.75 ± 0.03 (4.5–5.0)*	45	4.29 ± 0.04 (3.6-4.9)*	< 0.001

Table 1 from Gryaznova and Savchenko 2017.

 Table 1. Morphometric parameters of the sand and pale sand martins of Central Siberia (live and freshly obtained birds, collection specimens)

(LW) Length of the wing, (LT) length of the tail, (TG) tail split, (TM) length of the tarsometatarsus, (LB) length of the bill from the forehead, (LBN) length of the bill from the front tip of nostril, (*n*) number of specimens. The parentheses show the range. (*) Collection specimens.

Schweizer et al. (2018) measured museum specimens from the breeding ranges of both species, 120 individuals of *R. diluta* and 131 individuals of *R. riparia*. The measurements analyzed were wing length (maximum chord), tail length, and depth of tail fork. The authors tested whether the subspecies within *R. diluta* or *R. riparia* were differentiated and found no clear separation at the subspecific level.

Nesting habitat and behavior

An extensive contact zone is found in southern Central Siberia. Gryaznova and Savchenko (2017) examined 93 colonies of *R. riparia* and *R. diluta* and added information on 16 colonies based on museum collections. Of the 109 colonies, 80 were exclusively inhabited by *R. diluta*, 12 by *R. riparia*, and 17 by both species. Mixed colonies were common in the sympatry zone. The authors noted that the colonies of *R. diluta* are located in higher cliffs than colonies of *R. riparia*, an average of 3 m vs. an average of 1.5 m, respectively. Mixed colonies were found at heights of 1.8 - 2.2 m. The colonies of *R. diluta* were located where vegetation was sparser and steppelike.

Scherbakova and Korobitsyn (2020) examined nest hole positions in a mixed colony of *R*. *riparia* and *R*. *diluta* in the Tom river in southern Russia. Of 745 holes, 489 were occupied by *R*. *diluta* and 256 by *R*. *riparia*. The nests were located in single species segments or together but at separate heights, the Pale Sand Martin *R*. *diluta* occupied the higher nest holes in the colony (Figure 1). The authors recorded the timing of arrival to the colony, *R*. *diluta* arrived at the nesting site approximately a week earlier than *R*. *riparia*, but that did not affect the timing of breeding, which began at similar times for both species. Using a videoscope, they recorded 53 clutch sizes of *R*. *diluta* and 45 of *R*. *riparia*, and found no significant differences between species (*R*. *diluta* 4.0 +/- 0.08 eggs, *R*. *riparia* 4.04 +/- 0.08 eggs). None of the monitored pairs were mixed between the two species.

Figure 1. Diagram of the nesting hole position in a mixed colony of *R. riparia* (black dots) and *R. diluta* (gray dots). The bottom line represents the low horizon. Figure taken from Scherbakova and Korobitsyn (2020).

Genetics

Schweizer et al. (2018) sequenced one mitochondrial (ND2), one autosomal (FIB7), and one Zlinked nuclear (MUSK) marker from 87 individuals sampled from across the ranges of both *R. riparia* and *R. diluta* (Figure 2). They supplemented the data with 123 mitochondrial sequences from Pavlova et al. (2008). Bayesian Inference phylogeny built with ND2 and a BEAST tree built with the concatenated dataset confirmed the reciprocal monophyly of *R. diluta* and *R. riparia*. The data showed strong genetic structure within *R. diluta*, differentiating the subspecies *R. d. diluta* from Central Asia, *R. d. indica* from northwestern India, *R. d. tibetana* from the Tibetan Plateau, and *R. d. fohkienensis* from southeastern China (Figure 3, left). Contrarily, there was no genetic structure within *R. riparia* (Figure 3, right).

Tang et al. (2021) studied gene flow among three subspecies of *R. diluta: R. d. diluta, R. d. fohkienensis*, and *R. d. tibetana*. They also included samples of *R. riparia* from eastern Asia. Analysis of genetic data (genotyping by sequencing) showed no signal of gene flow between *R. d. tibetana*, although limited shared ancestry between *R. d. diluta* and *R. d. tibetana*. Of interest for species limits between *R. diluta* and *R. riparia*, there was no signal of gene flow between them (Figure 4).



Figure 2. Breeding ranges of the subspecies of *Riparia diluta* and *R. riparia*. Black stars represent sample locations for sequences in Pavlova et al. (2008). Red stars represent new sample locations. Figure taken from Schweizer et al. (2018).



Figure 3. 50% majority consensus trees of Bayesian Inferences based on ND2 data. Left, tree with focus on the subspecies of *Riparia diluta*. Right, tree with an emphasis on *R. riparia*. Phylogeny from Schweizer et al. (2018).



Figure 4. Map with pie charts and bar plots representing genome-wide ancestry assignment with K=4 using NgsAdmix. Figure taken from Tang et al. (2021).

The swallow phylogeny from Schield et al. (2024) included three samples from *R. riparia* (one from western Paleartic, one from eastern Paleartic, and one from North America) and two samples from *R. diluta* (one from Mongolia and one from Russia). The analysis based on UCE loci showed reciprocal monophyly between both species with high support (100%).

Recommendation:

The sympatry of breeding colonies of *R. riparia* and *R. diluta* without any sign of interbreeding is reason enough to split *riparia* from *diluta*. Additionally, plumage coloration and genetics support the split. Therefore, I recommend adopting the split of *R. diluta* from *R. riparia* and aligning with global checklists. This split is well overdue.

a) Please vote YES or NO to the split.

There is little consensus on the English name currently in use for each of the two species. For *R. riparia*, the names are Bank Swallow (ebird/Clements and IOC), Sand Martin/Bank Swallow (Howard & Moore), and Collared Sand Martin (HBW-BirdLife). For *R. diluta*, the names are Pale Martin (eBird/Clements, Howard & Moore, and IOC) and Pale Sand Martin (HBW-BirdLife). In the Forty-fifth Supplement to the AOU Check-list (Banks et al. 2004), the committee considered and rejected the suggestion to change the English name of *Riparia riparia* from Bank Swallow to Sand Martin. For *R. riparia*, we either keep the current name in the AOS checklist (Chesser et al. 2024), Bank Swallow, which is the same one as in ebird/Clements and IOC, or adopt a different name through a separate proposal. I recommend keeping the English name for this species to include in the Notes. For *R. diluta*, I recommend adopting the name Pale Martin, as used by eBird/Clements, Howard & Moore, and IOC.

b) Please vote YES or NO to keep the English name Bank Swallow for *R. riparia*, and to adopt the English name Pale Martin for *R. diluta*.

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Submitted by: Rosa Alicia Jiménez, Universidad de San Carlos de Guatemala

Date of proposal: 10 March 2025

2025-C-5 N&MA Classification Committee p. 565

Transfer Fan-tailed Warbler Basileuterus lachrymosus to Euthlypis

Effect on NACC:

If this proposal is approved, the Fan-tailed Warbler *Basileuterus lachrymosus* would be transferred back to the genus *Euthlypis*. The genus transfer would not require a linear change in the checklist but would require a new genus heading for *Euthlypis*.

Background:

The Fan-tailed Warbler was long placed in the monotypic genus *Euthlypis*. However, following the most recent phylogeny (of the time) of the Parulidae (Lovette et al. 2010), it was transferred to the genus *Basileuterus* (Chesser et al. 2011). In the Lovette maximum likelihood phylogeny (based on 5847 mitochondrial and 4602 intron nucleotides), the Fan-tailed Warbler was shown to be the sister species of *Basileuterus* warblers (*rufifrons*, *melanogenys*, *belli*, *hypoleucus*, *culicivorus*, *trifasciatus*, *tristriatus*), with a bootstrap support of 91.

Proposal <u>2010-B-10</u> suggested changes within the family Parulidae, including transferring the Fan-tailed Warbler from *Euthlypis* to *Basileuterus*. This was just one change within a comprehensive proposal to accept the new classification recommended by Lovette et al. (2010). Seven committee members voted YES, two voted NO, and one abstained. However, two committee members who voted YES commented that *Euthlypis* could still be retained, although not necessarily considering the strong phylogenetic evidence (<u>NACC comments on proposal</u> <u>2010-B-10</u>). Therefore, *Euthlypis lachrymosa* was transferred to the genus *Basileuterus* and the species name was changed to *lachrymosus* (Chesser et al. 2011).

New information:

A recent phylogeny of the family Parulidae (Zhao et al. 2025), based on 4186 UCE loci, recovered the Fan-tailed Warbler as sister to the clade *Basileuterus* + *Cardellina* + *Myioborus* with 100% bootstrap support (Fig. 1, next page). The authors discussed that the position of the Fan-tailed Warbler in Lovette et al. (2010) was likely driven by mitochondrial data, which can be explained by mito-nuclear discordance. Given the unique morphology, distinctive behavior, foraging ecology, and strong support in the UCE analysis, the authors recommended resurrecting *Euthlypis* Cabanis, 1850.

Recommendation:

The new phylogeny based on genomic data recovered the Fan-tailed Warbler as separate from the genus *Basileuterus* with strong node support. The Fan-tailed Warbler was sister to a clade consisting of *Basileuterus* + *Cardellina* + *Myioborus*. For the classification to represent evolutionary relationships, this species cannot be retained in *Basileuterus*; therefore, *B. lachrymosus* should be transferred back to *Euthlypis*, and the species name should again be *lachrymosa*. I recommend a YES to the genus transfer.

Please vote YES or NO to the genus transfer.



Figure 1. Relevant part from Figure 2 of Zhao et al. (2025). Concatenated tree of the taxa with good quality DNA based on filtered UCE dataset. Values at nodes are ultrafast bootstrap support values, * indicates full support.

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Submitted by: Rosa Alicia Jiménez, Universidad de San Carlos de Guatemala

Date of proposal: 12 March 2025

2025-C-6 N&MA Classification Committee

pp. 466-467

Treat Black-crested Titmouse *Baeolophus atricristatus* and Tufted Titmouse *B. bicolor* as a single species

Effect on NACC:

If approved, this proposal would merge the species *Baeolophus atricristatus* and *B. bicolor* into a single species.

Background:

The genus Baeolophus currently includes five species of titmice distributed in oak and juniper woodlands as well as mixed deciduous forests in the United States and Mexico. *Baeolophus* was recognized based on DNA-DNA hybridization data (Slikas et al. 1996, Banks et al. 1997) and is well differentiated from other parids (Sheldon et al. 1992, Gill et al. 2005, Johansson et al. 2013). Baeolophus bicolor (Tufted Titmouse) is widespread and abundant throughout much of the eastern and central United States, whereas B. atricristatus occurs from southernmost Oklahoma through much of central Texas and northeastern Mexico. The two forms come into contact in southern Oklahoma and central Texas (Fig. 1) where precipitation varies from wetter in the northeast to drier in the southwest. The area of overlap includes two well-studied transects: a younger contact zone in southwestern Oklahoma and an older contact zone in northern Texas (Curry and Patten 2014, Semenov et al. 2023). These species were long considered conspecific based on apparently free interbreeding in zones of overlap (Allen 1907, Dixon 1955, 1978, 1990). However, the AOU split them into the two currently recognized species (Banks et al. 2002) on the basis of genetic (Braun et al. 1984, Avise and Zink 1988, Sheldon et al. 1992) and vocal evidence (Dixon 1955, Coldren 1992). Here, we provide an overview of new information on this species complex and their hybrid zone dynamics, including modern genomic studies of hybridization and introgression, ecological variation, and phenotypic differences both temporally and spatially. Taken together, these data suggest that re-lumping the two species is the most appropriate treatment.

New Information:

Phenotypic Variation: Overall, *B. atricristatus* and *B. bicolor* are similar in body size and other morphometric measurements, but differences between allopatric populations in body size and crest length have been documented (Curry and Patten 2014). Phenotypic differences are most pronounced in color and song. The two forms have similar plumage for most feather tracts but differ prominently in the color of their forehead and crest. *B. atricristatus* has a buffy-white forehead and a longer, melanized crest that is black in adult males and dark gray in females and immatures. *Baeolophus bicolor* has a black forehead and a shorter gray crest. More subtle differences in back and rump color have also been documented (Dixon 1978, Curry and Patten 2014). Intermediate phenotypes are found where the two forms come in contact, with a gradual transition in both morphometric and plumage characters (Fig. 1). Intermediate phenotypes are largely constrained to the hybrid zones, whereas parental types are far more prevalent outside these areas (Dixon 1955, 1990).



Figure 1: Geographic distributions and phenotypic variation in the *Baeolophus atricapillus* x *Baeolophus bicolor hybrid zone.* (A) Geographic distributions and zone of contact of the two currently recognized species. (B) plumage phenotypic scoring index based on crest and forehead color. (C) and (D) show the location of the younger and older transects that have been studied, as well as how phenotypic indices vary spatially. Figure from Curry and Patten 2014.



Figure 2: Vocal variation in the *Baeolophus* contact zone, including spectrograms of between (A) *Baeolophus bicolor* and (B) *Baeolophus atricristatus*. (C) shows variation in song indices across the two contact zones combined, with *B. bicolor* in white and *B. atricristatus* in black. Figure from Curry and Patten 2019.

Slight vocal differences have also been documented between *B. atricristatus* and *B. bicolor* (Coldren 1992, Curry and Patten 2019). Namely, *B. atricristatus* songs typically have fewer notes per phrase, longer song duration, more phrases per song, longer note duration, shorter phrase durations, and higher frequency songs compared to *B. bicolor* (Figure 2A, 2B). Interestingly, the northern, younger transect exhibits vocal differences associated with environmental variation across the contact zone, whereas the southern transect does not (Curry and Patten 2019). Nonetheless, intermediate song types occur in both contact zones, with a gradual transition in overall song characters in both transects (Figure 2C).

Ecological and Habitat Variation: The contact zone between *B. bicolor* and *B. atricritatus* spans an ecological gradient that varies in precipitation and transitions from more deciduous forests in the east to arid and open woodlands in the west (Dixon 1955, Martinez and Veech 2024). Hybrid individuals appear to favor intermediate habitat characteristics (Martinez and Veech 2024), while microhabitat preferences are fairly similar between the two (Dixon 1955).

Molecular Studies: *Baeolophus bicolor* and *B. atricapillus* differ in mtDNA by 0.4–0.6% (Avise and Zink 1988), suggesting a crown age for the sister species pair of ~250,000 years. Recently, Semenov et al. (2023) conducted a thorough genomic analysis of both transects and parental types outside of the contact zone to examine hybrid zone dynamics. Specifically, they used a 'genotype-by-sequencing' (GBS) approach to generate a panel of thousands of single-nucleotide polymorphisms (SNPs) from 120 individuals. The authors then conducted a suite of population genetic structure and hybrid zone analyses to explore both broader geographic patterns of genetic differentiation and infer any evidence of hybridization, backcrossing, and introgression in both transects.

