AOS Classification Committee – North and Middle America

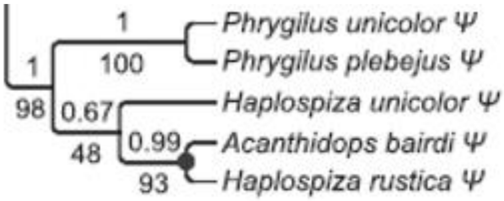
Proposal Set 2024-A

14 September 2023

Reconsider the generic placements of *Haplospiza rustica* and *Acanthidops bairdi*

Background:

Phylogenetic analyses have shown that five small finch-like birds (*Phrygilus unicolor*, *P. plebejus, Haplospiza unicolor*, *H. rustica*, and *Acanthidops bairdii*) form a well-supported clade within the family Thraupidae (Burns et al. 2014; Barker et al. 2015). Here is the relevant part of the tree from Burns et al. (2014):



and here are photos of the five species from the LSU collection, courtesy of Van Remsen:

SACC reconsidered the taxonomy of this clade and numerous other clades in a proposal to revise generic limits within the Thraupidae (see Remsen 2016: https://www.museum.lsu.edu/~Remsen/SACCprop730.htm). Due to the polyphyly of *Phrygilus* (type species *gayi* and several other species are placed in completely different parts of the tree), SACC transferred *P. unicolor* and *P. plebejus* to *Geospizopsis* Bonaparte, 1856 (type species *unicolor*), but *H. unicolor* and *H. rustica* were maintained in *Haplospiza* (*A. bairdi* does not occur in South America, so its placement was not addressed).

(A formal alternative to SACC's transfer of *P. unicolor* and *P. plebejus* to *Geospizopsis* would have been to place all five species in this clade in the same genus (Burns et al. 2016); in this case, *Haplospiza* Cabanis, 1851, would have priority over both *Geospizopsis* and *Acanthidops* Ridgway, 1882. However, two problems would arise from placing the five species in *Haplospiza*.

First, this would place two species with the same species name (*unicolor*) in this genus, which would necessitate designating a new name for the more recently described species. This leads us to the second problem, which is that the type species of *Haplospiza*, known since its description as *Haplospiza unicolor* Cabanis, 1851, was described more recently than the species formerly known as *Phrygilus unicolor* (d'Orbigny and Lafresnaye, 1837). If these species become congeneric, the rules of priority mandate that the former *Phrygilus unicolor* would become *Haplospiza unicolor*, and the former *Haplospiza unicolor* would receive a new name, resulting in the transfer of the name used for one species since 1851 to another species, which would obviously have destabilizing effects. For these reasons, this taxonomic arrangement was not recommended in the SACC proposal, despite morphological and phylogenetic data that suggest it as a plausible alternative (Remsen 2016).)

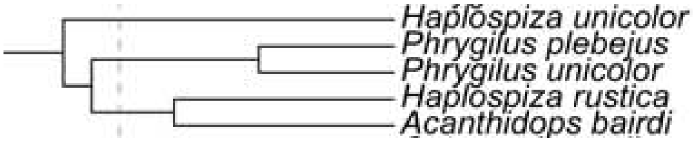
<u>NACC's current treatment and possible alternative treatments</u>:

Although two species in this clade, *H. rustica* and *A. bairdi*, occur in North America, NACC's proposal to revise generic limits within the Thraupidae (2019-C-6), did not address the placement of these two species. This issue has come up before the IOU's Working Group on Avian Checklists (WGAC) because Clements and Birdlife have transferred *H. rustica* to *Spodiornis*, whereas the other checklists maintain this species in *Haplospiza*. The transfer of *H. rustica* to *Spodiornis* was previously rejected by WGAC, but it has now been proposed that *H. rustica* be transferred to *Acanthidops*.

The current treatment of these species is based on the phenotypic similarity of the two species of *Haplospiza* and the phenotypic difference of *A. bairdi*, particularly in bill shape. As is evident from the photos, morphology of the three species is similar, but *A. bairdi*, although similar in plumage, is smaller and its bill has a distinctive pointed shape (hence the English name Peg-billed Finch), in contrast to the finch-like bills of both species of *Haplospiza*.

In this proposal, we consider several options for the generic placement of *H. rustica* and *A. bairdi*. These options include (1) transfer of *Acanthidops bairdi* to *Haplospiza*, creating a 3-species *Haplospiza*; (2) transfer of *Haplospiza rustica* to *Acanthidops*, creating a 2-species *Acanthidops* and a monotypic *Haplospiza* containing only *H. unicolor*; (3) transfer of *H. rustica* to *Spodiornis*, thereby placing each species in a monotypic genus; and (4) leaving the generic assignments as is, pending more robust data.

Option 1, transferring *Acanthidops bairdi* to *Haplospiza* and thereby creating a 3-species *Haplospiza*, would be consistent with the topology of the Burns et al. (2014) tree, as above, but the node uniting the three species has poor support (48% bootstrap and 0.67 pp). Moreover, this arrangement is not supported by the Barker et al. (2015) tree, despite apparently being based on the same data used by Burns et al. (2014):

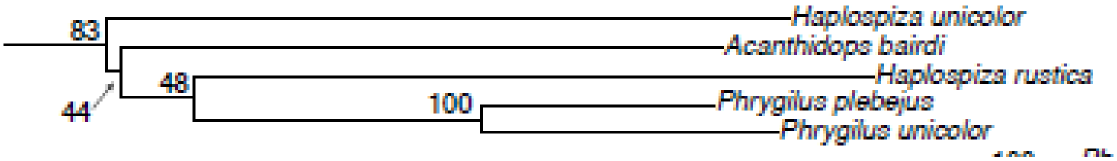


Given the lack of support for a clade consisting of *H. unicolor*, *H. rustica*, and *A. bairdi* in both the Burns et al. (2014) and Barker et al. (2015) phylogenetic trees, it is strongly recommended that we reject this alternative.

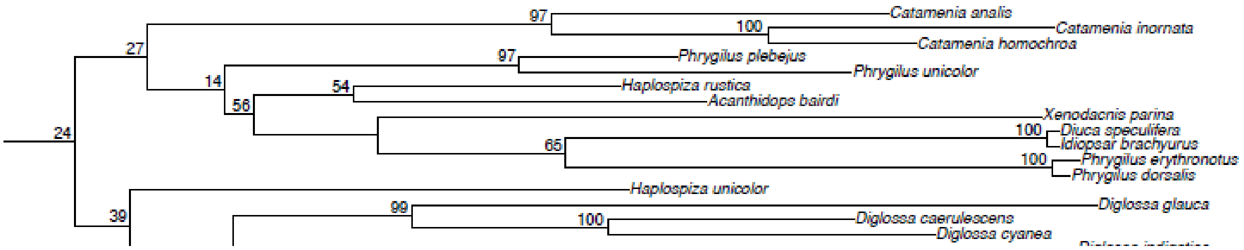
Option 2, transferring *Haplospiza rustica* to *Acanthidops* and thereby creating a 2-species *Acanthidops* and a monotypic *Haplospiza*, would appear to have support from the Burns et al. (2014) and Barker et al. (2015) trees, both of which strongly support a sister relationship between *rustica* and *bairdi* (93% bootstrap and 0.99 pp in Burns, 1.0 pp in Barker). However, as noted above, this arrangement is not supported by morphological data and a closer look at the genetic data reveals the shortcomings of the phylogenetic support. Although *Haplospiza rustica* and *Acanthidops bairdi* are both bamboo specialists, *H. unicolor* also specializes on bamboo and is much more similar morphologically to *H. rustica*. Vocalizations of *H. rustica* and *H. unicolor* are also similar, making it difficult to imagine what phenotypic characters could be used to diagnose two genera, one of which consists of *H. rustica* and *A. bairdi*, and the other of *H. unicolor*.

Although Burns et al. (2014) sequenced six genes (two mitochondrial and four nuclear) for their study of the Thraupidae, not all genes were sequenced for all species, and coverage of nuclear genes typically included only one species per genus except in cases in which lack of monophyly was suspected. Here, the two mitochondrial genes (cyt-b and ND2), were sampled for all five species, one nuclear gene (FGB-I5) was sampled for the two species of *Haplospiza* and *A. bairdi*, and the other three nuclear genes were sampled only for *H. rustica* and *A. bairdi*. Thus, no nuclear data were available for the two species of *Phrygilus*, and sequence of only one nuclear gene was available for *H. unicolor*.

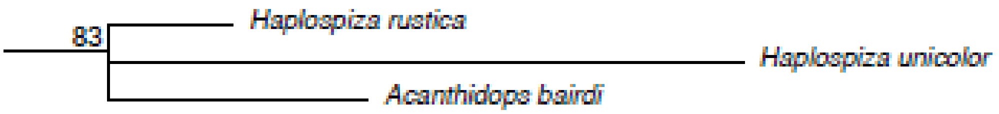
Looking at trees for the individual genes (available in the supplementary figures for Burns et al.), the five species formed a moderately well-supported clade (83% bootstrap) in the ND2 tree, in keeping with the overall tree, but *H. rustica* and *A. bairdi* were not sister taxa. Instead, the two species of *Phrygilus* were strongly supported sisters, *H. rustica* was a weakly supported sister to them, *A. bairdi* a weakly supported sister to this clade, and *H. unicolor* sister to the rest of the species:



In the cyt-b tree, *H. rustica* and *A. bairdi* were sisters but with only 54% bootstrap support, and *H. unicolor* was placed in an entirely different part of the tree. Because mitochondrial genes should produce similar trees, the quite different position of *H. unicolor* in the cyt-b tree relative to the ND2 tree (and other trees) is surprising, suggesting that even the weak support obtained for the *rustica-bairdi* sister relationship may have been inflated by the distant placement of *H. unicolor*:



In the FGB-I5 tree, the two species of *Haplospiza* and *A. bairdi* formed a moderately well-supported clade (83% bootstrap), as would have been expected given that the tree did not include *P. plebejus* and *P. unicolor*, but there was no support for a sister relationship between *H. rustica* and *A. bairdi*:



In the other three nuclear trees, *H. rustica* and *A. bairdi* were strongly supported as sister species, but of course these genes were not sequenced for *P. plebejus*, *P. unicolor*, and *H. unicolor*, making the *H. rustica-A. bairdi* sister relationship in these trees more-or-less a foregone conclusion.

In summary, support for a sister relationship between *H. rustica* and *A. bairdi* evaporates upon close examination of the data: only one tree that included taxa other than *H. rustica* and *A. bairdi* supported them as sister species, and the support for this was poor, at 54%, and was perhaps inflated by the strange position of *H. unicolor* in this tree. Thus, the strong support for the *rustica-bairdi* sister relationship in Burns et al. (2014) and Barker et al. (2015) appears to have been driven by the genes for which no other species in this clade were sequenced, calling this result into question. Therefore, it is strongly recommended that this alternative also be rejected.