Semenov et al. (2023) first conducted a STRUCTURE analysis, which indicated that B. bicolor and *B. atricapillus* are distinct genetic clusters outside of the contact zone (Fig. 3A). In both the younger and older contact zones, individuals exhibit mixed ancestry, gradually exhibiting increasing *B. bicolor* ancestry as one moves from west to east along the ecotone (Fig. 3A). This is also evident in a PCA plot, where allopatric populations are distinct and hybrids and backcrosses of mixed ancestry are intermediate in their genetic composition (Fig. 3B). A geographic cline analysis estimated that the younger (northern) hybrid zone is nearly four times narrower (width = 43.8 km, 2 log likelihood limits = 25.5–73.3 km) compared to the older (southern) hybrid zone (width = 178.9 km, 2 log likelihood limits = 121.5–218.8 km). The author compared these findings to expectations and simulations of different hybrid zone dynamics, including a tension zone in which zone width is determined by the interplay between the dispersal of parental genotypes into the region of hybridization and selection against admixed genotypes that are maladaptive (Slatkin 1973, Barton and Hewitt 1985). Specifically, the authors compared their empirical findings to a model of unrestricted hybridization and neutral diffusion following the theoretical predictions of the tension zone model using a dispersal distance of 0.248 km (Rylander et al. 2020) and hybrid zone ages of 60 and 150 years for the younger zone (Sutton 1967) and 4,000 years ago for the older zone (Dixon 1978). Based on these parameter settings, Semenov et al. (2023) inferred the estimated width for a hybrid zone of neutral diffusion to be 21-34 km for the younger and 174 km for the older transect. As such, the observed hybrid zone widths (26-73 km for the younger transect, and 122-219 km for the older transect) better match a model of neutral diffusion than one of a tension zone that balances



Figure 3: Genomic analyses of *Baeolophus* hybrid zone dynamics from Semenov et al. (2023) including (A) Structure plot and (B) PCA plot.

dispersal of parental types into the hybrid zone with selection against hybrids. In other words, these hybrid zones appear to exhibit more interbreeding, advanced generation hybrids, and backcrossing than would be expected if hybrids were at a selective disadvantage compared to parental types.

Semenov et al. (2023) further demonstrated that within the contact zone, there are few (8% in younger transect) to no (0% in older transect) individuals of pure parental ancestry of either type. The study documented no individuals that could be assigned as F1 hybrids; rather, the vast majority of individuals were F2 or more advanced generation hybrids and backcrosses. The lack of F1s is somewhat surprising but could be attributed to the considerable width of the contact zone. In order for F1s to occur, two pure parentals of either type must produce offspring, and it seems that pure parentals are restricted to either end of the contact zone. As such, individuals in the contact zone are either late-generation backcrosses or advanced F2 hybrids. Increased sampling would likely reveal F1s, but they do seem rare given that this study included 80 individuals from the two contact zones combined and found no F1 hybrids. These patterns are visualized via triangle plots of their data, which demonstrates how individuals in the contact zone and types in either contact zone. Such high levels of introgression suggest that there are few if any barriers to gene flow between these types when they come into

contact and that they produce viable offspring that can then go on to reproduce with other hybrid and parental types. The authors provided a visual aid (Figure 4A) to illustrate how heterozygosity and hybrid index can be interpreted for different ancestry types within a contact zone.



Figure 4: Triangle plots illustrating observed heterozygosity and hybrid indexes for individual *Baeolophus* titmice found in both the young and old contact zones. Panel (A) shows how to interpret triangle plots in terms of what is expected for parental, backcross, F1, and advanced hybrid individuals.

Recommendation:

Under the biological species concept, I recommend a YES vote to lump *B. atricapillus* and *B. bicolor* given the shallow level of overall genetic divergence (~0.5% mtDNA) and strong evidence of a hybrid swarm where the forms overlap—including many F2 hybrids and rampant backcrossing. Although there may be some evidence of differences in habitat type and phenotypes, this is to be expected in a widespread species that spans broad ecological gradients. With these detailed genomic analyses in hand, I believe these forms are more consistent with subspecies that exhibit slight phenotypic and ecological differences that are geographically localized, but little reproductive isolation where they come into contact, with free interbreeding between parental and admixed individuals.

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Submitted by: Nicholas A. Mason, Louisiana State University

Date of proposal: 13 March 2025

2025-C-7 N&MA Classification Committee p. 280

Transfer Alpine Swift Apus melba to Tachymarptis

Effect on NACC

If approved, this proposal would transfer Alpine Swift Apus melba from Apus to Tachymarptis.

Background

Typical swifts (Apodini) in the genus *Apus* (Scopoli 1777) represent around 20 species widely distributed across Africa, Europe, and Asia. The Alpine Swift (*Apus melba*), a rare visitor to our area, is sometimes separated from other *Apus* species and placed in the genus *Tachymarptis* (Roberts, 1992) based on its larger size, differences in nestling foot structure, and feather lice (Brooke, 1970; Brooke, 1972). The current AOS Checklist (7th edition) places the Alpine Swift in the broader genus *Apus*. However, as of 2023, three of the four global checklists treated Alpine Swift (and Mottled Swift *A. aequatorialis*) in the genus *Tachymarptis* (Dickinson and Remsen, 2013; Gill et al., 2024; HBW and BirdLife International, 2024), whereas eBird/Clements retained it in *Apus*. In 2023, the Working Group on Avian Checklists (WGAC) voted on this discrepancy and chose to recognize the genus *Tachymarptis*, although one vote opposed the transfer. Subsequently, Clements et al. (2024) transferred *A. melba* to *Tachymarptis*, bringing all global lists into agreement.

New Information

Previous molecular studies have shown mixed support for a sister relationship between Apus and Tachymarptis. Thomassen et al. (2005) placed the Alpine Swift within Apus, whereas Price et al. (2004) suggested a sister relationship. More recently, Päckert et al. (2012) reconstructed a nearly complete species-level phylogeny of Eastern Hemisphere swifts (Apodini) using two mtDNA genes and four nuclear markers, also finding evidence for a sister relationship between Apus and Tachymarptis (Fig. 1). Their data also indicated that genetic divergence (uncorrected p-distance) between the two genera is similar to the divergence observed between Apus and Cypsiurus (Appendix 1). Beyond genetics, Päckert et al. (2012) argued that the distinctiveness of Tachymarptis is supported by other factors, including differences in host-specific feather lice, the unique foot structure of Alpine Swift nestlings, and notable vocal differences from



Figure 1. Phylogeny from Päckert et al. (2012).

Apus (Cramp, 1985). Indeed, the voice of *Apus* is quite uniform among species and very different from that of the Alpine Swift (Boesman, pers. comm.). The spectrogram of the Alpine Swift (Fig. 2) shows much narrower-frequency calls than the typical call of *Apus* (Fig. 3).



Figure 2. Alpine Swift, Portugal. ML477326381.



Figure 3. Apus apus, Spain. ML597256831.

Recommendation

The simplest approach would be to refrain from splitting the genus *Apus*. However, I suggest that the committee approve this transfer. Adopting this classification would align with the four global checklists and the recommendation put forth by WGAC. Furthermore, the species is a rare vagrant in our area, with only five records in the Caribbean, all from Barbados (Ławicki and van den Berg, 2015).

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Submitted by: Nicholas Vinciguerra, Museum of Southwestern Biology

Date of proposal: 14 March 2025

	C par	C bal	Taeq	T mel	А рас	A acu	A hor	A nip	A aff	A bal	A bar	A caf	A bra	A bat	A ber	A nia	A ale	A uni	A ap	A pal
C. parvus																				
C. balasiensis	4%																			
T. aequatorialis	6%	5%																		
T. melba	7%	5%	3%																	
A. pacificus	5%	4%	3%	3%																
A. acuticauda	6%	4%	4%	3%	2%															
A. horus	6%	4%	3%	3%	3%	3%														
A. nipalensis	6%	4%	4%	3%	3%	3%	2%													
A. affinis	6%	5%	4%	4%	4%	4%	3%	1%												
A. balstoni	6%	5%	3%	4%	3%	4%	3%	3%	3%											
A. barbatus	6%	4%	3%	3%	3%	3%	2%	2%	3%	1%										
A. caffer	5%	3%	4%	3%	3%	3%	2%	3%	3%	2%	2%									
A. bradfieldi	5%	4%	3%	3%	2%	3%	2%	2%	2%	1%	0%	1%								
A. batesi	6%	4%	3%	4%	3%	3%	2%	3%	3%	2%	2%	1%	1%							
A. berliozi	5%	4%	3%	3%	2%	3%	2%	2%	3%	1%	1%	2%	0%	2%						
A. niansae	5%	5%	3%	4%	3%	4%	3%	3%	3%	2%	2%	2%	1%	2%	1%					
A. alexandri	7%	5%	5%	5%	4%	4%	3%	3%	4%	3%	3%	2%	2%	3%	3%	3%				
A. unicolor	5%	4%	3%	4%	3%	3%	3%	2%	3%	1%	1%	2%	1%	2%	1%	1%	2%			
A. apus	6%	5%	3%	4%	3%	4%	3%	3%	3%	2%	2%	2%	1%	2%	1%	2%	3%	1%		
A. pallidus	6%	5%	4%	4%	3%	4%	3%	3%	3%	2%	2%	3%	1%	2%	1%	2%	3%	1%	1%	0
	Cypsi	urus vs	Apus	Cy	psiurus	s vs Tac	hymarµ	otis	Tacl	nymarp	tis vs A	pus								

Appendix 1. Divergence (p-distance) between species of *Cypsiurus*, *Tachymarptis*, and *Apus* (based on Päckert et al. 2012).

	, ,	21	5	,	
min p-distance (%)	3%	5%		3%	
max p-distance (%)	7%	7%		5%	

2025-C-8 N&MA Classification Committee p. 576

Treat Red-crowned Ant-Tanager Habia rubica as more than one species

Effect on NACC:

Acceptance of this proposal would remove *Habia rubica*, which would be restricted to South America, from the NACC area, and would add four or five newly recognized species to the checklist.

Background:

The Red-crowned Ant Tanager *Habia rubica* (Cardinalidae) is a highly polytypic taxon with marked geographical variation; up to 14 subspecies have been recognized, most of which were described based on variation in the hue and intensity of plumage color (Hilty, 2011). Its current distribution ranges from central Mexico to northeastern Argentina and southeastern Brazil and encompasses regions with very different ecological conditions or separated by recognized biogeographical barriers (Hilty, 2011).

Ridgway (1902) placed *Habia rubica* in the tanagers, which included 21 genera. One of them was *Phoenicothraupis* (Cabanis 1850). According to Ridgway (1902), the genus *Phoenicothraupis* (described by Cabanis 1850 with the type *Saltator rubicus* Vieillot) had three species: *Phoenicothraupis rubica* (with five subspecies: *P. r. rubicoides*, *P. r. nelsoni*, *P. r. vinacea*, *P. r. affinis*, *P. r. rosea*), *Phoenicothraupis salvini* (with five subspecies), and *Phoenicothraupis fuscicauda* (monotypic). Ridgway (1902) described the genus *Phoenicothraupis* as follows:

Medium-sized Tanagers superficially resembling the more uniformly colored species of *Piranga*, but outermost (ninth) primary shorter than second (instead of decidedly longer than third); adult males with a scarlet crown-patch and with more or less red on under parts (sometimes confined to the throat); females and young brown or olive above, paler below. Bill as in the more slender-billed species of *Piranga* but narrower (width at base scarcely if at all exceeding basal depth), the gonys relatively shorter, and distinctly, though slightly, convex, and maxillary tomium without any indication of a tooth-like projection. Nostrils narrower. Rictal bristles strong, conspicuous, and frontal bristles (over nostrils) well developed. Wing about three and three-fourths to a little more than four times as long as tarsus, much rounded (seventh to fourth primaries longest, ninth shorter than second); primaries exceeding secondaries by much less than length of tarsus. Tail shorter than wing by much less than length of tarsus, sometimes nearly as long as wing, more or less rounded, the rectrices rather broad, with rather loose webs and somewhat pointed tips. Tarsus decidedly longer than middle toe with claw; outer claw reaching about to or a little beyond base of middle claw, the inner claw falling short of the latter; hind claw shorter than its digit.

Coloration.—Adult males reddish brown, reddish gray, or dusky, with bright red throat and crown, the feathers of the latter sometimes developed into a more or less obvious crest; females and young usually brownish above, paler beneath, with or without a yellowish-bufl'y or tawny crown-patch; adult female sometimes similar to

the male, but duller.

Range.—Southern Mexico to southern Brazil, Paraguay, Bolivia, and western Ecuador.

Phoenicothraupis was placed in *Habia* by Hellmayr (1936) and subsequent classifications. The genus *Habia* was until recently placed in the Thraupidae, but we now treat it in the Cardinalidae (Burns et al. 2014).

The AOS currently treats *Habia rubica* as single species (AOU 1983, AOU 1998). Hilty (2020) recognized 17 subspecies as follows:

- *H. r. rubica*: southeastern Brazil (southern Minas Gerais) to eastern Paraguay and northeastern Argentina
- H. r. bahiae: tropical eastern Brazil (Bahia)
- *H. r. rubicoides*: southern Mexico (Puebla and eastern Veracruz) to northern Nicaragua
- *H. r. holobrunnea*: subtropical eastern Mexico (southern Tamaulipas to Veracruz and northern Oaxaca)
- *H. r. nelsoni*: southeastern Mexico (Yucatán Peninsula north of southern Campeche)
- *H. r. alfaroana*: northwestern Costa Rica (Guanacaste Peninsula)
- *H. r. vinacea*: Pacific slope of southwestern Costa Rica (Nicoya Peninsula) to eastern Panama
- *H. r. affinis*: Pacific slope of southern Mexico (Oaxaca)
- *H. r. rosea*: Pacific slope of southwestern Mexico (Nayarit and Jalisco to Guerrero)
- *H. r. rubra*: Trinidad
- *H. r. crissalis*: coastal mountains of northeastern Venezuela (Anzoátegui to Sucre)
- *H. r. mesopotamia*: Venezuela (Río Yuruán region of eastern Bolívar)
- *H. r. coccinea*: eastern base of eastern Andes of north-central Colombia and western Venezuela
- *H. r. rhodinolaema*: southeastern Colombia east of the Andes to northeastern Peru and far northwestern Brazil
- *H. r. peruviana*: tropical eastern Peru to central Bolivia and adjacent western Brazil
- *H. r. hesterna* River (eastward to Rio Xingu), southward to northern Mato Grosso
- *H. r. perijana*: Sierra de Perijá (Colombia/Venezuela border)

New information:

Three recent studies were published on *Habia rubica*. One (Lavinia et al. 2015) was a phylogeographic analysis that suggested that this species originated in South America, where there are at least two clearly differentiated clades: one in the Atlantic Forest of Brazil and another in the Amazon basin. However, limited taxon-sampling precluded detailed investigation of diversification within Central America and southern Mexico. The other two studies (Ramirez-Barrera 2018, 2019) provided new evidence, one using multilocus data and the other, plumage

color.

Lavinia et al. (2015) sequenced mtDNA and nDNA from 100 individuals from Mexico to Argentina. Their results are shown below (Bayesian and maximum parsimony, Fig. 1). Their geographic sampling did not include Panama and much of western Mexico. The most important result was the identification of two lineages in South American that split ca. 3.5 MA and two lineages in Middle America. Their analyses of vocalizations and plumage coloration found differences between the four main groups consistent with the molecular data.



Fig. 1. Bayesian majority rule consensus tree obtained from the analysis of 1743 bp of the concatenated mitochondrial dataset (mtDNA: COI + cyt *b*) showing four major clades recovered within *Habia rubica*. Subspecies are indicated to the right. "Indicates maximum node support of Bayesian posterior probability (PP) of 1.0 and maximum parsimony bootstrap (MP) of 100%; "denotes PP \ge 0.95 and MP \ge 95%; other values are indicated with numbers. Support values from most of the internal nodes were omitted for clarity. The tree was rooted with *Ramphocelus carbo* (not shown for simplicity). The map on the upper left shows the distribution of *H. rubica* and the collection sites. The colors of the symbols represent the major phylogroups. Distribution was based on BirdLife International and NatureServe (2013). (For interpretation of the web version of this article.)

Ramirez-Barrera et al. (2018) amplified mitochondrial and nuclear markers from 125 individuals of *H. rubica* covering the species' distribution, the other three species of *Habia* (*fuscicauda*, *atrimaxillaris*, *gutturalis*), and 16 samples from *Chlorothraupis* (*C. olivacea*, *C. carmioli* and *C. stolzmanni*). They found that *H. rubica* can be divided into three main clades: (1) western Mexico, (2) eastern Mexico to Panama, and (3) South America. Within these main clades they recognized seven main phylogroups, as shown in the next figure:



Figure 1. Geographical distribution, phylogenetic consensus tree, and haplotype network. (A) Geographical distribution (indicated by pink shading) and sampling points of *H. rubica*; the mitochondrial DNA sampling is represented by the color of the dots and the nuclear DNA sampling is highlighted with a black dot on the dot's color. ArcGIS (ArcMAP 10.2.2; Esri, Redlands, CA, USA). (B) Phylogenetic consensus tree representing the relationship among populations of *H. rubica*, based on Bayesian inference from a multilocus dataset. Values above branches denote posterior probabilities (PP). (C) Haplotype network, where the phylogroup "D" corresponds to individuals from the Chiapas-Yucatan peninsula to Costa Rica and "d" corresponds to individuals from Guatemala and El Salvador (the numbers inside of circles indicate the number of individuals that shared each haplotype).

Ramirez-Barrera et al.'s (2018) species delimitation analysis (BP&P) is shown on the following page; note the high speciation probabilities (0.97 to 1.0).

Ramírez-Barrera et al. (2019) analyzed genetic, coloration, and morphometric data from specimens from collections in Mexico and the United States and used the Multiple Matrix Regression with Randomization (MMRR) approach to evaluate the influence of geographic and environmental distances on genetic and phenotypic differentiation at both the phylogroup and population levels. They found that geographic isolation was the main factor structuring genetic variation within populations of *Habia rubica*; this suggests that climate did not playing a major role in within-species genetic differentiation.



Figure 2 Bayesian species delimitation. (A) Bayesian species delimitation results assuming seven species (lineages) from multilocus phylogeny of *H. rubica* (Finetune = 1). (B) Bayesian species delimitation results assuming seven species (lineages) from multilocus phylogeny of *H. rubica* (Finetune = 0, parameters estimated previously). The speciation probabilities are provided for each node under each combination of priors for τ and θ : top, priors $\theta \sim G(1, 10)$ and $\tau 0 \sim G(1, 10)$; middle, priors $\theta \sim G(2, 2000)$ and $\tau 0 \sim G(2, 2000)$; bottom, priors $\theta \sim G(1, 10)$ and $\tau 0 \sim G(2, 2000)$. We consider speciation probability values >0.95 as strong support for a speciation event.

Full-size 🖾 DOI: 10.7717/peerj.5496/fig-2

Recommendation:

We present two options:

(1) Separate *H. rubica* into seven species: This is based on phylogenetic evidence and some differences on plumage color.

- 1. *Habia rosea* (Nelson, 1898): Pacific coast of western Mexico (Jalisco, Nayarit, and Colima; lineage A in Figure 2)
- 2. *Habia affinis* (Nelson, 1897): Pacific coast of southwestern Mexico (Michoacan, Guerrero, and Oaxaca; lineage B in Figure 2)
- 3. *Habia holobrunnea* (Griscom, 1930): E Mexico from S Tamaulipas S to N Oaxaca (lineage C in Figure 2
- 4. *Habia rubicoides* (Lafresnaye, 1844): S Mexico (from Puebla, E Oaxaca, Tabasco, and Chiapas), Guatemala and Belize S to Honduras, El Salvador, and Nicaragua (lineage D in Figure 2).
- 5. *Habia vinacea* (Lawrence, 1867): Panama (lineage E in Figure 2)
- 6. *Habia rhodinolaema* (Salvin and Godman, 1883): Amazon basin (lineage F in Figure 2)
- 7. *Habia rubica* (Vieillot, 1817): southeastern Brazil, Argentina, and Paraguay (lineage G in Figure 2)

(2) As in Option 1 but treat lineages A and B as the same species (*Habia rosea – Habia affinis*). This option is to separate *Habia rubica* into six species based on two main arguments, the first being the low speciation probability value (<0.95) presented by the clade comprising the subspecies *H. r. rosea* and *H. r. affinis* in the BP&P analyses performed with multilocus data (Ramírez-Barrera et al. 2018). The second argument is the consistency of this grouping through two independent tests of the same analysis and with adjustment of specific parameters. At the morphological level, both subspecies are described as a polytypic group characterized by having paler plumage than the other subspecies of *H. rubica* (del Hoyo 2020). At the geographical level, the distribution of these two subspecies from western Mexico is clearly delimited by three large mountain ranges: the Eje Neovolcánico Transversal, the Sierra Madre del Sur, and the Sierra Madre Oriental. These geographical formations seem to have great influence on the genetic structure of the populations, acting as barriers to gene flow, which has possibly promoted the differentiation between the populations of eastern and western Mexico.

Species	Proposal 1	Species	Proposal 2			
1	1 Habia rosea (Nelson, 1898)		Habia affinis (Nolson, 1807)			
2	Habia affinis (Nelson, 1897)	-				
3	Habia holobrunnea Griscom, 1930	2	Habia holobrunnea Griscom, 1930			
4	Habia rubicoides (Lafresnaye, 1844)	3	Habia rubicoides (Lafresnaye, 1844)			
5	Habia vinacea (Lawrence, 1867)	4	Habia vinacea (Lawrence, 1867)			
6	Habia rhodinolaema (Salvin and	E	Habia rhodinolaema (Salvin and			
	Godman, 1883)	5	Godman, 1883)			
7	Habia rubica (Vieillot, 1817)	6	Habia rubica (Vieillot, 1817)			

We recommend Option 1 for the following reasons:

• The phylogenetic evidence supporting the differentiation between *H. r. rhodinolaema* and *H. r. rubica* in South America is consistent across two independent studies (Lavinia et al. 2015, Ramírez-Barrera et al. 2018), which present broad sampling and cover most of the distribution of both phylogroups. In addition, significant differences in traits such as song and coloration have also been reported (Lavinia et al. 2015), which support the probable differentiation between the two phylogroups. Furthermore, there is a geographic correspondence between the distribution ranges of the identified phylogroups (del Hoyo 2020), which could also indicate that geographic barriers in South America have influenced their genetic differentiation.

• The deep genetic structure reported between the phylogroups of Central America and eastern Mexico (Ramírez-Barrera et al. 2018) shows high support for the phylogenetic hypothesis obtained with multilocus data. This genetic structure corresponds to barriers to dispersal and gene flow such as the Talamanca Mountain Range in Costa Rica, the Motagua-Polochic- Jocotán fault system, and the Isthmus of Tehuantepec in southern Mexico, which could be promoting the reported genetic isolation and genetic differentiation. Analyses of differences between these groups for traits such as song and coloration could not be tested in

detail due to the low sampling available; however, a clear difference is reported between these phylogroups and the phylogroups distributed in South America (Lavinia et al. 2015).

• The five phylogroups distributed from central Mexico to South America show evidence of genetic and phenotypic differentiation, as well as geographic correspondence in their distributions. We consider this evidence sufficient to identify at least five clearly differentiated species. This would allow us to better explain the relatively weak patterns of variation among the subspecies described for this geographic range of *H. rubica*.

• The phylogroups distributed along the western slope of Mexico also show robust molecular differentiation supported by a phylogenetic hypothesis based on multilocus data that shows a profound divergence between those distributed in the north and south of this region (Ramírez-Barrera et al. 2018). This evidence is supported by very complete sampling, which covers the entire distributional range of *H. rubica* and leaves no room for doubt about the genetic structure of the species in this region. In addition, there is evidence of geographic correspondence with barriers such as the Transversal Neovolcanic Belt, the Sierra Madre del Sur, and the Sierra Madre Oriental, which limit the distribution of populations and have kept them isolated for long periods of time, which has favored the deep genetic differentiation (Ramírez-Barrera et al. 2018). There is no evidence of song differentiation as in the previous cases; however, both phylogroups are recognized as a polytypic group whose coloration is markedly paler than that reported in the rest of the species (del Hoyo 2020), which could add evidence on the degree of differentiation that these groups present.

• *Habia rubica* is widely described as a polytypic species with a very wide distribution; however, it has also been described as a species in which "differences between the racial groups are not always clear-cut or pronounced" (del Hoyo 2020). "Several of the numerous races are weakly differentiated and seem barely worth recognizing" (del Hoyo 2020). This apparently weak phenotypic differentiation, coupled with the complicated field identification of the different subspecies (especially those with sympatric distribution), makes it necessary to consider all those genetic, geographical, and phenotypic elements (e.g., pink coloration of phylogroups from western Mexico) as sufficient arguments to be able to recognize these groups as independent species.

Voting:

Please vote on the following:

- (A) Separate *H. rubica* into more than one species (YES/NO).
- (B) If voting YES on part A, specify whether you favor 6 species, 7 species, or a different number of species (with details).

English names:

If the proposal passes, a follow-up proposal on English names is needed. We should also coordinate with SACC on this proposal.

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Submitted by: Blanca E. Hernández-Baños & Sandra M. Ramírez-Barrera

Date of proposal: 14 March 2025

2025-C-9 N&MA Classification Committee p. 668

Treat Gray-crowned Goldfinch *Carduelis caniceps* as a separate species from European Goldfinch *C. carduelis*

Effect on the NACC:

If this proposal is accepted, *Carduelis carduelis*, an introduced species in the NACC area, will be split into two species: *C. carduelis* and *C. caniceps*. *C. caniceps* is extralimital, though it should be noted that there are occasional reports of escaped individuals (i.e., ML301392991). The split would thus not add a species to the checklist, but it would require changes to the Notes and the geographic distribution in the species account for *C. carduelis*.

Background:

The two groups have usually been treated as conspecific as they were said to hybridize broadly in southwestern Siberia and narrowly in Iran. Recently, however, del Hoyo and Collar (2016) treated them as separate species based on plumage differences.

Plumage Differences:

There are multiple subspecies within each group with *C. carduelis* most authorities recognize 10 subspecies, and *C. caniceps* three to four. Within each group the differences are minor and some authors have only recognized six subspecies in *carduelis* (Shirihai and Svensson 2018). The two groups, however, differ markedly with *carduelis* having a black crown and line behind the ear coverts (lacking in *caniceps*), whiter face, warm brown (rather than cold gray) breast, mantle, wing coverts, and lower back, white tips to secondaries and tertials versus white vanes and no white tips, and a shorter bill.

Genetics:

The only paper to include both *carduelis* and *caniceps* groups is Zamora et al. (2006), which found shallow mtDNA divergence between the two (using samples from Spain and Nepal), approximately the same divergence they found for other sister species (including the now lumped redpolls, *flammea* and *hornemanni*).

New Information:

Recently the WGAC voted 6-1 to split the two based on the plumage and vocal (song) differences.

Vocalizations:

Boesman (2016) found the *caniceps* group lacked the tinkling notes in song phrases that are present in the *carduelis* group giving it a harsher quality (sample sizes not given). The *caniceps* group consistently sings a series of repeated notes while the *carduelis* group rarely does so. These vocal differences, like the plumage differences, appear to be uniform across the ranges of both groups. In contrast to the song, calls were found to be similar with both groups having a tonal tinkling quality.



Ardeola 53(1), 2006, 1-17

Figure 1: Maximum likelihood tree from Zamora et al. (2006).

8 ZAMORA, J, MOSCOSO, J, RUIZ-DEL-VALLE, R, LOWY, E, SERRANO-VELA, J L, IRA-CACHAFEIRO, J AND ARNAIZ-VILLENA, A.

FIG. 2.—Parsimony tree. Bootstrap (1000 replicates) and branch length values are above and underlined below the branches respectively. Tree length = 742; consistency index = 0.36; retention index = 0.54. [Årbol de parsimonia. Los valores de bootstrap (1000 réplicas) y longitudes de rama aparecen respectivamente sobre y bajo las ramas. Longitud del árbol = 742; índice de consistencia = 0,36; índice de retención = 0,54.]



Araeola 55(1), 2006, 1-17

Figure 2: Parsimony tree from Zamora et al. (2006)

Hybrid Zone:

Two hybrid zones have been described, one southeast of the Caspian Sea in Iran has been described as narrow with a wider hybrid zone in southeastern Siberia and northeastern Kazakhstan (Johansen 1944; Vaurie 1956). In looking at photos the WGAC had a hard time finding hybrids and concluded that the hybrid zones must be narrower than previously thought.

Siberia and Kazakhstan

In looking through photos on inaturalis (n=+1000) and eBird (n=24), I was able to find a few hybrids, but the parental forms seemed to dominate throughout the region. Photographs of both groups could be found during the breeding season close together in the northeastern portion of the Altai Mountains of Siberia.

Examples of hybrids:

https://www.inaturalist.org/observations/191083975 https://www.inaturalist.org/observations/196355613 https://www.inaturalist.org/observations/199004505 https://www.inaturalist.org/observations/218858313

I likely overlooked backcross hybrids but I did find at least one likely individual indicating these do occur. <u>https://www.inaturalist.org/observations/208716587</u>

Iran:

In looking through photos from this area on inaturalist (n=17) and eBird (n=.28) most appeared to be phenotypically pure and distinctive, however hybrids could be found over a wide range though these appeared to be rare.

Hybrids: https://ebird.org/checklist/S93687203

https://www.inaturalist.org/observations/175232170

https://macaulaylibrary.org/asset/351417871

Possible subtler hybrids could also be found but these could be difficult to identify by looking at the photos. <u>https://ebird.org/checklist/S70149419</u>

They two also co-occur together at the same times and they looked phenotypically pure at the same site, i. e. <u>https://ebird.org/checklist/S56832974</u>

Recommendation:

Without more in-depth studies and as these two taxonomic groups are native to areas outside the NACC, have distinct morphological and song differences and the near unanimous acceptance by the WGAC, I weakly recommended the split of *C. caniceps* from *C. carduelis*. For English names Gray-crowned Goldfinch has been used for the *caniceps* group and is currently used by Clements/eBird, whereas European Goldfinch has been retained for the *carduelis* group. If this proposal passes, I recommend using these English names as well.

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Submitted by: David Vander Pluym

Date: 15 March 2025

Transfer Yellow-breasted Chat (Icteria virens) from Icteriidae to Icteridae

Effect on NACC:

Acceptance of this proposal would result in the transfer of *Icteria virens* to the family Icteridae. Because Icteriidae, the current family of *I. virens*, consists solely of this species, making this change would result in the removal of the family Icteriidae from the checklist.

Background:

The Yellow-breasted Chat (Icteria virens) is one of the most unusual songbirds of North America, currently classified in AOS taxonomy in the monotypic family Icteriidae. Unique features include relative size and shape, bold color pattern, bill shape, and behavior. Its song is reminiscent of a mimid, with a long series of bizarre chucks, clucks, rattles, whistles, and other short phrases it strings together. Despite the loud nature of this song, the bird is difficult to see because it mostly sings while hiding in dense, shrubby habitat. However, males will also sing during unique courtship flights which include a 30-foot ascent followed by a descent, with their legs dangling down. All these unique features have presented a challenge to identifying its taxonomic affinities; thus, the species has been classified in various families across passerines. The species was originally collected and illustrated by Catesby, and Linnaeus (1758) classified the bird as a thrush, placing it in the genus Turdus. A hundred years of taxonomic indecision followed with the species classified as a wheatear, thrush, flycatcher, tanager, manakin, weaver, vireo, and finally a warbler. Among these early naturalists, Vieillot (1807) collected a series of specimens and studied its behavior. He assigned the species to the new genus Icteria and thought its bill shape unusual, but similar to some troupials ("more closely approaches the troupial than any other bird, thanks to its strong bill with a fine, sharp tip and no notches"). In reality, the bill is not that similar to that of a troupial, and Vieillot ended up placing the species with the weavers.