Option 3, placing each of the three species in different genera, as in the Clements and Birdlife treatments, would create three monotypic genera, including two for phenotypically very similar species *H. unicolor* and *H. rustica*. Although some authorities (e.g., Hellmayr 1938) previously recognized genus *Spodiornis* for *rustica*, Hellmayr's summary of the differences between *Haplospiza* and *Spodiornis* actually demonstrates the great similarity between them: "*Haplospiza* Cabanis comes very close to *Spodiornis* Sclater, but may be separated by its thicker, basally more inflated bill and more pointed wing." Most of us frown on monotypic genera unless the species are much more distinctive than these two, so to recognize monotypic genera in such similar species would be unusual. Moreover, wing pointedness is hardly a generic character, and the malleability of bill shape in the Thraupidae, including in most cases much more pronounced differences than the minor difference between *H. unicolor* and *H. rustica* (as evident in the photos), is well established.

The genetics tell a similar story: according to the timescale in Barker et al. (2015), *H. rustica* and *A. bairdi* separated ca. 4 million years ago and *H. unicolor* some 6 mya (and this figure is probably elevated by the odd placement of *H. unicolor* in the cyt-b tree). To recognize four genera (including *Geospizopsis*), three of which would be monotypic, within such a comparatively recent, 5-species radiation would be well out of keeping with the standard for other genera in the Thraupidae, or any other family that comes to mind. Thus, it is strongly recommended that this alternative also be rejected.

This leaves us with **Option 4**, to keep the generic limits as they currently stand until better genetic data are available. This is consistent with the phenotypic data and appears to be the only responsible option given the lack of resolution in the phylogenetic trees. This taxonomic arrangement also maintains stability in the classification until relationships among species of *Haplospiza*, *Acanthidops*, and *Geospizopsis* are clarified by additional genetic sampling. **I recommend that we accept this option**, maintaining *rustica* in *Haplospiza* and *bairdi* in *Acanthidops* pending genetic data that better resolve relationships in this clade.

Literature Cited:

Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette (2015). New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. The Auk 132:333–348.

Burns, K. J., Shultz, A. J., Title, P. O., Mason, N. A., Barker, F. K., Klicka, J., Lanyon, S.M. & Lovette, I. J. (2014). Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. Molecular Phylogenetics and Evolution, 75:41–77.

Burns, K. J., P. Unitt, and N. A. Mason (2016). A genus-level classification of the family Thraupidae (Class Aves: Order Passeriformes). Zootaxa 4088:329–354.

Hellmayr, C. E. (1938). Catalogue of Birds of the Americas. Field Museum of Natural History Publications, Zoological Series, vol. 13, part 11.

Remsen, J. V., Jr. (2016). Revise generic limits in the Thraupidae. Proposal 730 to the South American Classification Committee, American Ornithologists' Union. https://www.museum.lsu.edu/~Remsen/SACCprop730.htm

Submitted by: Terry Chesser

Date of Proposal: 30 May 2023

Make changes to our classification of the herons (Ardeidae): (a) Modify the linear sequence and existing taxonomic structure within the family; (b) Revise the genus-level taxonomy of the bitterns (*Ixobrychus*, *Botaurus*); (c) Revise the genus-level taxonomy of *Bubulcus ibis* (Cattle Egret) and related species; and (d) Remove the hyphen from the group name Night-Heron

(a) Modify the linear sequence and existing taxonomic structure within the family

Background:

Our current linear sequence of the family Ardeidae is unchanged since the seventh edition of the Checklist (AOU 1998), where the notes for the family are as follows:

> Recent studies of genetic and vocal characters (Sheldon 1987[a], Sheldon et al. 1995, McCracken and Sheldon 1997) support the traditional arrangement used here in most ways; the relationships of *Butorides* might be with the Nycticoracini rather than the Ardeini.

Curiously, as might be deduced from this note, the family was divided into tribes rather than subfamilies. Four tribes were recognized (genera in our area are in parentheses):

1. Botaurini: Bitterns (*Botaurus* and *Ixobrychus*)
2. Tigrosomatini: Tiger-Herons (*Tigrisoma*)
3. Ardeini: Typical Herons (*Ardea*, *Egretta*, *Bubulcus*, *Butorides*, *Agamia*, and *Pilherodius*), and
4. Nycticoracini: Night-Herons (*Nycticorax*, *Nyctanassa*, and *Cochlearius*).

Numerous molecular studies of herons have been published more recently than AOU (1998), including Sheldon et al. (2000), Chang et al. (2003), and Huang et al. (2016), but many questions remain concerning relationships among species and genera in this family and higher-level divisions (subfamilies or tribes) within the family. Kushlan and Hancock (2005), for example, divided the family into five subfamilies:

1. Tigrisominae (tiger herons)
2. Botaurinae (bitterns)
3. Ardeinae (typical herons, including night herons)
4. Agamiinae (Agami Heron *Agamia agami*), and
5. Cochleariinae (Boat-billed Heron *Cochlearius cochlearius*).

New Information:

Hruska et al. (2023) recently published a phylogenetic paper on herons based on sequences of UCEs and mitochondrial DNA. They sampled 55 species of heron, although success with both UCEs and mtDNA was variable: 46 species were included in their UCE tree (Fig. 1), and 47 species in their mtDNA trees (Figs. 2, 3).

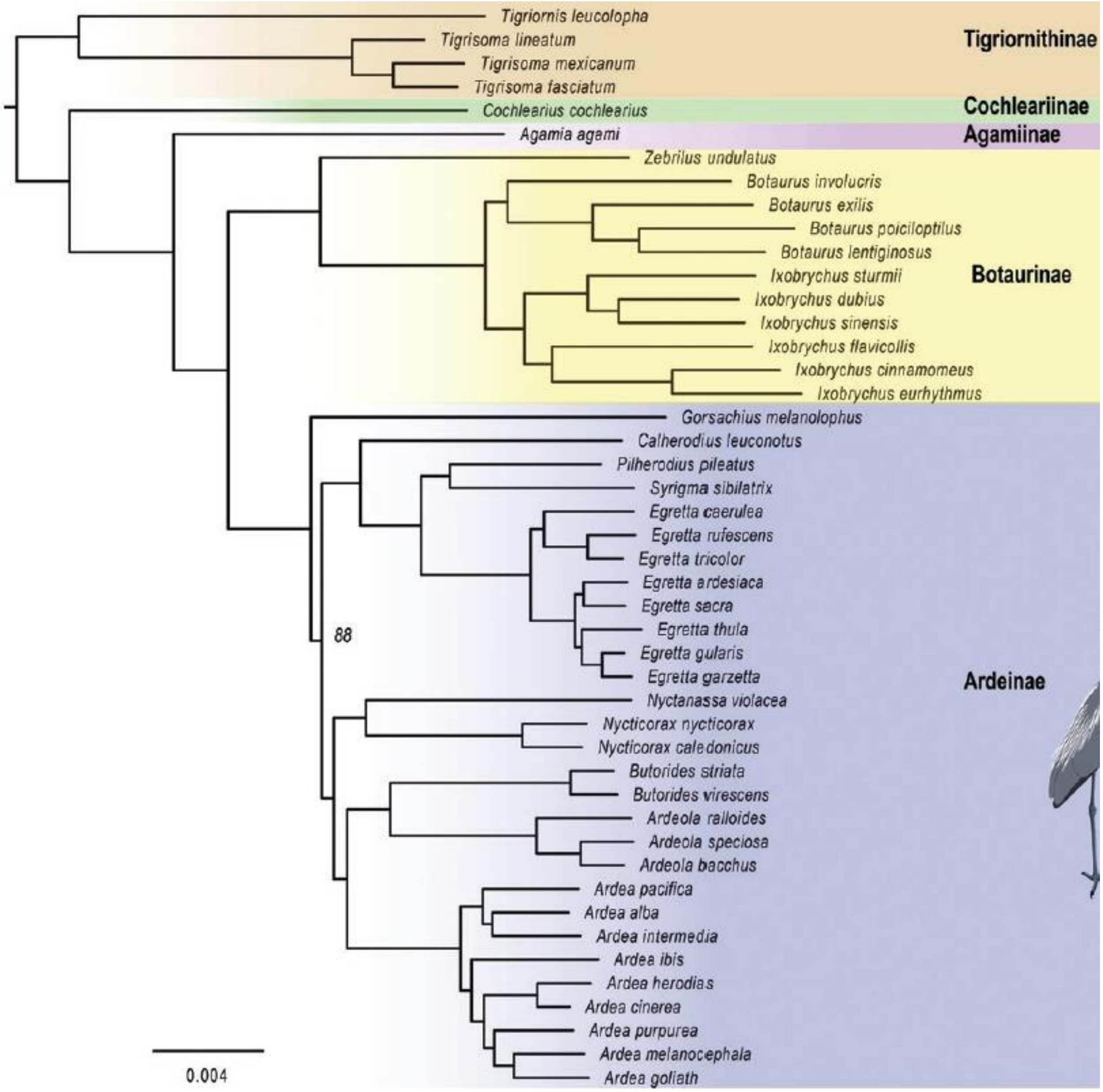


Fig. 1. Phylogenetic tree based on sequences of UCEs (Hruska et al. 2023). All nodes received 100% bootstrap support except as noted.

This phylogeny recovered the subfamily structure of Kushlan and Hancock (2005), although the species composition of subfamilies differed somewhat and the subfamily name Tigriornithinae (Bock 1956) was used instead of Tigrisominae for the tiger-herons. Support for relationships in the UCE tree was universally high: all nodes received 100% bootstrap support with the exception of the node uniting all species of the Ardeinae except for *Gorsachius melanolophus*, which was 88%. The mitochondrial phylogenies (Maximum Likelihood and Bayesian) recovered the same subfamily structure (except that *Agamia agami* was not sampled, and so Agamiidae was not identified) and the same relationships among subfamilies, although many bootstrap values were not as high, and the trees lacked resolution in some areas:

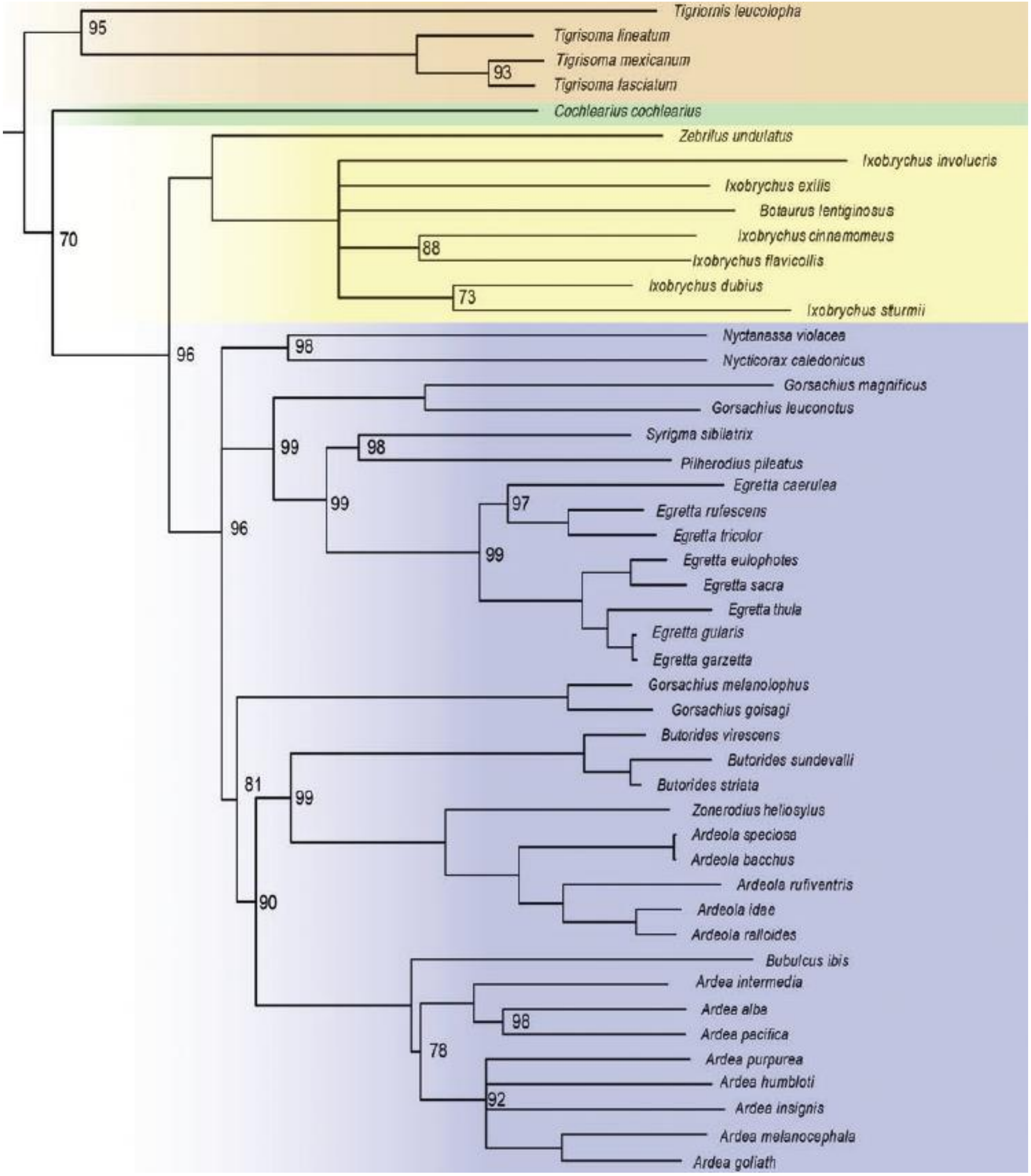


Fig. 2. Phylogenetic tree based on Maximum Likelihood analysis of sequences of mtDNA (Hruska et al. 2023). All nodes received 100% bootstrap support except as noted.

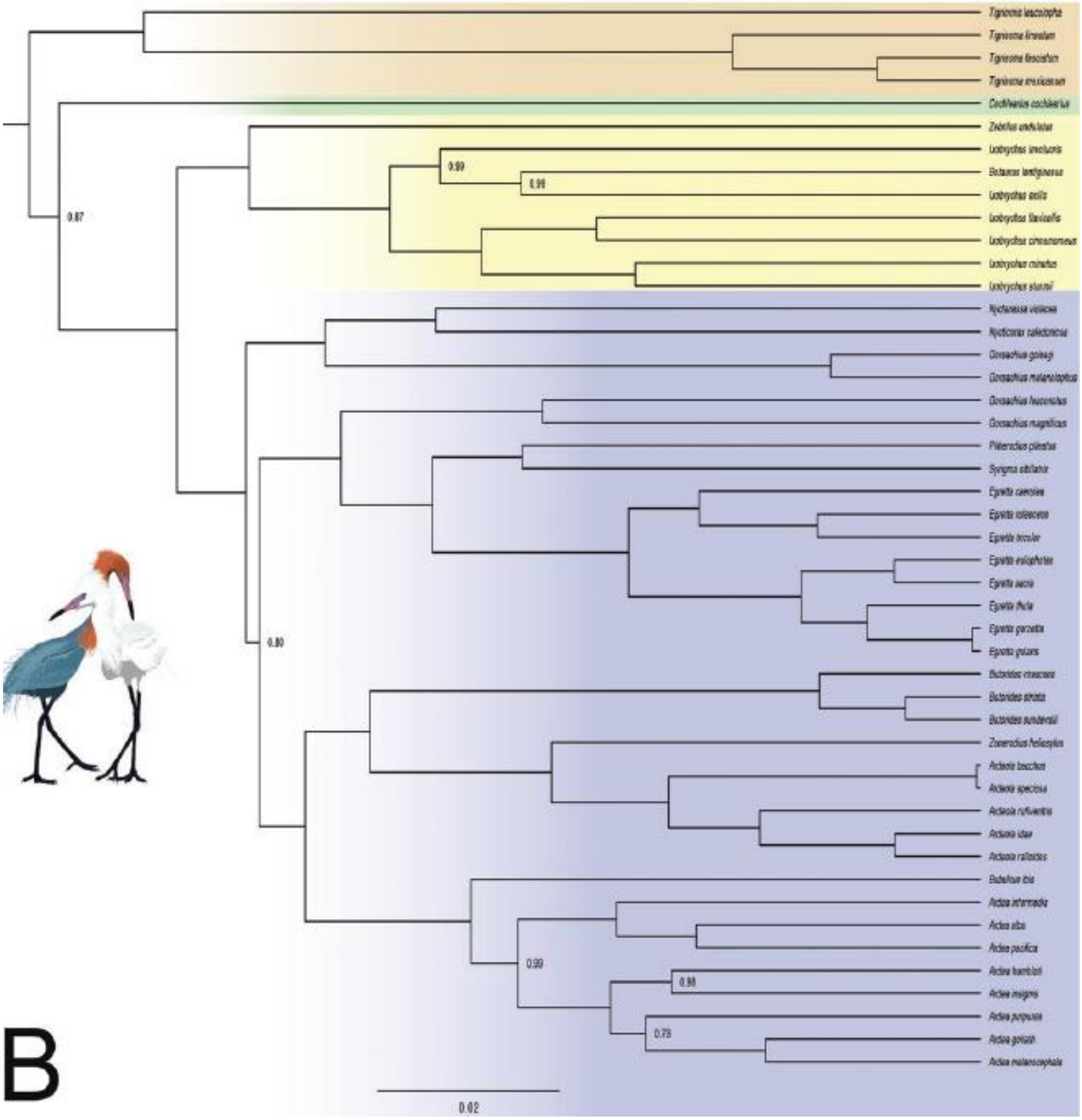


Fig. 3. Phylogenetic tree based on Bayesian analysis of sequences of mtDNA (Hruska et al. 2023). All nodes received 100% bootstrap support except as noted.

Recommendation:

I recommend that we adopt the linear classification posted at the end of this proposal, as well as the following sub-family classification (to replace the tribes used in AOU 1998):

1. Tigriornithinae (tiger herons)

2. Cochleariinae (Boat-billed Heron *Cochlearius cochlearius*)
3. Agamiinae (Agami Heron *Agamia agami*)
4. Botaurinae (bitterns)
5. Ardeinae (typical herons, including night herons)

Note that Tigriornithinae Bock, 1956, the subfamily name used by Hruska et al. (2023), apparently has priority over Tigrisomatinae and Tigrisominae. The latter names, as far as I'm aware, were first used by Payne & Risley (1976) and Kushlan & Hancock (2005), respectively. (Thanks to David Donsker for tracking down these references.)

(b) Revise the genus-level taxonomy of the bitterns (*Ixobrychus*, *Botaurus*)

The NACC list includes three species of *Ixobrychus*: Least Bittern *I. exilis* and two Old World species that occur as accidentals, Yellow Bittern *I. sinensis* and Little Bittern *I. minutus*. Molecular studies have consistently found *I. exilis* to be more closely related to *Botaurus* than to most other species of *Ixobrychus*. In the DNA-DNA hybridization tree of Sheldon (1987a), for example, it was sister to American Bittern *B. lentiginosus* rather than to the other two species of *Ixobrychus* (*I. minutus* and *I. cinnamomeus*) included in the study. Moreover, in the DNA barcode paper of Päckert et al. (2014), who sampled seven species of *Ixobrychus* and three of *Botaurus*, *I. exilis* was sister to the three species of *Botaurus* (with 1.0 p.p.) rather than to any of the other six species of *Ixobrychus*:

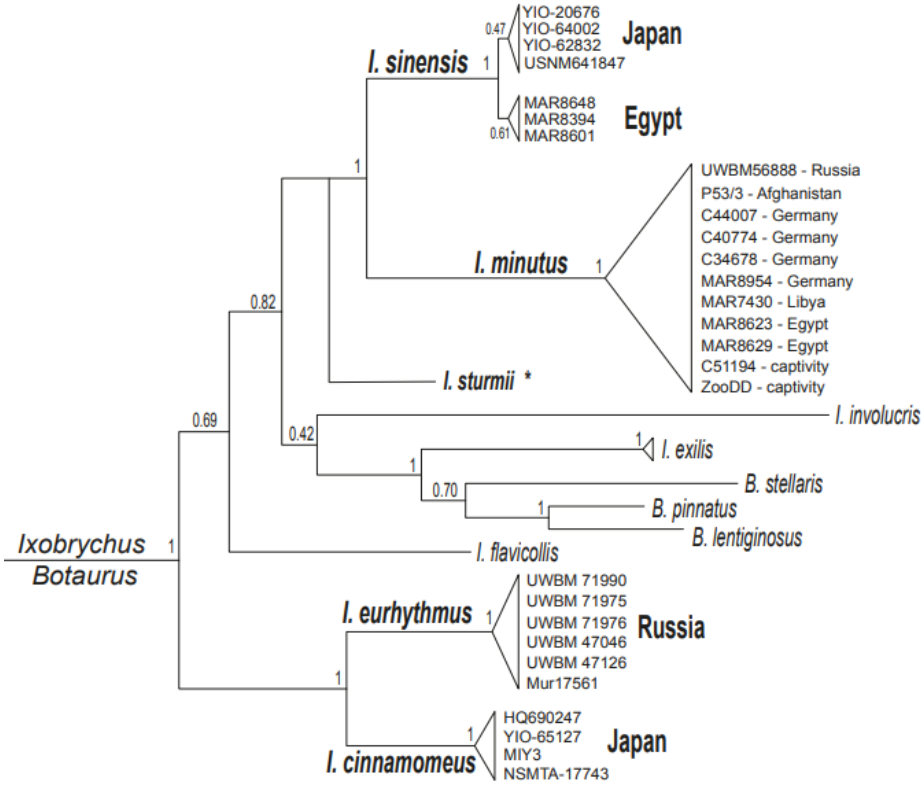


Fig. 4. Mitochondrial barcode tree from Päckert et al. (2014) showing the sister relationship between *Ixobrychus exilis* and the three species of *Botaurus*.