Baird (1858) thought the species fit within the warblers, and he placed the species within its own section (Icterieae) within the warbler family (This is the source of the family name Icteriidae currently in use). He only had two sections in the warbler family. The first of edition of the AOU checklist (1886) agreed with Baird and put *Icteria virens* with warblers, and all subsequent editions of the checklist also placed it with warblers. Nevertheless, some editions of the checklist have included reservations, and many authors continued to note unusual features of the chat that don't align with warblers or other groups (Clark 1974, Eisenmann 1962, Ficken and Ficken 1962, Mayr and Short 1970, Lowery and Monroe 1968).

The first molecular studies that address the chat's phylogenetic position included allozymes by Avise et al. (1980) and DNA-DNA hybridization of Sibley and Ahlquist (1982). Both had limited sampling but concluded that the Yellow-breasted Chat fits with the warblers. Later, in their more comprehensive DNA-DNA hybridization study, Sibley and Ahlquist (1990) reached the same conclusion, but with a long branch connecting *Icteria* as the sister to the warblers and a short internode between the warbler/chat clade and the blackbird clade. When DNA sequencing came along, the bird was included in several studies with various degrees of taxon and character

sampling (e.g., Klicka et al., 2000; Lovette and Bermingham, 2002; Yuri and Mindell, 2002; Klein et al., 2004; Klicka et al., 2007). Some of these confirmed a sister relationship with warblers, others showed a closer relationship to blackbirds or sparrows, and some were unable to place the species definitively, other than confirm it belonged within nine-primaried oscines. Many also noted a long branch separating it from other groups of nine-primaried oscines.

Barker et. al. (2013) performed more comprehensive DNA sequencing analyses that included at least one species of each genus of the New World nine-primaried oscines, resulting in over 200 sampled species. They sampled 2 mitochondrial and 4 nuclear gene regions for all but a few of these species and performed both concatenated and species-tree analyses. Their results conflicted in the placement of *Icteria* relative to other taxa. The concatenated analyses showed 100% bootstrap support for clade identifying the Yellow-breasted Chat as the sister taxon to the blackbird clade (Icteridae). However, when looking at individual gene trees, only the RAG1 tree had greater than 75% bootstrap support for this relationship. In addition, species-tree analyses did not recover the Icteria-blackbird relationship. Instead, Teretistris was the sister to blackbirds in the species-tree analyses, albeit with poor support. Because of the uncertainty around the position of the Icteria relative to other taxa, Barker et al. (2013) opted to put Icteria in its own family - Icteriidae. The authors put the age of Icteriidae at about 11 million years, similar to that of other families in their study. In a later study, Barker et al. (2015) used the same data, but also added mtDNA of nearly all species of nine-primaried oscines. This study used a family-level backbone tree based on the 2013 study, so it shows the same conflicting relationships of Icteriidae as the Barker et al. (2013) study, with Icteriidae as sister to blackbirds in some trees, and Teretistris as sister in others. Based on all of these results, Chesser et al. (2017) opted to follow the recommendations of Barker et al. (2013) and move *Icteria virens* to the monotypic family Icteriidae.

New Information:

More recently, Oliveros et al. (2019) looked at relationships across passerines using UCE data. This study included more characters (4,060 UCE loci), but sparser taxon sampling with regard to nine-primaried oscines than the Barker et al. (2013, 2015) studies. Oliveros generally included 1-3 species of most of the relevant nine-primaried oscine families, including two species of blackbirds and two species of warblers, as well as the Yellow-breasted Chat. Importantly, neither of the two species of *Teretistris* (currently recognized as Teretistridae in our taxonomy) was included. Their trees showed that *Icteria virens* was strongly supported (100%) as the sister to the clade containing the two blackbird species that were sampled (*Icterus cucullatus* and *Sturnella neglecta*). However, Oliveros et al. (2019) lacked samples of *Teretistris*, which was the taxon that confounded the relationships in the Barker et al. (2013) study. The split between the blackbird clade and the Yellow-breasted Chat was about 10 million years, slightly younger than the age of the chat lineage identified by Barker et al. (2013), but still within the range of other nine-primaried oscine families.

Other relevant new information includes Matthews et al. (2018), which found a species of feather mite on the Yellow-breasted Chat that is more closely related to mite species found on blackbirds than on warblers. In addition, a putative hybrid between a Yellow-breasted Chat and possibly a species of oriole has been photographed and described (Grube 2020; <u>https://ebird.org/species/x00478</u>).

Recommendation:

I recommend a NO vote to this proposal. Although the Oliveros et al. (2019) trees and some of the Barker et al. (2013) trees identified a sister relationship between *Icteria* and the blackbirds, I think further study is needed to definitely show a sister relationship between blackbirds and the Yellow-breasted Chat. The concatenated tree and only one of the gene trees studied by Barker et al. (2013) had strong support for this relationship; however, the other trees in Barker et al. (2013) did not recover this relationship. The Oliveros et al. (2019) study did not include *Teretistris*, which was the taxon that caused conflict in the Barker et al. (2013) trees. In addition, the branch length connecting the chat to any other taxa is relatively long. Lastly, naturalists and researchers have long noted the phenotypic and behavioral uniqueness of this species. Despite a lot of investigation and speculation on the placement of the Yellow-breasted Chat, I'm not aware of anyone that formally suggested this species is part of the blackbird family based on an analysis of phenotypic or behavioral characteristics. I recognize that monotypic taxa can be irritating because they don't by themselves identify phylogenetic relationships; however, they do help highlight and illustrate relictual taxa, another important property of the process of diversification and extinction.

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Submitted by: Kevin J. Burns

Date of Proposal: 17 March 2025

Also see this link for a good discussion of early taxonomic history of Yellow-breasted Chat: <u>http://birdaz.com/blog/2014/07/11/who-made-that-bird-a-warbler-anyhow/</u>

2025-C-11 N&MA Classification Committee pp. 569-581

Merge Nesospingidae and Spindalidae into an expanded Phaenicophilidae

Effect on NACC:

Acceptance of this proposal would result in the removal of two families, Nesospingidae and Spindalidae, from the checklist, and the transfer of species currently in those two families to the family Phaenicophilidae.

Background:

This proposal would place the nine species in these three families into a single family, Phaenicophilidae. Currently, Phaenicophilidae consists of four species (*Phaenicophilus palmarum*, *P. poliocephalus*, *Xenoligea montana*, *Microligea palustris*), Nesospingidae consists of a single species (*Nesospingus speculiferus*), and Spindalidae consists of four species (*Spindalis zena*, *S. nigricephala*, *S. dominicensis*, and *S. portoricensis*). All of these species are found on islands in the Caribbean, primarily the Greater Antilles. *Microligea* and *Xenoligea* were traditionally considered warblers, whereas the rest have long been classified with the tanagers (Ridgway 1902, Hellmayr 1936, Storer 1970, Lowery and Monroe 1968).

Burns (1997) sequenced mitochondrial DNA of most tanager genera and found a close relationship among Phaenicophilus, Spindalis, and Nesospingus, and also showed that these three genera fell outside the traditional tanagers. Klein et al. (2004) found a close relationship between the "warblers" Microligea and Xenoligea and the "tanager" Phaenicophilus palmarum. Despite differences in body size, this Microligea/Xenoligea/Phaenicophilus clade agrees with plumage characters; all species share an olive back, wings and tail; gray underparts; and a broken white eve ring. Taken together, the Burns (1997) and Klein et al. (2004) studies suggested that none of the taxa discussed in this proposal belong to either the tanagers or the warblers and that they form a previously unrecognized endemic Caribbean radiation. Nevertheless, all taxa were not included together in the same study until Barker et al. (2013) performed a comprehensive DNA sequencing analysis that included at least one species of each genus of New World nine-primaried oscines, resulting in over 200 sampled species. Their study included one individual for each genus discussed in this proposal. Barker et al. (2013) sampled 2 mitochondrial and 4 nuclear gene regions and performed both concatenated and species-tree analyses. These analyses confirmed the monophyly of a group containing Microligea, Xenoligea, and Phaenicophilus. In both the concatenated analysis and the species tree analysis, these three genera formed a strongly supported clade. Barker et al. (2013) also found a sister taxon relationship between Nesospingus and Spindalis in both the species-tree and concatenated analyses; however, this relationship was not strongly supported. All genera in this proposal formed a clade in the concatenated analysis, but this was not strongly supported. The relationship was also not strongly supported by any of the individual gene trees and was not recovered in the species-tree analyses, with Calyptophilus disrupting monophyly. In the species tree analyses, Calyptophilus is sister to the Phaenicophilus/Microligea/Xenoligea clade, without strong support. Spindalis/Nesospingus is sister to this clade, again without strong support. We currently treat Calyptophilus as a separate family, Calyptophilidae. In a later study, Barker et al. (2015) used the same data, but also added mtDNA of nearly all species of nineprimaried oscines. However, they did not include the other species of *Phaenicophilus* or the other three species of *Spindalis*. The 2015 study used a family-level backbone tree based on the 2013 study, so it shows the same relationships as the 2013 paper for the taxa pertinent to this proposal. Based on the findings and recommendations of the Barker et al. (2013) study, Chesser et al. (2017) opted to recognize the three families we currently use: Phaenicophilidae, Spindalidae, and Nesospingidae. Barker et al. (2013) estimated the age of Phaenicophilidae at about 11.5 million years, about the average age of nine-primaried oscine families currently recognized. Spindalidae and Nesospingidae are the youngest families, but still relatively old at just under 10 million years.

New information

More recently, Oliveros et al. (2019) looked at relationships across passerines using UCE data. This study included more characters (4,060 UCE loci), but sparser taxon sampling with regards to nine-primaried oscines than the Barker et al. (2013, 2015) studies. Oliveros generally included 1-3 species of most passerine families. Relevant to this proposal, their sampling included the following taxa: *Nesospingus speculiferus*, *Spindalis zena*, *Microligea palustris*, and *Phaenicophilus palmarum*. In all but one of their many analyses, they recovered a strongly supported clade for these four species. Thus, they showed monophyly for a clade uniting families Nesospingidae, Spindalidae, and Phaenicophilidae, consistent with the enlarged Phaenicophilidae proposed here. Sister to this clade was *Zeledonia*, which we currently recognize as its own family Zeledonidae. *Calyptophilus* (which disrupted the monophyly of the proposed enlarged Phaenicophilidae in some of the Barker et al. (2013) trees) was sampled by Oliveros et al. (2019) and is strongly supported as the sister taxon to clade containing *Zeledonia* and the proposed Phaenicophilidae clade. Apparently, no one has conducted an analysis that includes all nine species discussed in this proposal. I don't think this would change relationships, but it's definitely a study worth doing.

Other than molecular work, I'm not aware of any studies that suggest uniting all the taxa in these three families (Phaenicophilidae, Nesospingidae, and Spindalidae). Regarding plumage patterns and colors, three species in Phaenicophilidae and all Spindalidae males have black and white patterns on their heads. Although *Microligea palustris* lacks black on the head, it shares the broken white eye ring with other members of Phaenicophilidae. Overall back color of all Spindalidae and Phaenicophilidae are a similar yellowish olive green, and McDonald (1988) noted that female Jamaican Spindalis *S. nigricephala* is similar in appearance to *Phaenicophilus* fledglings. *Nesospingus* looks different from all the other species due to its brown upperparts and white underparts that are somewhat streaked. In addition, the dark wings have a white wing spot at the base of two of the primaries. I suppose the streaks on *Nesospingus* are somewhat reminiscent of some female *Spindalis*. Although Western Spindalis also has a white wing spot similar to that of *Nesospingus*, it looks like this involves different primaries in the two species. Overall, I don't find these plumage similarities too compelling.

Recommendation

Unlike the situation with *Icteria* (see previous proposal), all relevant taxa were sampled in the UCE study, and a strongly supported clade was consistently identified. Placing all these species in the same family would have the advantage of recognizing this endemic, Caribbean radiation.

Although I am confident in this relationship, there are also reasons for keeping these in separate families. Having separate families would emphasize the uniqueness of each of these groups. Moreover, merging them into one family obscures the age of these different lineages. If all these families were merged into an expanded Phaenicophilidae, the reconstituted family would be among the oldest families of New World nine-primaried oscines. The approximate age is 12-13 million years, making them older than families such as Icteridae, Parulidae, and Passerellidae (Oliveros et al. (2019), Fig. 2). Basically, this is a radiation that is both old and endemic to the Caribbean, but it is hard to recognize both of these facts in a classification scheme. In the end, I recommend a YES vote to merge these into one family, but I am on the fence about this one and could be persuaded to vote either way. If we vote to merge, the name Phaenicophilidae (Sclater 1886) has taxonomic priority over the other two family names.

If we vote to merge Nesospingidae, Spindalidae, and Phaenicophilidae into a single family, should we recognize the former families as subfamilies? I think that we should recognize subfamilies but that two subfamilies are a better option than three: Phaenicophilinae for *Phaenicohilus, Xenoligea*, and *Microligea* and a second subfamily for *Nesospingus* and *Spindalis*. To me, this is preferred to separate subfamilies for *Nesospingus* and *Spindalis* since each of those are already in separate genera and making a single subfamily for the two together emphasizes their sister taxon relationship.

Please vote on the following:

- (a) merge Nesospingidae and Spindalidae into an expanded Phaenicophilidae
- (b) if YES on (a), recognize Nesospinginae, Spindalinae, and Phaenicophilinae as subfamilies of Phaenicophilidae (3 subfamilies)
- (c) if YES on (a), recognize Nesospinginae/Spindalinae (whichever has priority) and Phaenicophilinae as subfamilies of Phaenicophilidae (2 subfamilies)

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Submitted by: Kevin J. Burns

Date of Proposal: 17 March 2025

2025-C-12 N&MA Classification Committee p. 510

Treat Turdus daguae as a separate species from White-throated Thrush T. assimilis

Note: This proposal is being considered concurrently with a SACC proposal to treat the *T. assimilis-T. albicollis* complex as more than two species. We will need to coordinate with SACC on the taxonomy and, if splits are made, English names, which may mean that the results of votes on this proposal will not be published in this year's supplement.

Effect on AOS-CLC area:

Splitting *T. daguae* from *T. assimilis* would result in one additional species for the AOS area.

Description of the problem:

The *assimilis/albicollis* complex is found throughout much of Middle and South America and comprises four main subspecies groups. The *assimilis* group is found in the highlands from northern Mexico in all mountainous regions south to central Panama. The taxon *daguae* is currently considered a subspecies of *assimilis* and is found in the lower foothills of the Chocó biogeographic region, from southwestern Ecuador north to eastern Darién. In the Amazon Basin and the Guiana Shield, three subspecies represent the *phaeopygus* group of *T. albicollis*. These reach as far north/west as the Sierra de Santa Marta and as far south as northern Bolivia, Mato Grosso, and Pará. The nominate *albicollis* group is found in southeastern Brazil, Argentina, and Uruguay, with an isolated population (subspecies *contemptus*) in the Andes of Bolivia, in close proximity to lowland *phaeopygus*.

Taxonomic history:

The taxonomic history was covered thoroughly in NACC proposal 2022-A-4. Briefly, *daguae* was described as a species in 1897 by Berlepsch, but of course in a different era and different species concept. Peters (1964) considered all four groups to be members of one species, *T. albicollis*. Most authorities have considered *daguae* as a subspecies of *T. assimilis* (of Middle America) based on plumage similarity. A few recent authorities (e.g., HBW BirdLife) have considered *daguae* as a subspecies of *T. albicollis* (of South America) based on vocal similarity or more recently as a separate species (Ridgely & Greenfield 2001).

In early 2021, the Working Group Avian Checklists (WGAC) addressed the placement of *daguae* and voted 6-0 to consider *daguae* as a species separate from both *T. assimilis* and *T. albicollis*. However, two WGAC committee members noted that they wanted to hear from NACC and SACC and would reconsider their votes if those committees disagreed with that conclusion. Later in 2021, Van Remsen submitted a proposal to split *daguae* concurrently to both NACC (proposal #2022-A-4) and SACC (proposal #922). Those proposals both failed (respective votes: 4-7 and 4-4), with both committees retaining *daguae* as a subspecies of *T. assimilis*. WGAC has not reconsidered its vote since these NACC and SACC proposals.

The SACC proposal is here: https://www.museum.lsu.edu/~Remsen/SACCprop922.htm

The WGAC proposal was based on the same information as in the NACC and SACC proposals. We encourage the committee members to read the NACC/SACC proposal, and especially the comments by committee members on both proposals.

New information:

No new information since 2021. We are here again addressing this issue in advance of the publication of the WGAC checklist, to attempt to minimize discrepancies between NACC and WGAC. Committee members in both NACC and SACC who voted against changes to taxonomy raised two main issues: 1) genetic sampling was insufficient, both spatially and in number of loci, and 2) no formal analysis of vocalizations was conducted. Although both issues could use additional research, we present additional information on both, that together clarify some of the issues raised by committee members.

Regarding genetic sampling, most data come from the mitochondrial tree presented by Núñez-Zapata et al. (2016) and included in NACC 2022-A-4 / SACC 922. That tree showed a sister relationship but with a deep divergence between *daguae* and *assimilis*. All samples of *daguae* came from southern Ecuador, far from any potential contact zone, but note that based on distribution we do not believe that these taxa come into contact. SACC committee members also noted that there may be multiple species within *T. albicollis* and that Núñez-Zapata et al. (2016) sampled only the nominate subspecies group of southeastern Brazil, Argentina, Uruguay, and Andean Bolivia. We checked this to be certain, as both subspecies groups occur in Bolivia, and based on the sampling localities in Núñez-Zapata et al. (2016), confirmed that both Bolivian samples were from Andean localities, so represent *contemptus* of the *albicollis* group. We can confirm, therefore, that the Amazonian *phaeopygus* group was not sampled.

Another paper (Batista et al. 2020) sampled ultraconserved elements (UCEs) across the diversity of *Turdus*, including multiple taxa in the *assimilis/albicollis* complex, but the previous proposals noted that it, unfortunately, did not sample *daguae*. Batista et al. (2020) did sample UCEs from *T. albicollis*; however, both subspecies included (*phaeopygus* and *spodiolaemus*) are part of the same Amazonian subspecies group. UCE data indicated that *T. albicollis* and *T. assimilis* are sister taxa but with a deep divergence. That UCE tree, from their supplemental data, is shown below.

Turdus albicollis spodiomaemus TAL24 (Sao Gab, Cach. AM BR) Turdus albicollis phaeopygus TAL13 (Para BR) Turdus assimilis U4275 (Panama) Turdus assimilis U4159 (Guatemala)

A portion of supplemental Figure 2 from Batista et al. 2020, showing UCE-based phylogenetic relationships in the *albicollis/assimilis* complex. The node separating *albicollis* from *assimilis* was estimated to be 3.16 Mya.

The supplemental data from Batista et al. (2020) show that they extracted mitochondrial data from their UCE reads and combined these with existing mitochondrial data to estimate a phylogeny that included the four major clades in the complex. Although the standard mitochondrial gene tree issues apply, their results pointed to deep divergences between all four groups and resolved the taxon sampling issues raised previously.



A portion of Figure S5 from Batista et al. (2020) showing the phylogenetic relationships in the *Tudus assimilis/albicollis* complex based on the mitochondrial gene cytochrome-b. We have highlighted the subspecies groups of interest here with red bars. The scale bar on this mtDNA phylogeny figure is difficult to interpret, as the scale bars below 5 Mya are missing, but by our estimate, the node separating *albicollis* from *assimilis* is approximately 4 Mya (so, just older than from the UCE data) and the node separating *daguae* and *assimilis* is approximately 2.5 Mya. Of note, the node separating *phaeopygus/spodiolaemus* and nominate *albicollis* is approximately 3.5 Mya. The samples highlighted in blue are those determined by the authors to represent particularly deep intra-specific splits. Note that the node ages of the four major clades in the *assimilis/albicollis* complex are comparable to or older than other well-established species in the genus.

Phenotypic variation

In addition to the plumage differences noted in earlier proposals, Vallely and Dyer (2018) mentioned that *daguae* shows a dusky bill tip lacking in *assimilis*, which they illustrate as having a solid yellow bill. However, online photos show considerable variation in dusky coloration on the bill in *assimilis*, which may be age- or sex-related. The few available photos of *daguae* show a considerably darker bill, solidly dark in almost all cases. Herzog et al. (2016) illustrated *phaeopygus* as having a solidly dark bill, versus a yellow bill with a dark tip in *contemptus* of the *albicollis* group. Photos online show *phaeopygus* having either a dark bill or a yellow mandible contrasting with a dark maxilla.

Vallely and Dyer (2018) illustrated both gray and brown birds for *T. assimilis* and noted that these populations are known from adjacent localities in Honduras. Collar et al. (2024) illustrated subspecies *T. assimilis atrotinctus* of the Caribbean slope of Honduras and Nicaragua as being dark gray and mentioned in the text that subspecies *leucauchen* is also dark gray. In our search of online photos and field guide references, it appears that the brown populations are found in most of Mexico, and extend south on the Pacific slope to southern Guatemala. These are nominate *assimilis* and some related subspecies, which are paler and more uniformly brown than other subspecies. Dark gray birds are found on the Caribbean slope from the humid slope of southeastern Mexico, south through Guatemala, Honduras, and Nicaragua, and again in the mountains of most of Costa Rica except the far south (nicely illustrated in Howell & Webb 1995). In the southern Pacific slope of Costa Rica and through its range in Panama there is another brown subspecies, *cnephosus*, but this one is more contrasting and paler below than the northern nominate brown subspecies. Most of the above phenotypic differences were also noted by Hellmayr (1934), but we note that from the mtDNA, these are all genetically very similar.

Lastly, a "small and dark" subspecies, *coibensis*, is known from Isla Coiba, but its genetic affinities are unknown. In his description of *coibensis*, Eisenmann (1950) gave the diagnosis as "closest to *daguae*", especially in the underpart and bill color, and noted that it is different than cnephosus in that regard. Wetmore (1957) wrote that coibensis differs from daguae in being "larger, more olive above and graver below, with the unmarked white area on the foreneck less in extent", so some plumage differences exist. Wetmore (1957) also provided morphometrics for coibensis, which could be compared with other taxa. Eisenmann (1950) used this plumage similarity as evidence that daquae was conspecific with assimilis, with coibensis as the geographic intermediate. However, he also combined all these taxa under an expanded albicollis. Ridgely & Gwynne (1989) noted that coibensis has a blackish bill and is ruddier above than *cnephosus*, and also that it is the most numerous forest bird on the island, guite different in this respect from the mainland populations. We now know that Isla Coiba has some very interesting biogeography; for example, the endemic Coiba Spinetail is most closely related to South American taxa, so we think it is more likely that something interesting is going on with coibensis, possibly a future candidate for species status. If daquae is split, we think coibensis should be tentatively retained with assimilis, given that it is vocally much like the assimilis group (see below). Some photos of this taxon are here: https://macaulaylibrary.org/asset/615988098 and here https://macaulaylibrary.org/asset/451105661

Regarding morphometrics, Hellmayr (1934) noted that *daguae* is notably smaller than other taxa. This was described in more detail in NACC 2022-A-4, but also illustrated nicely in the PCA plot from Núñez-Zapata et al. (2016) shown below.



Fig. 3 Multivariate analyses based on six morphometric measures from subspecies of *T. assimilis*. **a** PCA analysis; the first two components are shown. **b** Proportion of variability explained by each component. **c** Scatterplot of the discriminant function between subspecies of *T. assimilis*

Vocal variation

Below are comparisons of songs from the four major groups in the *T. assimilis / T. albicollis* complex. Top to bottom: 1) *phaeopygus* group, 2) nominate *albicollis*, 3) nominate *assimilis*, 4) *daguae*. Note the similar form and structure of *daguae* to *T. albicollis*. Note that *daguae* seems to lack the doubling of notes and the notes are more level.



To our knowledge, the only quantitative analysis of vocal variation within the *T. assimilis / T. albicollis / T. daguae* complex comes from Boesman (2016), which is worth reading: <u>https://birdsoftheworld.org/bow/ornith-notes/JN100305</u>

Below are links to exemplar songs that highlight the differences mentioned by Boesman (2016) and our comments on these differences. We note that Nacho Areta made some excellent comments on the SACC proposal that support the distinct song of *daguae*. We agree that *daguae* sounds much more like Amazonian *phaeopygus* than like *assimilis*. Ridgely & Greenfield (2001) had the following to say about the song of *daguae*: "Song a long-continued musical caroling with somewhat monotonous effect similar to White-necked Thrush's [*T. albicollis*] but pace a little faster (very different from White-throated Thrush [*T. assimilis*])".

A great example of most vocalizations in *assimilis*, showing especially the distinctive song: <u>https://macaulaylibrary.org/asset/72851</u>

Here is a good song from *daguae*: <u>https://xeno-canto.org/275527</u> which certainly sounds higher pitched than the rest to us, and very different from *assimilis*. A few more examples here: <u>https://xeno-canto.org/species/Turdus-daguae?view=3</u> and here:

https://media.ebird.org/catalog?taxonCode=whtthr2&mediaType=audio&view=list&sort=rating_r ank_desc&tag=song

Good song example from *phaeopygus* group: <u>https://macaulaylibrary.org/asset/158569851</u> Good song example from nominate *albicollis* group:<u>https://macaulaylibrary.org/asset/615294056</u> The one available song recording of *coibensis* sounds typical of *assimilis*: <u>https://macaulaylibrary.org/asset/69480131</u>

Boesman (2016) looked only at songs (which are of course critical), but there appear also to be considerable differences in the calls. There are at least three main call types in this clade, one whistled and longer, a short rough "churt" note, and an odd chattering call.

The whistled call note is clear and rising-falling in *assimilis*: https://macaulaylibrary.org/asset/231691361

but has a rising emphasis at the end in *daguae*: <u>https://macaulaylibrary.org/asset/288967681</u>. However, some *assimilis* may approach this: <u>https://macaulaylibrary.org/asset/72851</u>, including *coibensis*: https://macaulaylibrary.org/asset/69480121.

This call is much lower-pitched in Amazonian *albicollis* (calls after 3:15 mark): <u>https://macaulaylibrary.org/asset/188608</u>

and, to be thorough, here is that call from nominate *albicollis*, which is also short and low-pitched: <u>https://macaulaylibrary.org/asset/466693731</u>

In a cursory search, the short "churt" call sounds fairly similar across taxa, but more work should be done here.

The Amazonian taxa most commonly give the odd chattering repeated call, which is uncommon or rare in other taxa. A good example from *phaeopygus* is here: <u>https://macaulaylibrary.org/asset/245273</u>

Here is that call in *assimilis*: <u>https://macaulaylibrary.org/asset/591450671</u> which sounds much clearer and whistled than in *phaeopygus*, mirroring the differences in the whistled call.

This is the only example we can find for *daguae*: <u>https://xeno-canto.org/64330</u> which sounds very different than *assimilis*, and more like *phaeopygus*, but with one recording it's hard to be certain that this is a consistent difference.

The call of *coibensis* is described as "a guttural call like birds of the western highlands" and a "complaining *chur-r-r* or *pru-rr-r*" (Wetmore et al. 1984).

Distribution:

Turdus assimilis has a broad elevational distribution, occurring in mid-elevations and low elevations from northern Mexico through central Panama. This species is found in many foothill localities in Costa Rica and Panama, being more widespread in the Pacific lowlands than in the Atlantic lowlands. Farther south in this distribution, it is found primarily at middle elevations but occasionally wanders to the lowlands. In central Panama, it is found in the isolated hilly regions of Valle de Antón, Altos de Campana, and Cerro Hoya (all west of the Canal Zone). A few eBird records from the Canal Zone and Cerro Azul, based on photos, represent the *assimilis* group. Ridgely & Gwynne (1989) noted that the birds in the Canal Zone are wanderers from elsewhere, with numbers peaking in November-January, and also mention that "E.S. Morton found it to almost completely disappear from Cerro Campana during the dry season." Therefore, it seems that small numbers of the foothill birds from west of the Canal Zone disperse eastward, including likely the Cerro Azul records, and that Altos de Campana is the easternmost breeding population.

The Pacific slope of the Darién is the northernmost extent of *daguae*. Wetmore et al. (1984) cited specimens from Cerros Pirre and Tacarcuna, where they considered *daquae* to be fairly common. They also mentioned a specimen from Cerro Sapo in the coastal Serranía del Baudó. Ridgely & Gwynne (1989) also assigned both the Pirre and Tacarcuna birds to daguae. In eBird, all records in the Darién south of the Chucunaque River appear to be daguae, including records in the foothills of the Serranía de Pirre; records in the Cerro Tacarcuna lack photos. Of interest are eBird records on the Cerro Chucantí in western Darién. Just as we were wrapping up this proposal we noticed that a "Turdus assimilis" was marked as a background species in a recording from this site, and it sounds to us like a typical daguae, thus extending the distribution of this taxon slightly westward: https://xeno-canto.org/2974. Thus, it appears that assimilis and daguae are spatially isolated by intervening lowlands in central Panama (specifically, the lowlands around the Río Chepo), with assimilis extending as far south and east as Cerro Azul, where it occurs around 800 m, and *daguae* extending as far north and west as Cerro Chucantí, where most records are > 700 m (with one record, lacking documentation, at 100 m). The highlands of central and southern Panama are connected by the Serranía de San Blas, but we are not aware of records of either assimilis or daguae from this region; notably, this mountain range has a high elevation of ~748 m, lower than the elevations of both assimilis and daguae on the most adjacent mountains to the "gap" between these taxa and perhaps not suitable for populations of either taxa. Thus, we find no evidence for sympatry within the complex.

Regarding *coibensis*, Wetmore et al. (1984) cited specimen records from some of the islands between Coiba and the mainland, namely Isla Brincanco and Isla Rancheria, so it seems that this subspecies approaches the mainland. However, this taxon is found down to sea level, even in mangrove swamps, unlike foothill *cnephosus* (Wetmore et al. 1984).