In the UCE tree (Fig. 1 above) from Hruska et al. (2023), *I. exilis* was strongly supported (100% bootstrap) as sister to the two species of *Botaurus* sampled for UCEs (*B. lentiginosus* and *B. poiciloptilus*); this clade was sister to another species traditionally placed in *Ixobrychus* (*I. involucris*), also with 100% bootstrap support. Thus, the two New World species of *Ixobrychus* were strongly supported as more closely related to *Botaurus* than to the Old World species of *Ixobrychus*. In the Bayesian mtDNA tree (Fig. 3), these species were reasonably well supported (0.99 p.p. for both species) as more closely related to *Botaurus lentiginosus* than to other species of *Ixobrychus*, although this section of the ML mtDNA tree (Fig. 2) was unresolved. Based on these results, Hruska et al. (2023) recommended that both *I. exilis* and *I. involucris* be transferred to *Botaurus*. An alternative to this would be to place *I. exilis* into a separate monotypic genus, which would presumably also necessitate placing *I. involucris* in a monotypic genus, but names may not be available for these genera.

Another alternative, given that some of the small bitterns of *Ixobrychus* are more closely related to *Botaurus*, thus blurring the morphological lines between the traditional limits of these genera, would be to merge all species of these two genera into a single genus. This would avoid placing *exilis* in a separate genus from the extremely similar *minutus* and *sinensis*, all previously thought to constitute a superspecies. There is also a fair amount of plumage and size variation among species of *Ixobrychus*, such that *I. flavicollis*, for example, overlaps some *Botaurus* in size. Although the nodes uniting *Ixobrychus* and *Botaurus* in the UCE and mtDNA trees above are deeper than those uniting other single genera, Hruska et al. (2023) noted that rates of sequence evolution in bitterns (both *Ixobrychus* and *Botaurus*) were faster than those in other herons, supporting the previous finding of Sheldon (1987b) and indicating that branch lengths in the Botaurinae are likely inflated. Although it seems that an expanded *Botaurus* (*Botaurus* Stephens, 1819, has priority over *Ixobrychus* Billberg, 1828) would be heterogeneous both phylogenetically and phenotypically, the branch lengths would be at least somewhat offset by the faster rates of evolution and an expanded *Botaurus* would be little more phenotypically heterogeneous than a *Botaurus* expanded to simply include *exilis* (and *involucris*).

An additional consideration involved in the option of simply transferring *exilis* to *Botaurus*, is that *minutus*, the type species of *Ixobrychus*, was not sampled in the UCE study of Hruska et al. (2023), introducing some uncertainty as to whether *minutus* is part of the clade of species not being transferred to *Botaurus* (i.e., whether *minutus* is truly not closely related to *exilis/Botaurus*). The data regarding the relationship of *minutus* to *exilis-Botaurus* are suggestive but not definitive. In the DNA-DNA hybridization tree of Sheldon (1987a), *I. minutus* and *I. cinnamomeus* were not part of the *I. exilis-Botaurus lentiginosus* clade, although the relationships of *minutus* and *cinnamomeus* were unresolved. In the mtDNA barcode tree (Päckert et al. 2014) the 11 samples of *I. minutus* formed a clade (with 1.0 pp) sister to the seven samples of *I. sinensis*, which was sampled by Hruska et al. (2023) and was deeply embedded in the clade not being transferred. Päckert et al. (2014) also found *exilis* to be sister to the three species of *Botaurus* sampled, again with 1.0 pp. Thus, there's reasonably strong support for *minutus* not being closely related to *exilis-Botaurus* in the mitochondrial data, and some support in the nuclear data. In my view, this would be a more serious issue if we were proposing to make substantial changes to *Ixobrynchus*, such as splitting it into two or more genera, rather than simply transferring one species to *Botaurus*. However, the majority of species currently in *Ixobrychus*, including type species *minutus*, would simply be retained in *Ixobrychus*, undergoing no change of status under this option.

For this issue, votes are needed as follows:

1. Revise the taxonomy of the bitterns, YES or NO

If YES on #1, then vote for either 2A or 2B (unless you favor a different option, which should be specified):

2A. Transfer *I. exilis* to *Botaurus*, retaining *I. sinensis* and *I. minutus* in *Ixobrychus*
2B. Subsume *Ixobrychus* into *Botaurus*, transferring all three NACC species

Recommendation:

Numerous molecular studies indicate that the taxonomy of the bitterns requires revision, so I strongly recommend a YES vote on Part 1. Regarding Part 2, this is a tough call, with good arguments for and against the proposed treatments. I slightly favor transferring only *I. exilis* to *Botaurus*, at least for now, because (1) it is the least disruptive option; (2) it limits the genus transfers to a species endemic to the Americas, rather than also involving two Old World accidentals (as would happen if all NACC species were transferred to *Botaurus*); and (3) this option seems more consistent with the depth of nodes in the phylogenetic trees, even adjusting for a more rapid evolutionary rate among the bitterns. I view point 2 above as a major obstacle to subsuming *Ixobrynchus* into *Botaurus* at this time. Should a global body such as WGAC endorse the merger of *Ixobrychus* into *Botaurus*, then point 2 above becomes moot and the balance is likely tipped towards transferring all species of *Ixobrychus* to *Botaurus*. In that case we could re-vote, but for now I recommend the transfer of *exilis* only.

(c) Revise the genus-level taxonomy of *Bubulcus ibis* (Cattle Egret) and related species

The Cattle Egret is now generally placed in the monotypic genus *Bubulcus* based on its behavioral and morphological distinctiveness. However, it has also been placed in other genera, e.g., *Ardeola* (Bock 1956), *Egretta* (Payne and Risley 1976), or *Ardea* (Kushlan and Hancock 2005). Sheldon's (1987a) DNA-DNA data (his Fig. 2) showed it to be part of an unresolved clade with six other species all currently placed in *Ardea*. The cyt-b data of Sheldon et al. (2000), who sampled 15 species, found *B. ibis* to be sister to the two species of *Ardea* sampled (*alba* and *herodias*). In the mtDNA barcode tree of Huang et al. (2016), *B. ibis* was sister to *A. alba* and these species were nested deep within *Ardea*.

In the UCE tree (Fig. 1 above) from Hruska et al. (2023), *B. ibis* was nested within *Ardea* as sister to one of the two main clades of this genus, which consisted of *herodias*, *cinerea*, *purpurea*, *melanocephala*, and *goliath*, the other main clade consisting of *pacifica*, *alba*, and *intermedia*. This result received 100% bootstrap support. Thus, according to the UCE tree, retaining the phenotypically distinctive *B. ibis* in *Bubulcus* would necessitate a split of *Ardea* into two genera. In their mtDNA trees (Figs. 2 and 3), however, *B. ibis* was sister to *Ardea*, which was separated into two main clades. One clade corresponded to the second clade detailed above, but the other clade, due to the different taxon sampling, consisted of *humbloti*, *insignis*, *purpurea*, *melanocephala*, and *goliath*. Although the *Ardea* + *Bubulcus* clade received strong support (100% bootstrap and 1.0 p.p.), support for *Ardea* as a clade if *B. ibis* was excluded was not as strong (78% bootstrap, 0.99 p.p.).

Based on their results, Hruska et al. (2023) recommended that *B. ibis* be transferred to *Ardea*. However, an alternative consistent with all their trees would be to maintain *Bubulcus* for *ibis* and to split *Ardea* as currently delineated into two genera, one minimally consisting of *pacifica*, *alba*, and *intermedia*, the other minimally consisting of *humbloti*, *insignis*, *herodias*, *cinerea*, *purpurea*, *melanocephala*, and *goliath*. The two unsampled species, *cocoi* and *sumatrana*, would presumably belong to the latter group, *cocoi* thought to be closely related to *herodias* and *cinerea* (see Huang et al. 2016), and *sumatrana* thought to be closely related to *insignis*. This would preserve *Bubulcus* for the behaviorally distinctive *ibis*, and would place two other white egrets, *alba* and *intermedia*, with *pacifica* in a separate genus, for which *Casmerodius* Gloger, 1841, appears to be the oldest available name. To me, the branch lengths in the various phylogenies in Hruska et al. (2023) do not provide strong support for either alternative: the nodes uniting the proposed three genera are deeper than most nodes within genera in the Ardeinae but not as deep as most nodes that unite separate genera. However, the genus *Ixobrychus* does contain nodes that are deeper than any within *Ardea* + *Bubulcus*, even without including *exilis* and *involucris*.

For this issue, votes are needed as follows:

1. Revise the taxonomy of *Bubulcus ibis* and related species, YES or NO. A NO vote would retain *B. ibis* in *Bubulcus* and retain all related species in *Ardea*, which would be paraphyletic according to the UCE phylogeny in Hruska et al. (2023).

If YES on #1, then vote for either 2A or 2B (unless you favor a different option, which should be specified):

2A. Transfer *B. ibis* to *Ardea*
2B. Retain *B. ibis* in *Bubulcus* and transfer *Ardea alba*, *A. intermedia*, and *A. pacifica* to *Casmerodius*

Recommendation:

Based primarily on the UCE data of Hruska et al. (2023), I think changes to the taxonomy are warranted, so I recommend a YES vote on Part 1. For Part 2, I recommend that *Bubulcus ibis* be transferred to *Ardea*. As with the *Ixobrychus* issue above, this is a close call over keeping *B. ibis* in *Bubulcus* and splitting *Ardea* into two genera, but I favor transferring *B. ibis* for reasons similar to those regarding the bitterns: (1) it is the least disruptive option; (2) it limits the genus transfers to a widespread species (*B. ibis*) that occurs in the Americas, rather than transferring, in addition to a widespread species (*A. alba*) that occurs in the Americas, an Old World species (*A. intermedia*) accidental to our area (the third species of *Casmerodius*, *A. pacifica*, is an Old World species not known from our area; and (3) there is ample precedence for placing *ibis* in genera other than *Bubulcus* (i.e., not recognizing it as so distinctive as to require its own genus). Also, if relying on phenotype to continue to recognize *Bubulcus*, there is the question of what phenotypic characters distinguish *Casmerodius* from *Ardea*. As with the bitterns, should a global body such as WGAC endorse the transfer of *alba*, *intermedia*, and *pacifica* to *Casmerodius*, then point 2 above becomes moot and the balance may be tipped towards this alternative. In that case we could re-vote, but for now I recommend the transfer of *B. ibis* to *Ardea*.

(d) Remove the hyphen from the group name Night-Heron

Background:

Seven extant species of night heron are typically recognized, two of which (Black-crowned Night-Heron and Yellow-crowned Night-Heron) occur in North America. Peters (1931) placed these seven species in four genera, Black-crowned Night-Heron *nycticorax* and Nankeen Night-Heron *caledonicus* in *Nycticorax*, White-backed Night-Heron *leuconotus* in *Calherodius*, White-eared Night-Heron *magnifica* in *Oroanassa*, Yellow-crowned Night-Heron *violacea* in *Nyctanassa*, and Japanese Night-Heron *goisagi* and Malayan Night-Heron *melanolophus* in *Gorsachius*. These were placed consecutively in the linear sequence in Peters (1931), presumably indicating a close relationship. The second edition of the relevant volume of Peters (Mayr and Cottrell 1979) emphasized this presumed close relationship by placing all species in the single genus *Nycticorax*. In AOU (1957) and earlier editions of the AOU Check-list, the group name of these species was Night Heron, but AOU (1983) added a hyphen to the name (Night-Heron) to indicate the presumed monophyly of these seven species.