Possibly of relevance, the eBird science map has different abundance patterns for the two taxa, with *daguae* being uncommon and *assimilis* being common. However, there are few occurrence records for *daguae*, which may impact the reliability of this difference. However, Ridgely & Gwynne (1989) stated that *daguae* is uncommon, whereas *cnephosus* is fairly common.



Recommendation:

Based on differences in mitochondrial DNA, morphometrics, voice, and plumage, we posit that the *T. assimilis*/*T. albicollis* complex as a whole comprises either one broad-ranging taxa with very well-differentiated subspecies or four species-level taxa: *T. assimilis* in the north, *T. daguae* in the Chocó, *T. phaeopygus* in the Amazon, and *T. albicollis* in southern South America. Given concordant differences in genetics, plumage, and (in some cases) song for each of the groups, we recommend a YES vote on elevating *daguae* to species rank.

If reconsidered by the SACC, we highly encourage them to consider splitting the complex into four species, based on the information outlined above regarding variation within *T. albicollis* as compared to the differences between other species-level taxa and *T. assimilis / T. daguae* and related *Turdus* species.

Regarding a name, we suggest that committee members read the previous NACC proposal and comments on both the NACC and SACC proposals. Clements/eBird lists *daguae* as White-throated Thrush (Dagua), and Dagua Thrush was used by Ridgely & Greenfield (2001). Hilty & Brown (1986) stated that *daguae* has been considered a separate species by others, under the name Dagua Thrush, so there is historical usage of this name. The name is based on the collecting locality, the Rio Dagua, which is a fairly small river, but the name is memorable and

unique, and there is plenty of precedence for using the collecting locality for the species name (e.g., Altamira Oriole, Tennessee Warbler), although those names are often criticized for not being particularly useful. Choco Thrush is a logical choice, given that it is endemic to this biogeographic region. There are, however, plenty of other birds with the "Choco" name, and two other *Turdus* are endemic or near-endemic to the Chocó region (*T. obsoletus* and *T. maculirostris*). Of these three species, the range of *daguae* most closely matches that of the bioregion. We lean towards Dagua Thrush, but this name should be considered in consultation with SACC.

Please vote on the following:

- 1) Elevate *daguae* to species rank (BirdLife / WGAC treatment). **We recommend a YES vote.**
- 2) Adopt the English name Dagua Thrush for *Turdus daguae*. **We recommend a YES vote**.
- 3) Adopt the English name Choco Thrush for *Turdus daguae*. **We recommend a NO vote.**

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Submitted by: Oscar Johnson, Florida Gulf Coast University, and Jacob C. Cooper, University of Nebraska at Kearney

Date of proposal: 20 March 2025

pp. 218-232

Revise the classification of the Columbidae: (a) revise the linear sequence, (b) recognize subfamilies, and (c) revise the group name of *Starnoenas cyanocephala* in light of its phylogenetic position

Background:

The linear sequence of Columbidae in the current AOS-NACC Check-list (Chesser et al. 2024a) is as follows:

Columba

- Columba livia
- Columba palumbus

Ectopistes

- Ectopistes migratorius

Patagioenas

- Patagioenas cayennensis
- Patagioenas speciosa
- Patagioenas squamosa
- Patagioenas leucocephala
- Patagioenas flavirostris
- Patagioenas inornata
- Patagioenas fasciata
- Patagioenas caribaea
- Patagioenas plumbea
- Patagioenas subvinacea
- Patagioenas nigrirostris
- Patagioenas goodsoni

Streptopelia

- Streptopelia orientalis
- Streptopelia roseogrisea
- Streptopelia turtur
- Streptopelia decaocto
- Streptopelia chinensis

Geopelia

- Geopelia striata

Columbina

- Columbina inca
- Columbina passerina
- Columbina minuta
- Columbina talpacoti

Claravis

- Claravis pretiosa

Paraclaravis

- Paraclaravis mondetoura

Starnoenas

- Starnoenas cyanocephala

Geotrygon

- Geotrygon versicolor
- Geotrygon montana
- Geotrygon violacea
- Geotrygon caniceps
- Geotrygon leucometopia
- Geotrygon chrysia
- Geotrygon mystacea
- Leptotrygon
 - Leptotrygon veraguensis

Leptotila

- Leptotila verreauxi
- Leptotila jamaicensis
- Leptotila cassinii
- Leptotila plumbeiceps
- Leptotila wellsi

Zentrygon

- Zentrygon carrikeri
- Zentrygon costaricensis
- Zentrygon lawrencii
- Zentrygon albifacies
- Zentrygon chiriquensis
- Zentrygon goldmani

Zenaida

- Zenaida asiatica
- Zenaida aurita
- Zenaida auriculata
- Zenaida macroura
- Zenaida graysoni

Changes since the publication of AOU (1998) include the transfer of *Ectopistes* adjacent to its sister genus *Patagioenas* (2024-B-11, Chesser et al. 2024b) and of *Zenaida* to lie among the

/is

quail-doves and relatives (2014-C-3, Chesser et al. 2014), and changes to the circumscriptions (and linear sequence) of a handful of genera (such as in the quail-doves—Chesser et al. 2014; the ground doves—2019-C-8, Chesser et al. 2019; and the New World pigeons—Banks et al. 2003). A recent NACC proposal to introduce the subfamily Starnoenadinae for *Starnoenas* based on the morphological and behavioral data covered by Olson and Wiley (2016) (and, by extension, recognize additional subfamilies), 2020-A-7, was not passed, pending the inclusion of that species in a molecular phylogeny.

New Information:

Multiple phylogenetic studies of Columbidae have been published in recent years, elucidating the relationships among the great majority of species in the family. Three major clades, recognized by various recent authors (e.g., Dickinson and Remsen 2013; Young et al. 2024a & b) as subfamilies, have been recovered fairly consistently: the New World ground doves (Claravinae—see Dickinson and Raty 2015); a cosmopolitan clade including both Old World and New World pigeons and various doves (Columbinae); and a diverse radiation across the Old World tropics and into Oceania (a greatly expanded Raphinae; Treroninae may be further partitioned from Raphinae [e.g. by Boyd 2025], although all members of the former are extralimital and the latter is currently represented on the Check-list by a single established introduced species, *Geopelia striata*). The relationships among these clades vary from study to study—for example, Boyd et al. (2022), using whole-genome sequence data for 61 species, recovered Claravinae sister to Columbinae, whereas the supermatrix approach of Oliver et al. (2023) resulted in Raphinae and Columbinae as sister taxa—but the subfamilies' contents relative to one another remain mostly stable (Fig. 1). (Columbinae and Raphinae are further divided into tribes by Oliver et al. 2023 and Young et al. 2024a & b.)

Oliver et al. (2023) assembled a supermatrix phylogeny of the Columbidae including roughly ³/₄ of columbid species and representatives of all recent genera apart from *Starnoenas*, *Cryptophaps*, and the recently extinct *Microgoura*, including sections of four nuclear and six mitochondrial loci. An excerpt of their BEAST MCC consensus tree, excluding Raphinae, is reproduced below (Fig. 2). The tree of Lapiedra et al. (2021) is similar.

Most recently, Oswald et al. (2025) clarified the position of the Blue-headed Quail-Dove *Starnoenas cyanocephala*, hitherto unsampled in a published molecular phylogeny. They recovered it as sister to Columbinae with strong support, with Claravinae sister to the aforementioned taxa, and these together all sister to Raphinae (Fig. 3). This corroborated the conclusions of Olson and Wiley (2016) that *S. cyanocephala* has no close relatives among other columbids in the Americas on morphological and behavioral grounds, albeit not their suggestion that its affinities lay with Australasian doves.

The only species under the remit of NACC not included in one of the above phylogenies are *Patagioenas caribaea, P. goodsoni, Geotrygon caniceps, G. leucometopia, G. mystacea, Leptotila wellsi,* and *Zentrygon carrikeri. Leptotila wellsi* was sampled by Peters et al. (2023), who found it sister to the clade comprising *L. cassinii* and *L. plumbeiceps.* The remaining species are yet to be included in a published molecular phylogeny (although all have presumed close relatives that have been; see Banks et al. 2013 regarding *Geotrygon* and *Zentrygon*).



Figure 1. Time-calibrated phylogeny of doves based on sequences of 6363 nuclear single-copy orthologues. Scale bar at base of figure represents age in millions of years ago and geographic periods are designated above scale bar. Grey and white columns represent time intervals significant to biotic interchange across the Australia–Antarctica–South American land bridge and subsequent loss of habitat connectivity used to inform host–parasite phylogeny comparisons (66–45, 45–30, and 30–0 Ma). Colours at tree tips represent modern geographic ranges of pigeon and dove species and circles at nodes represent estimated ancestral ranges corresponding with the globe at the top of the tree. Blue-green colour in basal circle represents an ancestral range combining Australia and South America, corresponding to the Australia–Antarctica–South American land bridge illustrated at top of the figure. Q = Quatemary. Ma = millions of years ago. World maps created using maturalearth (https://github.com/ropensci/maturalearth). (Online version in colour.)

Figure 1. Phylogeny of the Columbidae from Boyd et al. (2022).



Figure 2. Supermatrix phylogeny of the Columbidae from Oliver et al. (2023).



Figure 3. RaxML phylogeny of the Columbidae, including *Starnoenas cyanocephala*, from Oswald et al. (2025).

The current linear sequence of the Check-list is inconsistent with recent phylogenetic results in that it intersperses Claravinae, *Geopelia striata* (Raphinae), and *Starnoenas cyanocephala* between the two tribes of Columbinae (Columbini, represented on the checklist by *Columba* through *Streptopelia*, and Zenaidini, represented by *Geotrygon* through *Zenaida*). It likewise separates the closely related genera *Columba* and *Streptopelia* from one another. The linear sequences of species within certain genera (e.g., *Streptopelia*, *Patagioenas*) are also inconsistent with existing phylogenetic data.

Recommendation:

I recommend that the committee adopt the following revised linear sequence of Columbidae:

Claravis

- Claravis pretiosa

Paraclaravis

- Paraclaravis mondetoura

Columbina

- Columbina inca
- Columbina passerina
- Columbina minuta
- Columbina talpacoti

Starnoenas

- Starnoenas cyanocephala

Geotrygon

- Geotrygon versicolor
- Geotrygon montana
- Geotrygon violacea
- Geotrygon caniceps
- Geotrygon leucometopia
- Geotrygon chrysia
- Geotrygon mystacea

Leptotrygon

- Leptotrygon veraguensis

Leptotila

- Leptotila jamaicensis
- Leptotila verreauxi
- Leptotila wellsi
- Leptotila cassinii
- Leptotila plumbeiceps

Zenaida

- Zenaida asiatica
- Zenaida aurita
- Zenaida auriculata
- Zenaida macroura
- Zenaida graysoni

Zentrygon

- Zentrygon carrikeri
- Zentrygon costaricensis
- Zentrygon lawrencii
- Zentrygon albifacies
- Zentrygon chiriquensis
- Zentrygon goldmani

Ectopistes

- Ectopistes migratorius

Patagioenas

- Patagioenas fasciata
- Patagioenas caribaea
- Patagioenas subvinacea
- Patagioenas plumbea
- Patagioenas nigrirostris
- Patagioenas goodsoni
- Patagioenas speciosa
- Patagioenas squamosa
- Patagioenas leucocephala
- Patagioenas inornata
- Patagioenas flavirostris
- Patagioenas cayennensis

Spilopelia

- Spilopelia chinensis

Streptopelia

- Streptopelia orientalis
- Streptopelia turtur
- Streptopelia decaocto
- Streptopelia roseogrisea

Columba

- Columba palumbus
- Columba livia

Geopelia

- Geopelia striata

This linear sequence is based primarily on the results of Oliver et al. (2023) and Oswald et al. (2025) (albeit retaining the sequence of Banks et al. 2013 for *Geotrygon* and *Zenaida*, as several nodes in these genera in Oliver et al. 2023 had relatively low support) and incorporating the transfer of *Streptopelia chinensis* to *Spilopelia* by proposal 2025-A-9, following standard linear sequence conventions (taking into account non-NACC-area taxa). Although the trees of Oliver et al. (2023) and Oswald et al. (2025) differ in the branching order among the subfamilies Claravinae, Columbinae, and Raphinae, this happily doesn't affect the linear sequence, as Raphinae is more species-rich than Claravinae and Columbinae combined.

A minor drawback to this sequence is that the position of *Starnoenas* adjacent to *Geotrygon*, along with retained use of "quail-dove" for the former, could erroneously imply a close relationship between *Starnoenas* and "true" quail-doves to checklist users unaware of the underlying phylogeny. This could potentially be clarified by introducing the subfamilies used by recent authors, as follows: Claravinae for *Claravis* through *Columbina*, Starnoenadinae for *Starnoenas* (following Oswald et al. 2025), Columbinae for *Geotrygon* through *Columba*, and Raphinae for *Geopelia*. It may also be worth revisiting the recommendation by Olson and Wiley (2016) to change the group name of *Starnoenas cyanocephala* from quail-dove (which suggests a now conclusively disregarded relationship between the species and [other] quail-doves) to the unique partridge-dove "in recognition of the derivation of the scientific name and the Spanish vernacular given to it in Cuba" (see also proposal 2020-A-7).

I recommend that the committee:

- (a) adopt the above linear sequence,
- (b) adopt the aforementioned four subfamilies, and
- (c) revise the English group name of *Starnoenas cyanocephala* from quail-dove to partridge-dove, thus changing the species name to Blue-headed Partridge-Dove.

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Submitted by: Max T. Kirsch

Date of Proposal: 21 March 2025

Treat Piaya mexicana and P. "circe" as separate species from Squirrel Cuckoo P. cayana

Note: This proposal is a modified version of Proposal 2024-A-9. The principal change is the addition of an Appendix that provides results of extensive qualitative comparisons of the main four vocalization types of *Piaya cayana*, focusing on Mexican and Central American *mexicana* vs. *thermophila*, but with cursory comparisons from South American populations as well. The Appendix includes a summary and supporting screenshots of usable recordings of these vocalization types from Mexico and Central America, with a sampling from South America, from recordings on xeno-canto and Macaulay Library as of 19 March 2025.

Description of the problem:

A recent NACC proposal (2022-B-11) to split *Piaya mexicana* from *P. cayana* failed unanimously, largely due to a lack of genetic or vocal data, or information from the contact zone of *mexicana* and *thermophila*. A recent paper (Sánchez-González et al. 2023) addressed some of these issues, and proposal 2022-B-11 overlooked genetic data published in Smith et al. (2014). This proposal incorporates that genetic information and additional taxonomic information from Colombia and Venezuela that is relevant to the potential split of South American taxa. We encourage committee members to read proposal 2022-B-11 and comments on that proposal. In particular, proposal 2022-B-11 contains photos of specimens that are relevant to the current proposal. The introduction to this proposal includes much of the same text as in 2022-B-11 but expands on certain topics overlooked in 2022-B-11.

Piaya cayana (Linnaeus 1766) is a widespread polytypic species found from northern Mexico to Argentina, with as many as 14 subspecies recognized (Fitzgerald et al. 2020). The species is common in forested lowlands and foothills throughout its range. Details on relevant subspecies are outlined here. In Middle America, the darker subspecies thermophila Sclater, 1859, is found from eastern Mexico south to northwestern Colombia but is replaced on the Pacific coast of the Isthmus of Tehuantepec by the pale west Mexican subspecies mexicana (Swainson, 1827), which is found in dry forests from the Isthmus of Tehuantepec north to Sonora and Chihuahua. Fitzgerald et al. (2020) treated thermophila as a monotypic subspecies group, with a distribution extending south to northwestern Colombia, where replaced by another monotypic subspecies group, nigricrissa (Cabanis, 1862) of the Chocó from northwestern Colombia south to northern Ecuador on the Pacific slope, although nigricrissa reaches as far east as the eastern slope of the central Andes in Colombia (Chapman 1917). As the name suggests, *nigricrissa* has a darker blackish vent compared to thermophila, but it is otherwise similar. Fitzgerald et al. (2020) considered all remaining subspecies to be part of the cayana group. In northern Colombia, thermophila is replaced to the east by the pale rufous mehleri Bonaparte, 1850, in the dry forests of northern Colombia and Venezuela, and south into the Magdalena Valley of Colombia. The even paler rufous *circe* Bonaparte, 1850, replaces *mehleri* south of Lago Maracaibo. Either circe or mehleri is found east to the Río Orinoco delta, and insulana Hellmayr, 1906, is found on Trinidad. Subspecies mesura (Cabanis and Heine, 1863) replaces these pale rufous taxa south across the Río Orinoco in the northwestern Amazon Basin, likely meeting mehleri and nigricrissa via low passes in the Andes (Chapman 1917). Compared to nigricrissa, mesura is paler below and has red rather than greenish-yellow orbital skin (Ridgely and Greenfield 2001).

The nominate *cayana* is found in the humid Guiana Shield. Additional subspecies are found south through the remainder of South America.

HBW-BirdLife split *mexicana* from the remainder of *Piaya cayana* based on plumage and slight vocal differences and parapatric distribution; citations are Navarro-Sigüenza and Peterson (2004) and Howell (2013, in litt.): "[*mexicana*] differs from parapatric subspecies *thermophila* of *P. cayana* in its rufous underside of tail feathers with broad black subterminal bar and broad white terminal tip vs all-black underside of tail with broad white terminal tip (3); pale grey vs smoky-grey lower belly and vent (2); much brighter rufous upperparts and paler throat (1); usually greenish-grey vs greenish-yellow orbital ring (Howell 2013) (ns1); longer tail (effect size 2.01; score 2); "somewhat different" song (Howell 2013) (allow 1); and parapatric distribution (3)."

Piaya mexicana was described as a species by Swainson (1827), who gave the following characters (which largely mirror the differences described above): "Closely resembles *C. cayenensis* L. [=*Piaya cayana*], but the tail beneath is rufous, not black; the ferruginous colour of the head and neck is likewise much brighter." This treatment was maintained by authors through the beginning of the 20th century (Ridgway 1916, Cory 1919), until *mexicana* was lumped with *P. cayana* by Peters (1940). Ridgway expanded on the differences between *mexicana*: "Resembling *P. cayana thermophila*, but colored portion of under surface of rectrices cinnamon-rufous (instead of brownish black) with a dull black area immediately preceding the white tip, general coloration much lighter, and tail relatively much longer." Most authors since Peters (1940) have maintained *mexicana* as a subspecies of *cayana*.

Navarro-Sigüenza and Peterson (2004) used Piaya cayana as one of their case studies for contrasting a BSC classification (single species) with a PSC/ESC classification (two species) by splitting mexicana, using this rationale: "Populations along the Pacific lowlands from Sonora to the lsthmus of Tehuantepec are long-tailed, pale in coloration of the underparts, whereas the forms of eastern Mexico and Central America are shorter-tailed and darker in color. Although a narrow contact zone is present in eastern Oaxaca between the two forms, only one "hybrid" specimen is known, and the differences are maintained even in close parapatry." The reference to the "narrow" contact zone appears to be from Binford (1989), who reported a few specimens intermediate between thermophila and mexicana: "I have seen definite intermediates from Rio Ostuta (MLZ 45402), Las Tejas (MLZ 54387), and Tehuantepec City (UMMZ 137345 and 137350), but some specimens from the last two localities are mexicana. Birds from Tapanatepec, Santa Efigenia, and a point 18 mi south of Matias Romero are close to thermophila but very slightly paler, a condition that might represent response to the drier environment rather than intergradation" but noted that the "abruptness and apparent rarity of intergradation suggest that these two forms might be separate species; a detailed study is needed." This, combined with the unpublished information from Howell (2013) mentioned above, appears to constitute the basis for the HBW-BirdLife split of mexicana from the remainder of P. cayana. NACC proposal 2022-B-11 also contains photos of two potential intermediate specimens from this region.

Ridgway (1916) considered *mexicana* a species distinct from *cayana*, noting that "these certainly represent two specific types; certainly it is impossible that *P. c. thermophila* and *P. mexicana* can be conspecific, for perfectly typical examples of each occur together in the State

of Oaxaca, and none of the large number of specimens examined shows the slightest intergradation of characters." In the list of specimens examined for both *thermophila* and *mexicana* is the locality "Oaxaca; Tehuántepec", which is where we now know there is a limited contact zone. However, his note that there isn't the "slightest intergradation" does suggest that there is likely limited or no intergradation of characters outside of this contact zone.

New information:

Sánchez-González et al. (2023) and Smith et al. (2014) each analyzed 1-2 mitochondrial markers from across the range of *Piaya cayana*. Sánchez-González et al. (2023) recovered *mexicana* and *thermophila* as sister taxa, with a divergence time of 1.24 mya (1.8 – 0.8 mya, 95% HPD), with *nigricrissa* unsampled. The *mexicana* + *thermophila* clade was in turn sister to seven samples from Peru and Paraguay with a divergence time listed in the main text of about 4.7 mya (6.5–3.2 mya, 95% HPD). However, this latter divergence time estimate appears to be an error, based on the values shown in Figure 1. The 4.7 mya divergence date in the figure is that of *P. cayana* vs. *P. melanogaster*, whereas the divergence time of the Amazonian vs. the *mexicana* + *thermophila* clade is 1.7 mya. F_{ST} and D_{xy} divergence values are shown in their Table 1, and their phylogenetic tree, haplotype network, and sampling map are shown in their Figure 1, below. The F_{ST} results in Table 1 show F_{ST} with Nm (the number of migrants per generation) in parentheses. However, estimates of Nm based on F_{ST} are notoriously unreliable, especially from so few loci. See Whitlock and McCauley (1999) for discussion of this issue.



Fig. 1 Geographic distribution and phylogenetics of the Squirrel cuckoo *Piaya cayana* (A) mDNA Bayesian phylogenetic tree based on a ND2 (1041 bp) and a fragment of Cytb (622 bp) concatenated dataset. Numbers above branches indicate divergence time (in red), and bootstrap/posterior probability values (in black). The dark gray dotted circle represents the split between South American and Mesoamerican clades, while the light gray circle represents the split between the *mexicana* and *thermophila* lineages; B geographic dist

tribution (*P. c. thermophila* in green, *P. mexicana* in orange) and mitochondrial DNA population samples (black dots) in Mexico and Central America. Dotted lines depict both the accessible (or M) and projection areas for the models and the niche divergence analyses for the two evolutionary linages. Brown shading indicates areas at least 1000 m above sea level (m.a.s.l); and C haplotype network. Colors correspond to the vertical bar in the phylogenetic tree

 Table 1 Genetic differentiation for P. cayana.

	South America	Eastern	Western
South America	-	0.85042 (0.09)	0.81378 (0.11)
Eastern	3.177 (2.701)	-	0.90608 (0.05)
Western	3.241 (2.638)	2.431 (2.203)	-

Values above the diagonal correspond to Fst (Nm); values below the diagonal correspond to percentage values for Dxy (Da) α . Boldface values are significant at $\alpha = 0.05$

As part of a broader study on tropical diversification, Smith et al. (2014) sampled *Piaya cayana* from across its range, sequenced the ND2 mitochondrial gene, and used the species delimitation method bGMYC on the time-calibrated gene tree. Their results largely agree with those of Sánchez-González et al. (2023), although the sampling is very different. Smith et al. (2014) sampled across much of South and Middle America, but lacked samples from Colombia, eastern Brazil, or western Mexico (i.e., *mexicana*). Smith et al. (2014) recovered four bGMYC "species" (i.e., clades). Two of these clades contained most of their samples, and corresponded to 1) Middle American samples (*thermophila*) and 2) most of South America (much of the *cayana* group). The other two clades each contained a single sample; the first was their sample from western Ecuador (*nigricrissa*) which was sister to *thermophila*, and the second clade was a sample from Loreto, Peru, in the northwestern Amazon. The divergence time estimates were comparable between the two studies. These results are shown in the figure below.



Range map, ENM, time-calibrated gene trees, and delimited species for *Piaya cayana.* Range map shows distribution of each lineage with sampling localities as black circles (upper left). Ecological niche model (ENM) indicates areas with suitable climatic conditions from 0 (clear) to 1.0 (red); localities used to construct the ENM appear as black circles (upper right). Time-calibrated gene tree shows geographic clades (bottom left) and clades collapsed to show species delimited using bGMYC (bottom right).

Sánchez-González et al. (2023) also measured specimens of *thermophila* and *mexicana* and found significant average differences in four characters: bill width, bill length, tail length, and the length of the white tips on the tail feathers. A PCA of these characters largely separated the two taxa, with some overlap. These results are shown in their Figure 2 below.



Fig. 2 Morphometrics for the two Mesoamerican lineages. Orange color depicts mean and samples for the Western lineage (*P. mexicana*); green color indicates mean and samples for the Eastern lineage (*P. c. thermophila*). Mann–Whitney U test boxplots for comparison of the means for the different characters. Abbreviations: Bill

width (BW), Bill Length (BL), Bill Depth (BD), Tail Length (TAIL), Length of white tips in the tail (TIPS), Hallux Length (HAL), Tarsus Length (TL), and Wing Chord (WC). Right: principal component analysis plot showing the distribution of individuals in each lineage in the morphological space

There do not appear to be any published analyses of plumage or song from across the distribution of *P. cayana*, but multiple references outlined below discuss the plumages of each subspecies. Also, photos in 2022-B-11 nicely illustrate the plumage variation in the group. As for song, we noted in 2022-B-11 that "the song of *mexicana* appears to average higher pitched and more rapid than that of *thermophila*, but some recordings of songs of *thermophila* seem to match recordings of *mexicana*". Pam Rasmussen in her WGAC proposal noted that *mexicana* "seems to have the fastest 'chick' series with the sharpest (most vertical) notes, while South American taxa seem to have more slurred (more diagonal) notes, and east Mexican birds with longer, more resonant (less clipped) notes", and included the following sonograms to illustrate these differences. (Note that Pam has added extensive new vocal analyses in the Appendix.)





In addition, the limited genetic data suggest that if *mexicana* is split, then a split of South American taxa should also be considered, as this is a deeper split in the mitochondrial gene tree. This split is also currently being considered by WGAC. However, neither Smith et al. (2014) nor Sánchez-González et al. (2023) had samples from anywhere in Colombia, nor from the zones of contact between Middle American and South American groups. The sole sample from Venezuela in Smith et al. (2014) comes from south of the Río Orinoco in the far east of the country. Because it is very relevant to the species limits and range boundaries of groups, we here include what information is available on the distributions of the various forms that might come into contact. Fitzgerald et al. (2020) give the following distributional statements (and plumage differences) for the relevant subspecies that come into contact in Colombia and Venezuela. The first two taxa are each considered monophyletic subspecies groups by Fitzgerald et al. (2020):

thermophila Sclater 1859; type locality Jalapa, Veracruz, Mexico. Occurs on the Gulf and Atlantic slopes from Mexico south to Panama and northwestern Colombia.

Relatively dark rufous-chestnut above; belly and undertail coverts dark gray to black; underside of rectrices black, white tips to rectrices relatively narrow.

nigricrissa (Cabanis 1862); type locality Babahoyo or Esmeraldas, Ecuador. Occurs in western Colombia (east to the slopes of the central Andes), south of northwestern Peru. Similar to *thermophila*, but plumage darker; belly and undertail coverts blackish.

cayana group:

circe Bonaparte 1850; type locality Caracas, Venezuela. Occurs in Venezuela, south of Lake Maracaibo. Upperparts slightly more rufous than *mehleri*, but paler than nominate *cayana*.

mehleri Bonaparte 1850; type locality Santa Fé de Bogota (the same type locality as *mesura*?!). Occurs in northeastern Colombia, from the Gulf of Urabá to the Magdalena Valley and the west slope of the eastern Andes, east along the coast of northern Venezuela to the Paria Peninsula. More rufous than *mexicana*, with a lighter throat and breast that grade to light gray on the belly; underside of rectrices rufous.

insulana Hellmayr 1906; type locality Chaguaranas, Trinidad. Trinidad. Similar to *cayana*, but undertail coverts black.

cayana (Linné 1766); type locality Cayenne. Widespread, from eastern and southern Venezuela east through the Guianas, south to Brazil to the north bank of the lower Amazon. Belly ashy gray; undertail coverts darker gray; colors otherwise similar to *thermophila* except that the belly and undertail coverts are not as dark; underside of rectrices black with white tips.

mesura (Cabanis and Heine 1863); type locality Bogotá, Colombia. Occurs in eastern Colombia, Ecuador, and Peru. Similar in plumage to *nigricrissa*; smaller, but with overlap in size.

Chapman (1917) included more detail on the distribution of the Colombian taxa, and, critically, suggested an area of potential contact between *nigricrissa* and *mehleri* based on a fairly extensive specimen series. Some critical passages from Chapman (1917) are below. Note that *"columbiana"* is currently regarded as a synonym of *mehleri*.

Piaya cayana columbiana [=mehleri]

After comparison with an essentially topotypical series from Santa Marta, I refer to this form our specimens from the Magdalena Valley and western slope of the Eastern Andes as far south as Chicoral. These birds have the ventral region darker, the rectrices are blacker, and a bird from Puerto Berrio is deeper above than true *columbiana*. They thus show an approach toward *P. c. nigricrissa* of western Colombia, which, however, is darker above and has much more black on the ventral region.

Piaya cayana mesura

Two forms of *Piaya* inhabit the Bogotá region, *P. c. mesura* and *P. c. columbiana*. The first occurs on the eastern slopes of the Eastern Andes, and, singularly enough, on both eastern and western slopes of the Andes at the head of the Magdalena Valley; the second, occurs on the slopes of the Eastern Andes west of Bogotá and in the Magdalena Valley at least as far south as Chicoral.

Piaya cayana nigricrissa

Inhabits the Tropical and Subtropical Zones in western Ecuador and western Colombia, extending in Colombia eastward to the eastern slope of the Central Andes. Specimens from Antioquia east of the Western Andes approach *columbiana*, but on the whole, are nearer *nigricrissa*.

Chapman (1917) noted that *mesura* is "distinguished chiefly by the comparative blackness of all but the central tail-feathers, seen from below, a character that at once separates it from the other Colombian forms". This character is apparent in the photo of *mesura* in proposal 2022-B-11, especially in comparison to the specimen of *nigricrissa*. This, combined with Chapman's statement of intermediates between *nigricrissa* and *columbiana* [=*mehleri*] in Antioquia, suggests hybridization in central Colombia, likely between populations in the Magdalena Valley (*mehleri*) and the eastern slope of the central Andes (*nigricrissa*). As noted above, Chapman (1917) also indicated that samples at the far southern end of the Magdalena Valley pertain to *mesura*, which crosses over the eastern Andes in this region. An additional potential contact zone is in low passes in southern Ecuador (vicinity of Loja). It is not clear whether there are intergrades in these areas, which do not appear to be located at ecotones as in *mexicana* vs. *thermophila*.