New Information:

Most global checklists (e.g., Clements, IOC, and Howard & Moore) currently recognize three genera of night heron: *Gorsachius* for *magnificus*, *goisagi*, *melanolophus*, and *leuconotus*, *Nycticorax* for *nycticorax* and *caledonicus*, and *Nyctanassa* for *violacea*, although Birdlife has reverted to the taxonomy of Peters (1931). Regardless of the number of genera recognized, these species are still placed consecutively in the linear sequence.

All species of night heron were sampled for the Hruska et al. (2023) phylogenetic paper on herons, although success, as with other species, was variable. Their UCE tree included five species (*Gorsachius melanolophus* and *G. leuconotus* (placed in *Calherodius* in this tree), both species of *Nycticorax*, and *Nyctanassa violacea*), whereas their mtDNA tree included six species (the four species of *Gorsachius*, *Nycticorax caledonicus*, and *Nyctanassa violacea*, i.e., all species except *Nycticorax nycticorax*).

In the UCE tree (Fig. 1), *G. melanolophus* was sister to all other species of the subfamily Ardeinae, *C. leuconotus* was sister to one of the two main sub-clades of this subfamily, and *Nycticorax* and *Nyctanassa* were sister to the other main sub-clade of this subfamily. All relevant nodes received 100% bootstrap support. In the ML mitochondrial tree (Fig. 2), *Nyctanassa violacea* and *Nycticorax caledonicus* were sister species and formed one branch of the 3-way polytomy within the Ardeinae, with 98% bootstrap support. *Gorsachius magnificus* and *G. leuconotus* were sister species and were sister to the rest of the second branch of the polytomy (at 99% bootstrap), whereas *G. goisagi* and *G. melanolophus* were sisters and were sister to the rest of the third branch of the polytomy (at 81% bootstrap). The Bayesian tree (Fig. 3) differed somewhat: *N. violacea*, *N. caledonicus*, *G. goisagi*, and *G. melanolophus* formed a clade that was sister to the rest of the Ardeinae (1.0 p.p.), whereas *G. magnificus* and *G.*

leuconotus were sister species and were sister to a clade that included *Pilherodius*, *Syrigma*, and all species of *Egretta* (1.0 p.p.).

Recommendation:

Significantly, in none of the trees did the sampled species of night heron form a monophyletic group. Therefore, I recommend that we remove the hyphen from the group name “Night-Heron”. This is mandatory under our naming guidelines based on the trees in Hruska et al. (2023).

Summary Recommendation:

I recommend that we (a) adopt a new linear sequence and subfamily classification based on Hruska et al. (2023); (b) transfer *Ixobrychus exilis* (Least Bittern) to *Botaurus*; (c) transfer *Bubulcus ibis* (Cattle Egret) to *Ardea*; and (c) remove the hyphen from the group name Night-Heron. The new linear sequence and classification, incorporating the proposed changes in sections (b), (c), and (d), would be as listed below, although the linear sequence should be vetted thoroughly.

- subfamily: Tigriornithinae
  - genus: *Tigrisoma*
    - species: *Tigrisoma lineatum* (Rufescent Tiger-Heron, Onoré rayé)
    - species: *Tigrisoma mexicanum* (Bare-throated Tiger-Heron, Onoré du Mexique)
    - species: *Tigrisoma fasciatum* (Fasciated Tiger-Heron, Onoré fascié)
- subfamily: Cochleariinae
  - genus: *Cochlearius*
    - species: *Cochlearius cochlearius* (Boat-billed Heron, Savacou huppé)
- subfamily: Agamiinae
  - genus: *Agamia*
    - species: *Agamia agami* (Agami Heron, Héron agami)
- subfamily: Botaurinae
  - genus: *Botaurus*
    - species: *Botaurus exilis* (Least Bittern, Petit Blongios)
    - species: *Botaurus lentiginosus* (American Bittern, Butor d'Amérique)
    - species: *Botaurus pinnatus* (Pinnated Bittern, Butor mirasol)
  - genus: *Ixobrychus*
    - species: *Ixobrychus minutus* (Little Bittern, Blongios nain) A
    - species: *Ixobrychus sinensis* (Yellow Bittern, Blongios de Chine) A
- subfamily: Ardeinae
  - genus: *Pilherodius*
    - species: *Pilherodius pileatus* (Capped Heron, Héron coiffé)
  - genus: *Syrigma*
    - species: *Syrigma sibilatrix* (Whistling Heron, Héron flûte-du-soleil) A
  - genus: *Egretta*
    - species: *Egretta caerulea* (Little Blue Heron, Aigrette bleue)
    - species: *Egretta tricolor* (Tricolored Heron, Aigrette tricolore)
    - species: *Egretta rufescens* (Reddish Egret, Aigrette roussâtre)
    - species: *Egretta eulophotes* (Chinese Egret, Aigrette de Chine) A

        species: *Egretta thula* (Snowy Egret, Aigrette neigeuse)
        species: *Egretta garzetta* (Little Egret, Aigrette garzette)
        species: *Egretta gularis* (Western Reef-Heron, Aigrette à gorge blanche) A
    genus: *Nyctanassa*
        species: *Nyctanassa violacea* (Yellow-crowned Night Heron, Bihoreau violacé)
    genus: *Nycticorax*
        species: *Nycticorax nycticorax* (Black-crowned Night Heron, Bihoreau gris)
    genus: *Butorides*
        species: *Butorides striata* (Striated Heron, Héron strié)
        species: *Butorides virescens* (Green Heron, Héron vert)
    genus: *Ardeola*
        species: *Ardeola bacchus* (Chinese Pond-Heron, Crabier chinois) A
    genus: *Ardea*
        species: *Ardea alba* (Great Egret, Grande Aigrette)
        species: *Ardea intermedia* (Intermediate Egret, Héron intermédiaire) A
        species: *Ardea ibis* (Cattle Egret, Héron garde-boeufs)
        species: *Ardea cinerea* (Gray Heron, Héron cendré) A
        species: *Ardea herodias* (Great Blue Heron, Grand Héron)
        species: *Ardea cocoi* (Cocoi Heron, Héron cocoi)
        species: *Ardea purpurea* (Purple Heron, Héron pourpré) A

Acknowledgement: Parts b and c of this proposal benefitted greatly from comments from NACC members on a previous version, especially those of Van Remsen and Oscar Johnson.

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Sheldon, F. H., C. E. Jones, and K. G. McCracken (2000). Relative patterns and rates of evolution in heron nuclear and mitochondrial DNA. Molecular Biology and Evolution 17:437–450.

Submitted by: Terry Chesser

Date of Proposal: 18 July 2023, revised 20 December 2023

Revise the sub-family and genus-level classification of the Charadriidae

Background:

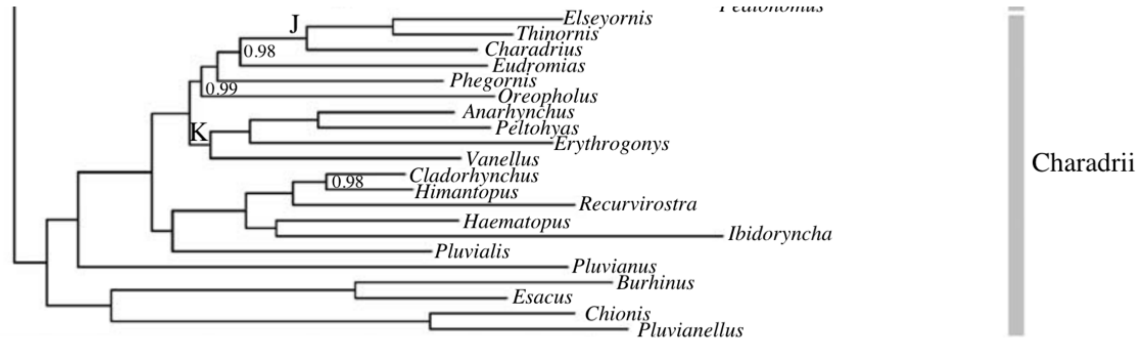
Charadriidae comprises nineteen species in two subfamilies in the NACC area. Of these, thirteen are in the long-recognized cosmopolitan genus *Charadrius*. The current linear sequence (Chesser et al., 2023) for the species in this family is:

<u>Subfamily Vanellinae</u>
Northern Lapwing, *Vanellus vanellus*
Southern Lapwing, *Vanellus chilensis*

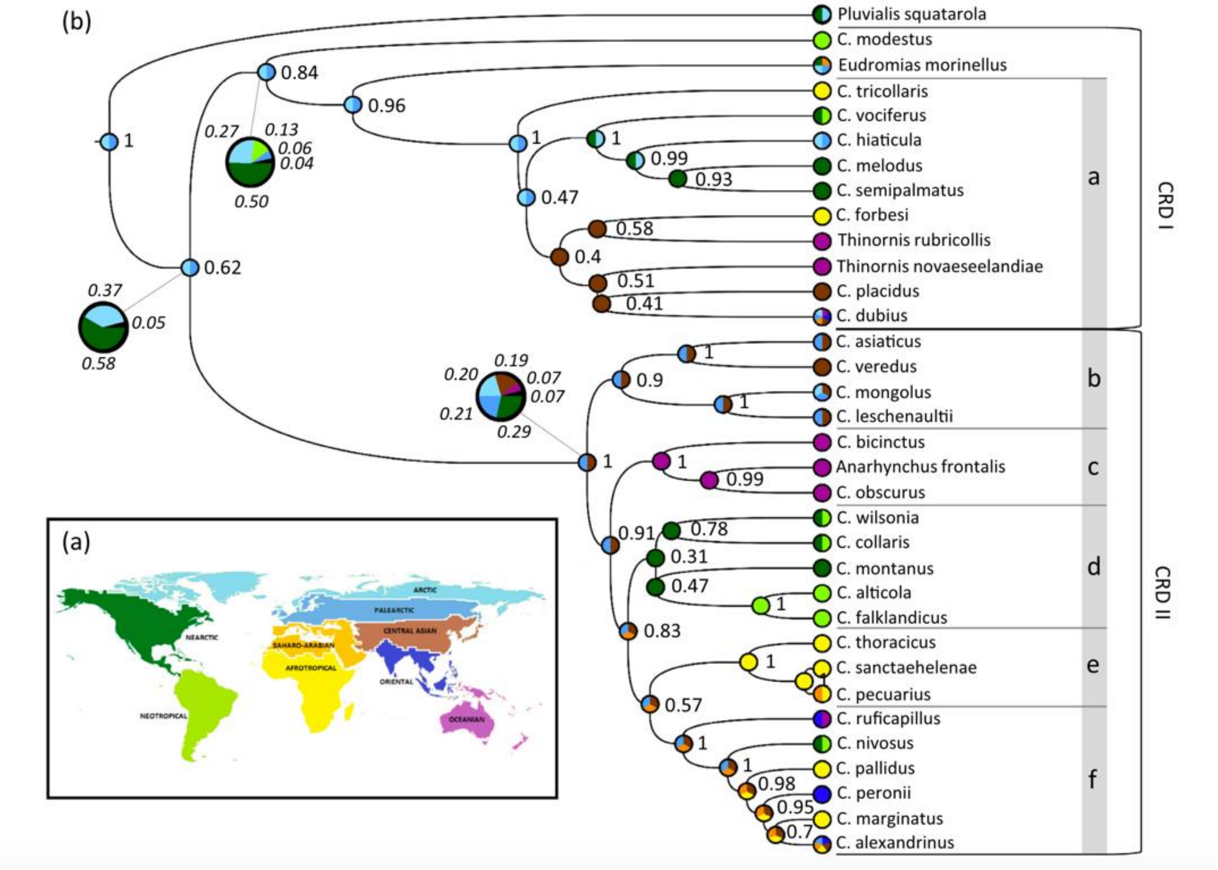
<u>Subfamily Charadriinae</u>
Black-bellied Plover, *Pluvialis squatarola*
European Golden-Plover, *Pluvialis apricaria*
American Golden-Plover, *Pluvialis dominica*
Pacific Golden-Plover, *Pluvialis fulva*
Eurasian Dotterel, *Charadrius morinellus*
Killdeer, *Charadrius vociferus*
Common Ringed Plover, *Charadrius hiaticula*
Semipalmated Plover, *Charadrius semipalmatus*
Piping Plover, *Charadrius melodus*
Little Ringed Plover, *Charadrius dubius*
Lesser Sand-Plover, *Charadrius mongolus*
Greater Sand-Plover, *Charadrius leschenaultii*
Oriental Plover, *Charadrius veredus*
Wilson's Plover, *Charadrius wilsonia*
Collared Plover, *Charadrius collaris*
Mountain Plover, *Charadrius montanus*
Snowy Plover, *Charadrius nivosus*

New Information:

A series of papers have come out addressing the phylogenetic relationships in the Charadriidae, with increasing amounts of data. However, all papers suffer from having few genetic markers, which hampers our ability to confidently make changes to genera, and two papers additionally suffer from limited taxon sampling. Baker et al. (2007) sampled three mitochondrial loci and one nuclear locus, targeting one sample per genus. Below is the relevant part of their tree. Note that *Anarhynchus* is in the same clade as *Vanellus*, the two of which are unrelated to the one *Charadrius* sample. Nodes without support values have a posterior value of 1.



Dos Remedios et al. (2015) sampled two mitochondrial and four nuclear loci from 29 *Charadrius* species. Their Bayesian consensus tree is shown below. Node values are posterior probabilities. Note the lack of any *Vanellus* samples, and the low node support in many parts of the tree. This phylogeny was the basis of NACC proposal 2019-A-8, which rearranged the linear sequence of species in *Charadrius* but did not change genus limits. The map and colored circles are a biogeographic analysis.



Another study (Barth et al. 2013) sampled eight mitochondrial and two nuclear loci from a decent selection of Charadriidae but focusing on placing the New Zealand Dotterel (*Charadrius obscurus*) in the phylogeny. Their results largely corroborate those of the other papers outlined here. Their Figure 1 phylogeny is shown below. Note that nodes without circles have low support and should be considered polytomies. Note also that *Vanellus* is embedded within *Charadrius*.

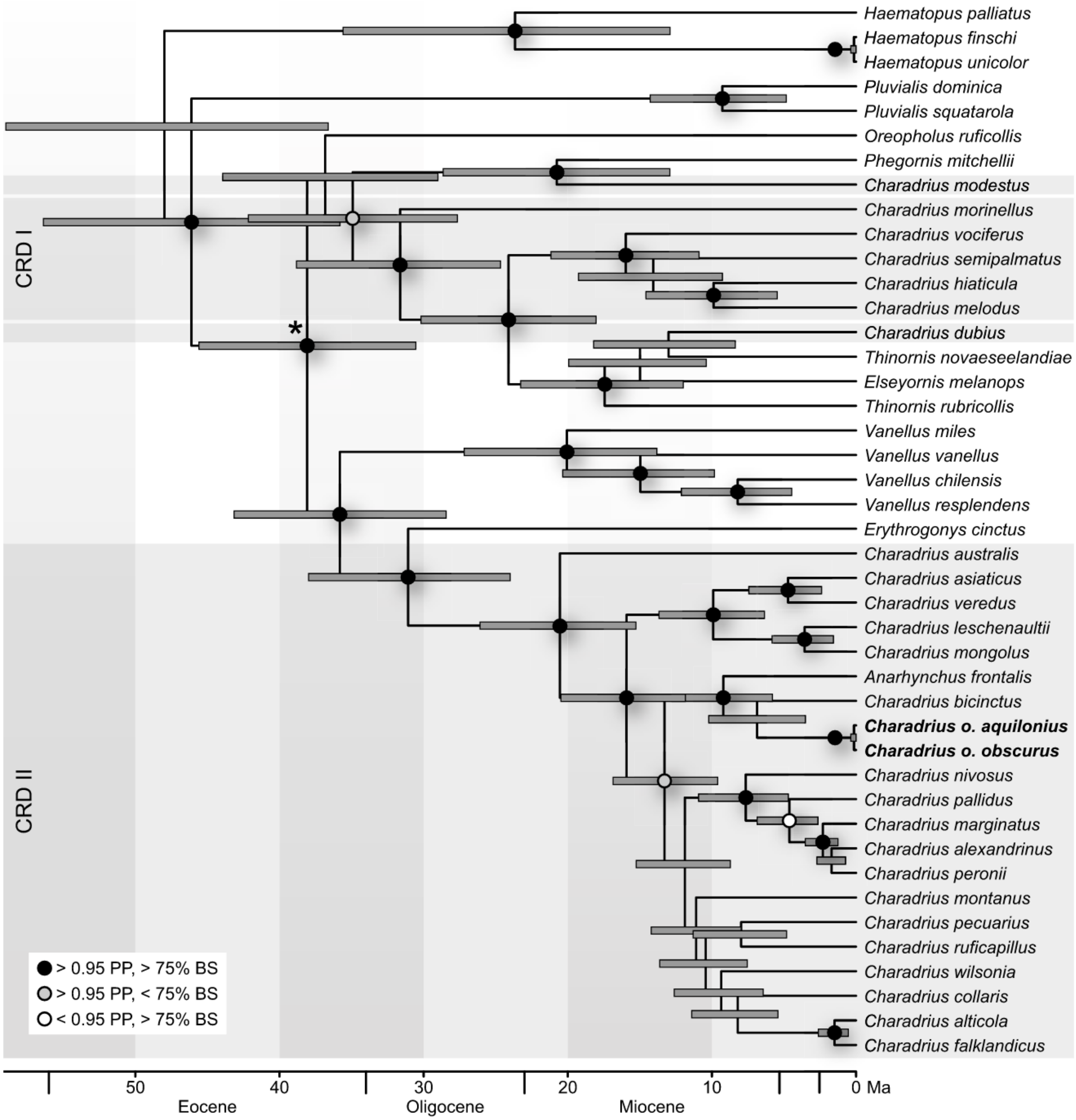
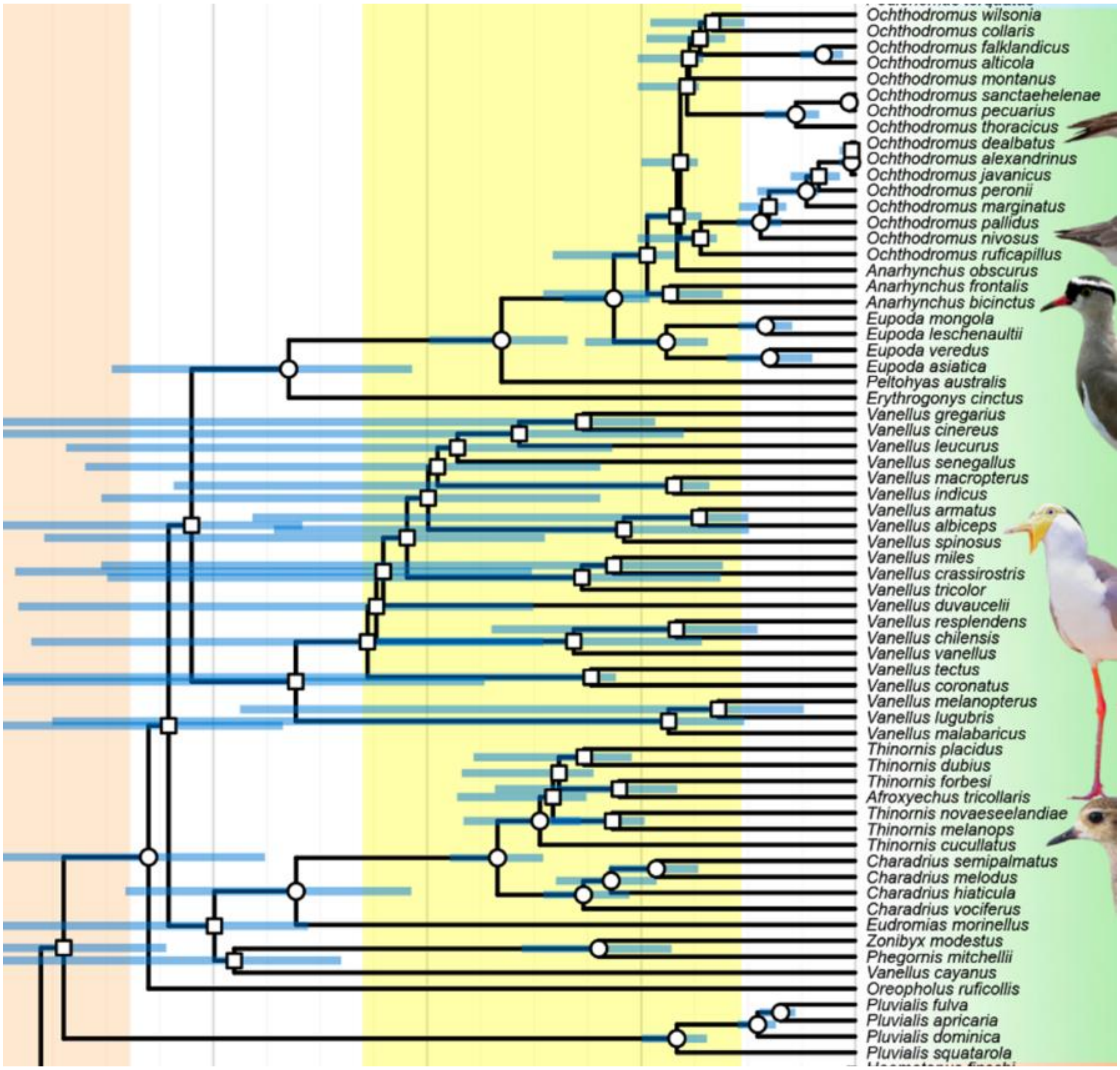