Another point, overlooked in 2022-B-11, is that *mehleri* of the northern coast of Colombia (and the taxon that presumably meets *thermophila* in northwestern Colombia) is pale rufous in color similar to *mexicana*. This was noted by Stone (1908), who stated that *mehleri* "is indistinguishable from *mexicana* above, and differs below only in the greater amount of black shading on the rectrices; the greatest difference is found in the much larger bill". Given that the very rufous coloration of *mexicana* is one of the primary characters suggesting species status for this taxon, this is of particular interest. Although proposal 2022-B-11 highlighted the similar pale rufous plumage of *mexicana* and *pallescens* of eastern Brazil, no specimen photos of *mehleri* were included in that proposal. The similar pale rufous coloration of *mehleri* and *mexicana* is readily apparent in photos, although the undertail of *mehleri* is darker overall, being more similar to other taxa in the *cayana* group in this regard. Photos of *mehleri* from northern Colombia:

https://macaulaylibrary.org/asset/206165711 https://macaulaylibrary.org/asset/366888881 https://macaulaylibrary.org/asset/393722091

Another critical issue overlooked in 2022-B-11 are differences in orbital skin color, something noted by Pam Rasmussen in her WGAC proposal and described in detail by Fitzgerald et al. (2020), but of course not apparent in specimens. In fact, this character might be a much better indicator of species limits in the group than overall plumage coloration, the latter of which seems to vary considerably based on climate. Based on Schulenberg et al. (2007), Restall et al. (2007),

Fitzgerald et al. (2020), and available photos online, variation in orbital skin color is as follows: blue-gray in *mexicana*; greenish-yellow in *thermophila*, *nigricrissa*, *mehleri*, *circe*, and *insulana*; and red in *mesura*, *cayana* (of the Guiana Shield), and all remaining South American taxa. Based on photos, it appears that populations with red orbital skin (*mesura* and *cayana*) approach those with greenish-yellow orbital skin (*nigricrissa*, *circe*, and *mehleri*) in multiple places with very abrupt turnover. These areas mostly correspond quite closely to the subspecies turnovers noted by Chapman (1917). These include in the southern Magdalena Valley near Neiva (greenish yellow *mehleri* to the north, red *mesura* to the south/east), the Rio Orinoco in Venezuela (greenish yellow *circe* on the left bank, and red *cayana* on the right bank), and perhaps somewhere across the Rio Meta in the dry Llanos Orientales of Colombia. The two (here *mehleri* and *mesura*) also appear to turn over within a few kilometers along the eastern flank of the eastern Andes near Yopal, Casanare, Colombia:

https://macaulaylibrary.org/asset/285186601 versus

<u>https://macaulaylibrary.org/asset/586198261</u>. eBird photos from Casanare department, Colombia in the dry llanos show a mix of red and greenish-yellow orbital rings in a patchwork, raising the possibility of local sympatry. We have found just one individual (from adjacent northern Meta department) that appears to show some green in an otherwise red orbital ring, which would argue for some limited hybridization in this area:

<u>https://macaulaylibrary.org/asset/217105071</u>. There is also abrupt turnover in this character within a few kilometers across low Andean passes near Loja in southern Ecuador (here *nigricrissa* and *mesura*). See <u>https://macaulaylibrary.org/asset/518051361</u> versus <u>https://macaulaylibrary.org/asset/600766311</u>.

This would all suggest that if a split is implemented, the division of only *thermophila* and *nigricrissa* from *cayana* is not a good course of action. In fact, we suggest based on orbital ring color and what appear to be very sharp turnovers between populations with red vs greenish-yellow orbital rings, that a group comprised of *circe, mehleri, insulana, thermophila* and *nigricrissa* could be split from *P. cayana*. In this case, the northern species would be either *P. circe* or *P. mehleri*, both described by Bonaparte in 1850, rather than *P. thermophila* Sclater, 1859. Because Bonaparte (1850) described *circe* and *mehleri* in the same publication, a first reviser action would likely be required to establish priority; we will refer to this species as *P. "circe"* through the rest of this proposal. Bonaparte's description of these taxa is here:



To provide a better visualization of where these taxa come into contact in Colombia, below is the eBird abundance map (<u>https://science.ebird.org/en/status-and-</u>

trends/species/squcuc1/abundance-map), with a red line approximately delineating the *cayana* and "*circe*" groups based on the distributional statements above. The abundances do seem to match the number of eBird records in these regions, so are likely a decent representation of the distribution. However, it would be great to get some insight on this issue from Colombian and Venezuelan ornithologists who are more familiar with this species in these potential areas of contact. If implementing this split, the range boundary between *P. "circe*" and *P. cayana* would be approximately as such:



In reading the older literature on this group there is a bewildering number of synonymies for each taxon, which is confounded by multiple taxa described from "Bogota" skins, and multiple examples of a name being applied to different populations by different authors. Much of this was sorted out by Chapman (1917) and Junge (1937) but we think some errors persist. As an example of this confusion, Stone (1908) applied *mehleri* Bonaparte, 1850, to the Central American populations (now considered *thermophila*) based on Sclater's (1860) determination that the type locality was in fact "Central America", not "Santa Fé de Bogota" as originally given by Bonaparte. Chapman (1917) then applied *columbiana* (type locality Cartagena, Colombia) to the northern Colombian population, considering *mehleri* Bonaparte, 1850. Later authors (e.g., Fitzgerald et al. 2020) applied *mehleri* Bonaparte, 1850, to the populations of coastal northern Colombia and Venezuela (i.e., *columbiana* of Chapman 1917). We mention this because we have not undertaken a thorough review of all synonymies for these taxa, and trust that later authors (e.g., Fitzgerald et al. 2020) have resolved these issues satisfactorily, such that if these taxa are split the correct names are applied to the daughter species.

One issue that we have attempted to clarify involves the type localities of *circe* and *mehleri*. Junge (1937) sorted out these type localities by reviewing the collecting localities on the tags of the type specimens. In contrast to earlier authors (see previous paragraph), he reported that the type of *circe* was collected in Caracas, Venezuela, and *mehleri* in Cartagena, Colombia. Both of these localities contain pale rufous birds with greenish-yellow orbital rings, so can be confidently associated with the northern group, not with the *cayana* group, based on orbital ring color. Phelps and Phelps (1958) thought that the type locality of *circe* was likely Mérida, Venezuela, and reported the distribution as being south of Lago Maracaibo, which seems to be the basis of the distributional statement in Fitzgerald et al. (2020). However, Junge (1937) compared the type of *circe* (from Caracas) to specimens collected "south of Lago Maracaibo" and concluded that they were similar enough to be considered same taxon. So, we suspect that it is *circe* that is found from western Venezuela (near Lago Maracaibo) as far east as the Delta Amacuro. Subspecies *mehleri* would then be restricted to northern Colombia and the Magdalena Valley.

Effect on AOS-CLC area:

Splitting *mexicana* from *cayana* would result in one additional species for the NACC area. Splitting "*circe*" from *cayana* would not result in any additional species for the NACC area, as *cayana* is extralimital. However, we think that it is still worthwhile for NACC to consider this split, as it would be better to consider species limits in the complex as a whole, based on current information.

Recommendation:

Although this is a borderline case, we recommend a **YES** on considering *mexicana* as a species separate from *cayana*. The split of *mexicana* is warranted due to mitochondrial genetic differences, consistent plumage differences, morphometric differences, a call type absent from *P. cayana,* sharper call notes, longer tail, paler coloration, and narrow contact zone with *thermophila*.

Since the first version of this proposal, WGAC considered this split and opted to split *mexicana* from *cayana*, which is why we are reconsidering this issue now.

Because of ambiguities concerning the taxonomic affinities of some of the subspecies, as well as the nomenclatural issue mentioned above (as Max noted, this could be resolved through a first reviser action in the supplement, although *circe* and *mehleri* are extralimital taxa), we do not recommend a split between the "*circe*" and *cayana* groups. This is a SACC issue, and if SACC were to split these groups, then we should reconsider.

If this proposal is adopted, we recommend the names Mexican Squirrel-Cuckoo and Common Squirrel-Cuckoo for *mexicana* and *cayana*, respectively. Please vote on the following. Note that a NO vote on (c) would require an alternative name to be suggested.

- (a) Treat Piaya mexicana as a separate species from P. cayana
- (b) Treat Piaya "circe" (including thermophila, nigricrissa, mehleri, and insulana) as a separate species from *P. cayana* (a provisional vote pending a new SACC vote on this, given that cayana only occurs in the SACC area)
- (c) Adopt the names Mexican Squirrel-Cuckoo for *P. mexicana* and Common Squirrel-Cuckoo for *P. cayana* recommend YES.
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- Submitted by: Oscar Johnson, Florida Gulf Coast University; Blanca E. Hernández-Baños, Universidad Nacional Autónoma de México; and Pamela C. Rasmussen, Cornell Lab of Ornithology

Date of proposal: 21 March 2025 (original proposal submitted on 5 September 2023)

Appendix to Proposal 2025-C-14:

Qualitative comparisons of online vocalizations of Piaya cayana

All clearly identifiable recordings of *Piaya cayana* from Mexico and Central America available as of 19 March 2025 on xeno-canto and Macaulay Library (mp3 and wav formats only) were downloaded, as was a representative sample of recordings from South America. To allow visualization of more notes in longer recordings, intervals were shortened and some recordings were truncated, where notes in truncated portions were similar to those represented in the sonagrams. For better visualization, some recordings were amplified or deamplified. Some recordings had multiple types of vocalizations and thus are used more than once in the different categories. Rarer vocalization types were not examined; these include growls, chatters, and isolated mewls. A vocalization type seemingly common to all, that can be represented as *chik-myeow*, was not noticed to differ between taxon groups and was therefore not further examined here. Recordings from the transition zone in Colombia and Venezuela between the *thermophila* (or *circe*) group and the mainly Amazonian *cayana* group were considered outside the present scope and not examined in detail. Supporting sonagrams are provided as a link to the pdf files in Google Drive.

Fitz-bew snarl

None of the 11 *fitz-bew* recordings of *mexicana* have more than two notes, but they are matched closely by some of this call type of the 8 *thermophila* from eastern Mexico and 44 from Central America. Most *thermophila* recordings, however, are clearly of multiple (3+) notes (and thus more of a chatter than a snarl, rendered here as *fitz-brrr*), and some of *thermophila* are intermediate and more difficult to categorize.



Here are four recordings of the *fitz-bew* snarl from *mexicana*:



And four from east Mexican *thermophila*, of which the Tamaulipas recording is much like those given by *mexicana*, whereas the other three are multi-noted, more like South American birds:



South American recordings, including the 13 of Chocó-Tumbes *nigricrissa* and a sample of 12 of the *cayana* group, usually show more and more distinct notes (with few exceptions) than *thermophila*, and are unequivocally transcribed as a chatter rather than a snarl.

Three recordings of *nigricrissa* cackles:



Four recordings of the cackle from the *cayana* group:



In summary, it seems that the *fitz-bew/fitz-brrr* note is somewhat clinal, but the evidence suggests that *mexicana* does not give the clearly multi-note *fitz-brrr* type note that is very common throughout South America, and that is also given sometimes by *thermophila*.

Chik-frrr:

This is a sharp loud single note quickly followed by a raspy growl. It is given very commonly by *mexicana*, at varying intensities and irregularly, sometimes consistently and sometimes mixed in series of single *chiks*. In *mexicana* the raspy growl occasionally does grade into the clear mew type that is similar to those given by other populations.

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Four recordings of the *chik-frrr* call from *mexicana*:

The raspy growl following the sharp *chik* note is not found in *thermophila* or SA, although one Brazil recording (ML 575032401) has short, slight growling sighs following most of the *chik* notes. These are shorter and sound somewhat different from those of *mexicana*, however.

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In summary, the chik-frrr call is unique to, and very commonly delivered by, mexicana.

Irregular piks:

Common and normally given singly in *mexicana*, although there are a few examples of doubled or multiple *pik* bursts in *mexicana* (ML 257862951, ML 611943099, ML 627692109, XC400276, XC584577).

Four examples of the irregular single *pik* notes in *mexicana*:

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And one of the few mexicana with multiple note bursts:

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While no examples of this call type were noted from east Mexican *thermophila*, the 10 from Central America are mostly single to double-noted.

Uncommon and normally given in quick bursts in South American taxa, each burst of 2-6, very often 4-5 notes, with only one example seen of a single *pik* note (though not all entire recordings available examined).

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Four examples of irregular *piks* from South American taxa:

In summary, irregular *pik* notes are very common and usually given singly in *mexicana*, but are uncommonly delivered and usually in quick bursts of several notes in the South American *cayana* group, but there are a few overlapping examples as detailed above. Delivery in Central American *thermophila*, for which there are few examples, may be intermediate, or closer to *mexicana*.

Series of regularly delivered pik notes:

These common vocalizations are always, as far as can be seen in the extensive sample (n=42), visually distinct on sonagrams in *mexicana* from the other taxa (32 from eastern Mexican *thermophila*). All taxa considered exhibit considerable variation in length of the series, from series a few seconds long (rarely) to 20 or more seconds. Normally each note is essentially indistinguishable from all other notes in the series, and the series rhythm is constant throughout, although sometimes the first or last note(s) may be offset slightly. The individual elements are thinner and sharper than those of other taxa, which are normally rounded at the apex. Those of other taxa that are not rounded at the apex still have obviously broader bases (e.g., temporal span from beginning to end) than do these notes in *mexicana*. In fact, with a little familiarity, one could correctly identify all *mexicana* recordings of this vocalization type on ML from those of all the other taxa just by inspection of the thumbnail sonagrams. The notes of this vocalization type are less distinctly different between *thermophila* and other southern taxa, although they tend to be more round-topped in *thermophila* and more slanted with a pointed top facing right in other taxa, but much further comparison and measurements are needed.



Four examples of regular *pik* notes of *mexicana*:

Four examples of regular piks from east Mexican thermophila:



Four examples of regular *piks* from the *cayana* group:



In summary, the regular *pik* series of *mexicana* are readily identified at least visually on sonagrams from those of other taxa, whereas those of the other taxa do not stand out as being so distinctive at least in cursory comparisons.

Overall summary of vocalizations:

The West Mexican taxon *mexicana*, split as a species by HBW/BLI in 2014 and also by WGAC/AviList more recently, is the most distinctive vocally of all *Piaya cayan*a taxa. In short, *mexicana* differs in:

- giving a two-note *fitz-bew* snarl rather than the *fitz-brrr* chatter very commonly given in other populations (although some *thermophila* give the two-note snarl as well);
- commonly giving a *chik-frrr* note, the first note sharp and the second a raspy mewl, that was not found to be given by any other taxon;
- very commonly giving isolated sharp *chik* notes, only rarely doubled or in bursts of multiple *chik* notes, whereas South American *cayana* group populations only rarely give single *chik* notes but uncommonly give bursts of multiple *chik* notes;
- very commonly giving regularly spaced series of *pik* notes that are temporally shorter and sharper than the more rounded or slanted *pik* notes given by the other taxa.

This adds to the body of evidence that supports considering *mexicana* as a separate species. However, the similarity of the chatter of *nigricrissa* to that of the *cayana* group more closely than to the snarl of *mexicana* (and some *thermophila*) does not agree well with the DNA phylogenies showing the Chocó region to be part of the Central American clade rather than the cis-Andean clade. Nor are the other vocal differences identified between *mexicana* and other taxa (all of which appear more vocally similar to each other than to *mexicana*) congruent with the available phylogenetic information on this complex.