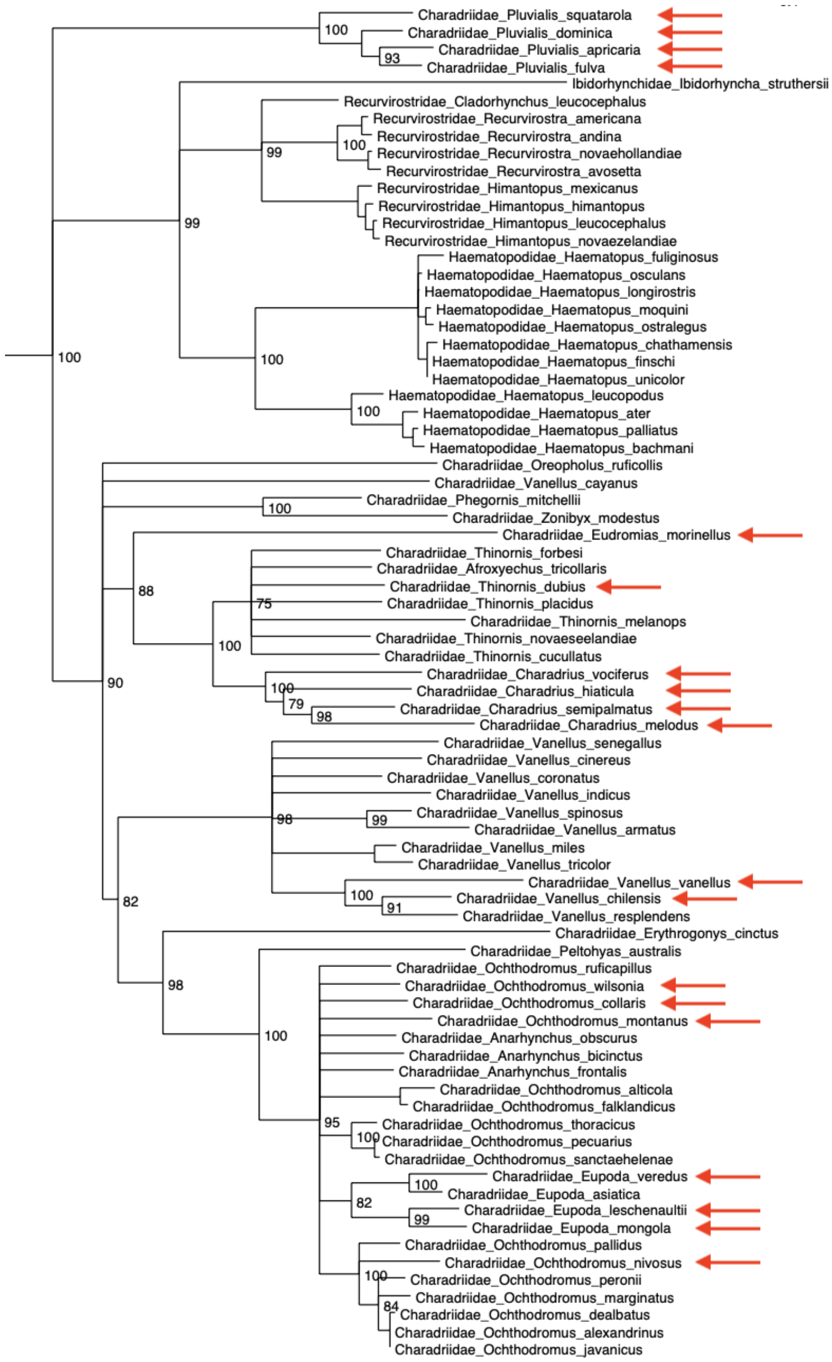
Figure 1. Placement of *C. obscurus* within a time-calibrated phylogeny of Charadriidae. Shown is the BEAST topology. Black dots indicate nodes with Bayesian Posterior Probability (PP) >0.95 and Bootstrap Support (BS) >75, grey dots indicate PP >0.95 and BS <75 and white dots PP <0.95 and BS >75. PP and BS values that are both lower than 0.95 and 75, respectively, are not indicated (for all support values, please see Fig. S1). Horizontal grey boxes (CRD I and II) highlight the non-monophyletic *Charadrius* groups. The asterisk marks the time-constrained split; node bars show 95% highest probability density (HPD).

Lastly, we come to the paper that is the basis for most of the changes in this proposal. Černý & Natale (2022) used a supertree approach that utilized much of the same data as in the previous papers (Baker et al. 2007, Barth et al. 2013, Dos Remedios et al. 2015), with the addition of more loci (27 total) and a matrix of 69 skeletal characters, to address the relationships of most species in the order Charadriiformes. The main issue I have with this paper is that the main figure (screenshot below) combines both the genetic and skeletal data with no indication of whether the relationships are supported by one or the other data types. I'm very skeptical of the older relationships in the main figure, given well known issues of convergence in skeletal datasets. Nodes with bootstrap support ≥70% are indicated by circles, and nodes with bootstrap support <70% are indicated by squares. As you can see, there are many squares on the nodes in this tree. This is no surprise, given the very high percentage of missing data in the molecular data matrix (68.5%!) with some samples represented by just a single locus (mean = 9.5 loci).



A portion of Figure 6 from Černý & Natale (2022), showing phylogenetic relationships in the Charadriidae. Note that the darker gray vertical lines are 10 Ma increments, and the faint gray lines are 2.5 Ma. Note that for converting this to a linear sequence, this tree should be "read" bottom-to-top.

Thankfully, the supplemental data for Černý & Natale (2022) does contain the molecular-only phylogeny, but it shows that many of the relationships, especially those deeper in the tree, are weakly supported by molecular data. To better illustrate those relationships that do have good support in the tree, I collapsed all nodes with posterior probabilities less than 0.75. Below is the relevant portion of the tree, with the species occurring in the NACC area indicated in red. Despite the weak support for many nodes, there is strong support for four main clades; 1) *Pluvialis*, 2) *Charadrius sensu stricto*, 3) *Vanellus*, and 4) the remainder of the *Charadrius*. There are a handful of species on long branches, whose relationships within the family are unresolved (e.g. "*Vanellus*" *cayanus*), but those are all extralimital to the NACC area.



As an aside, I’ve looked through the rest of this Charadriiformes tree and found just one other case of genus-level paraphyly (based on our current taxonomy). That topology places *Sterna forsteri* and *S. trudeaui* as sister to *Thalasseus* plus the rest of *Sterna*. However, this relationship is weakly supported, so I don’t think any changes should be considered for now.

Out of curiosity, I delved into the skeletal data used in this tree. Černý & Natale (2022) used data from Strauch (1978), which had been reanalyzed by Chu (1995). Chu (1995) presented phylogenies based solely on the skeletal data, which I’ve included below. As you can see, these deeper relationships strongly conflict with the molecular data, and as expected, place unrelated taxa close to each other in cases where morphology is similar (e.g., *Vanellus* closer to Recurvirostridae in some trees). Another tree from Chu (1995; not shown) with more tips and fewer markers, which includes more *Charadrius* tips, is less well-resolved but places *Vanellus* in a big polytomy with *Charadrius sensu lato*, so closer to where the molecular data indicate it belongs.

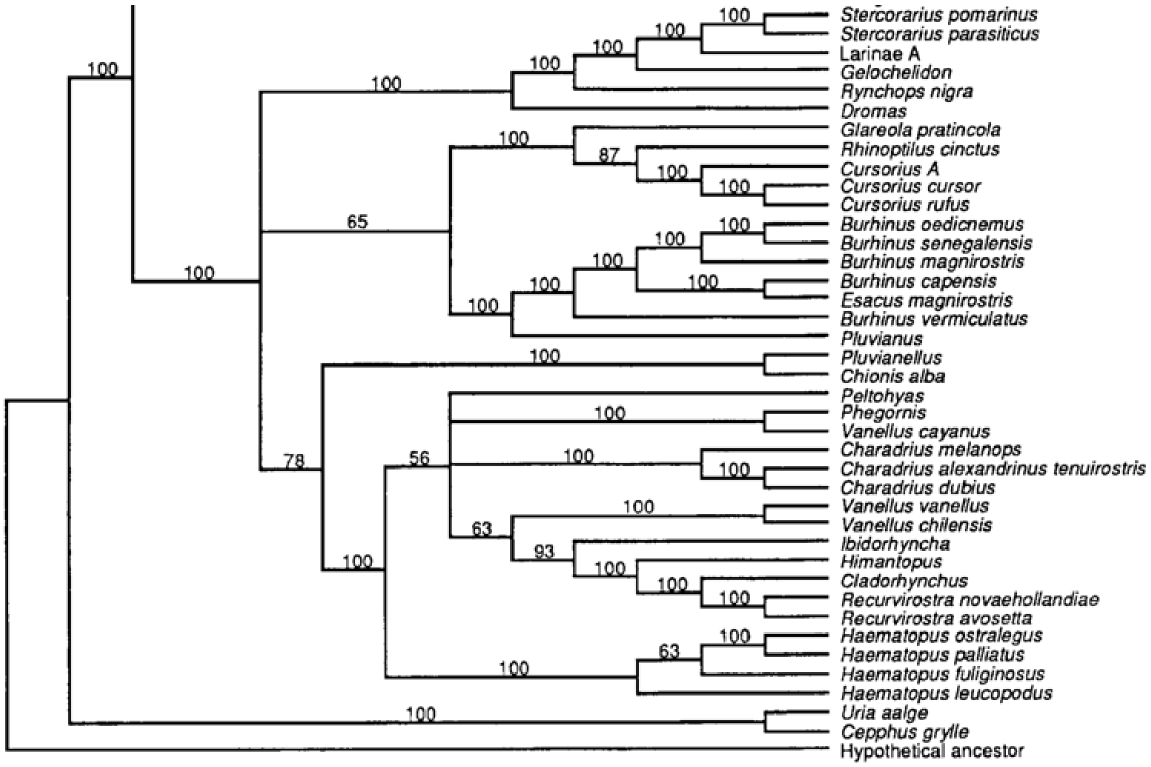


FIGURE 7. Fifty percent majority-rule consensus of the 855 shortest trees found during a reduced-matrix analysis of the revised Strauch matrix. Numbers adjacent to each node are the percentage of shortest trees having the resolution shown.

I think we have a few options. One would be to wait for better data, which was my initial reaction on seeing the phylogeny of Černý & Natale (2022). However, it seems that global authorities are moving forward with some changes to genera, and I think it would be worthwhile for NACC to consider making some of these changes. Although the molecular data do not resolve all the relationships in the group, they do indicate that our current treatment of *Charadrius* is highly paraphyletic, which would require a few changes. There are also a handful of species (e.g., *Charadrius morinellus*) that are on long branches that suggest that they could be split off as monotypic genera, even if their exact relationships are currently unresolved or poorly supported.

To make the taxonomy a bit easier to follow, I've listed here the author, year, and type species for each of the genera that are relevant to this matter, including those that could reasonably be resurrected for a clade. These are sorted by year.

Charadrius Linnaeus 1758, type *hiaticula*
Vanellus Brisson, 1760, type *vanellus*
Pluvialis Brisson 1760, type *apricaria*
Anarhynchus Quoy & Gaimard 1830, type *frontalis*
Eudromias Brehm 1831, type *morinellus*
Erythrogonys Gould 1838, type *cinctus*
Thinornis Gray, GR 1844, type *novaeseelandiae*
Ochthodromus Reichenbach 1852, type *wilsonia*
Eupoda Brandt, JF 1852, type *asiatica*
Aegialophilus Gould 1865, type *alexandrinus*
Peltohyas Sharpe 1896, type *australis*
Afroxyechus Mathews 1913, type *tricollaris*

Effect on AOS-CLC area:

Following the tentative recommendations below would lead to a new taxonomic arrangement and linear sequence for the Charadriidae, as follows:

Subfamily Pluvialinae
Black-bellied Plover, *Pluvialis squatarola*
European Golden-Plover, *Pluvialis apricaria*
American Golden-Plover, *Pluvialis dominica*
Pacific Golden-Plover, *Pluvialis fulva*

Subfamily Charadriinae
Eurasian Dotterel, *Eudromias morinellus*
Killdeer, *Charadrius vociferus*
Common Ringed Plover, *Charadrius hiaticula*
Semipalmated Plover, *Charadrius semipalmatus*
Piping Plover, *Charadrius melodus*
Little Ringed Plover, *Charadrius dubius*
Northern Lapwing, *Vanellus vanellus*
Southern Lapwing, *Vanellus chilensis*
Lesser Sand-Plover, *Anarhynchus mongolus*
Greater Sand-Plover, *Anarhynchus leschenaultii*
Oriental Plover, *Anarhynchus veredus*
Wilson's Plover, *Anarhynchus wilsonia*
Collared Plover, *Anarhynchus collaris*

Mountain Plover, *Anarhynchus montanus*
Snowy Plover, *Anarhynchus nivosus*

Recommendation:

Please vote on the following issues:

A. Transfer *Charadrius morinellus* to *Eudromias*
B. Transfer *Charadrius dubius* to *Thinornis*
C. Transfer *Charadrius mongolus*, *leschenaultii*, and *veredus* to *Eupoda,* and *wilsonia, collaris, montanus,* and *nivosus* to *Ochthodromus*
D. Transfer *Charadrius mongolus*, *leschenaultii*, *veredus, wilsonia, collaris, montanus,* and *nivosus* to *Anarhynchus*
E. Adopt the new linear sequence
F. Recognize the subfamily Pluvialinae for the species in *Pluvialis*
G. Transfer Vanellus to the subfamily Charadriinae
H. Recognize the subfamily Anarhynchinae for the species in *Anarhynchus*

Note that both C & D and G & H are mutually exclusive.

I recommend the following votes:

YES votes on A: *morinellus* is on a long branch that is much older than many other groups we consider genera (e.g., *Vanellus*). However, it is sister to a group containing *Charadrius sensu stricto*, so a strict conservative interpretation could maintain it within *Charadrius* for now. The Barth et al. (2013) phylogeny places the divergence time at just over 30 Ma, which suggests genus-level divergence.

NO on B (tentatively): Although this is the taxonomy in the phylogeny of Černý and Natale (2022), it was not adopted by global authorities, to my knowledge. I'm not very familiar with the species in *Thinornis* to make an educated recommendation on their phenotypic diagnosability. The Barth et al. (2013) phylogeny does place the divergence time at about 25 Ma, which is quite old and suggestive of separate genera. However, given that a global authorities have chosen to not recognize *Thinornis* and the one species in the clade (*dubius*) is largely extralimital to our area, I think it's better to maintain it in *Charadrius* for the time being.

NO on C: despite my initial hesitation on making revisions in this group given the haphazard quality of the phylogenetic data, there is strong evidence that this clade of former *Charadrius* is unrelated to the core group, and is at least as divergent as genera like *Vanellus*, so they could potentially go in their own subfamily. Černý and Natale (2022) recommend recognizing *Eupoda* but not *Ochthodromus*, but as shown in the phylogeny of molecular-only data, there is very little support for the internal relationships in the group. However, Barth et al. (2013) do also support this topology, with a somewhat old (~17 Ma) split from the rest of this clade. I am including this one here for sake of completeness, but also because there is a possibility that if the topology in Černý and Natale (2022) holds up with better data, that it could be a viable alternative. It doesn't matter at all for the taxonomy, but the etymology of *Ochthodromus* (“bank/shore-runner”) is much more appropriate for this group of plovers than is *Anarhynchus* (“backward-bill”).

YES on D. I highly recommend this option. The data are quite clear that this clade should not be in *Charadrius* and given that we don’t have a good handle on the internal topology, I think it’s safest to transfer all species to this genus for the time being. This is also taxonomy that global authorities are using, so it would put us in line with those global taxonomies. The one issue that I foresee here is that there could potentially be an older genus than *Anarhynchus* available for one of the species in this group. I did check the Richmond Index for the 28 synonyms of *Charadrius* listed in Birds of the World and none superseded *Anarhynchus*. Frank Rheindt and Pam Rasmussen have also done a thorough search for older available names (WGAC comments) and were unable to find older available names.

YES on E. Given the phylogenetic data that we have, this is the most accurate linear sequence for the group. This mostly just moves *Vanellus* between the two former *Charadrius* clades. I don’t think any changes should be made on the linear sequence within each of the groups, given the low resolution in the phylogenetic trees.

YES on F. I think it’s best to consider *Pluvialis* in a separate subfamily, Pluvialinae. This clade is on a very long branch and could potentially even be its own family.

G and H. I don’t have strong feelings on the best course of action for these subfamilies but given that *Vanellus* is embedded with the former *Charadrius*, some changes are necessary at the subfamily level. *Vanellus* is certainly morphologically distinct, but *Anarhynchus* clearly is not, given that we’ve long considered them in the same genus as *Charadrius.* One option would be to merge Vanellinae into Charadriinae (YES on G and NO on H), which would leave two subfamilies (in the NACC area) in Charadriidae but make a morphologically heterogenous Charadriinae. However, I think that this is preferable to creating three subfamilies each dominated by a single genus (i.e., NO on G and YES on H). These three subfamilies would be Charadriinae, Vanellinae, and Anarhynchinae. I don’t think this is a good option.

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Submitted by: Oscar Johnson, The University of Texas at El Paso

Date of proposal: 25 July 2023

2024-A-4 N&MA Classification Committee pp. 21-22

Recognize extralimital *Puffinus bailloni*, *P. bannermani*, and *P. persicus* as species distinct from Audubon's Shearwater *P. lherminieri*

Effect on NACC:

These three taxonomic groups are all extralimital to the NACC area and have been accepted as separate species by most world checklists and authorities on seabirds since the late 2000's. Acceptance of these splits by the NACC will result in changes to the distributional statement (restricting it to the North Atlantic) and notes for *P*. *lherminieri*.

Background:

Species limits within the former *Puffinus lherminieri*/*assimilis* group have long been contentious. Polytypic *P. bailloni* (4-7 taxa; Indian Ocean breeding *bailloni/atrodorsalis, nicolae/colstoni,* and Pacific Ocean breeding *dichrous*/*polynesiae* and *gunax*) were originally described as subspecies of *P*. *lherminieri* or as distinct species (depending on the taxon involved), whereas polytypic *P. persicus* (at least two taxa: nominate and *temptator*) and monotypic *P. bannermani* were originally described as distinct species. See figure 1 for breeding locations from Austin et al. (2004).

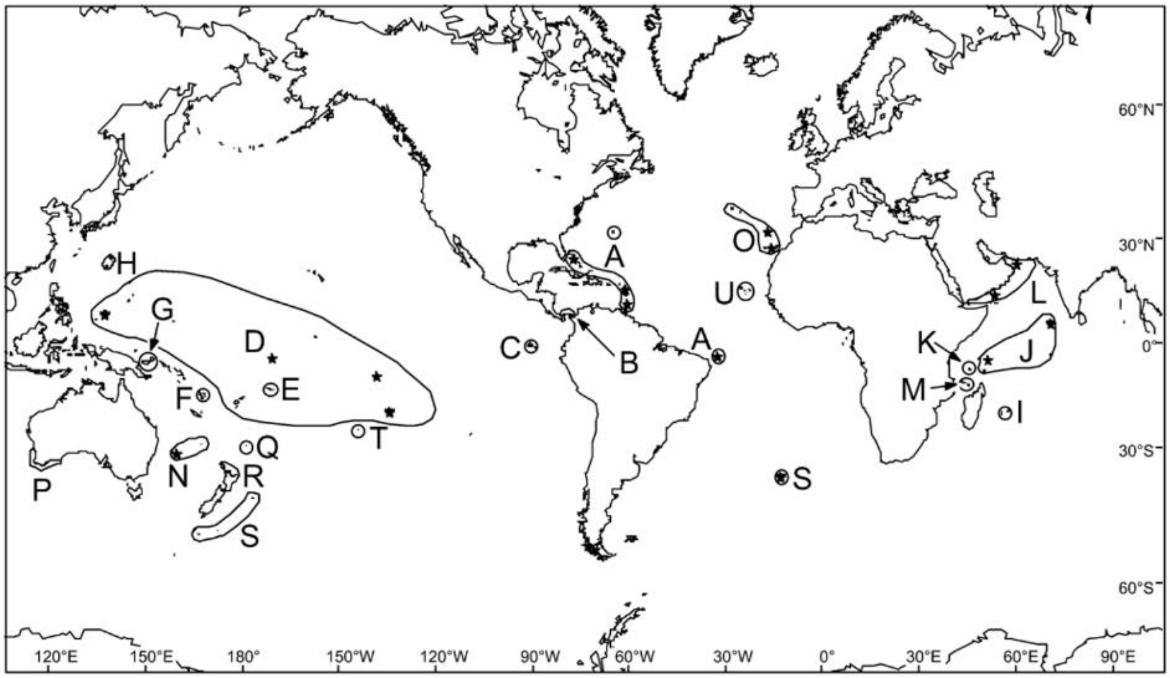

FIG. 1. Distribution of the *assimilis–lherminieri* complex. (A) *lherminieri*, (B) *loyemilleri*, (C) *subalaris*, (D) *dichrous*, (E) *polynesiae*, (F) *gunax*, (G) *heinrothi*, (H) *bannermani*, (I) *bailloni*, (J) *nicolae*, (K) *colstoni*, (L) *persicus*, (M) *temptator*, (N) *assimilis*, (O) *baroli*, (P) *tunneyi*, (Q) *kermadecensis*, (R) *haurakiensis*, (S) *elegans*, (T) *myrtae*, (U) *boydi*. Stars indicate sampling localities for widely dispersed taxa. From Austin et al. 2004

When described, *bannermani* was believed to be closely related to *newelli* and *auricularis* (Mathews and Iredale 1915). Post-description taxonomy remained unsettled before all were subsumed into *P. lherminieri* by Murphy (1927), which largely remained the status quo until

Jouanin and Mougin (1979), although keeping them within *lherminieri,* suggested that *bannermani* and *persicus* were potentially separate species. These splits were first adopted in Sibley and Monroe (1990), and taxonomy remained in flux through the 1990's. Austin et al. (2004) published a molecular phylogeny of the group using 917 bp of the mitochondrial gene cytochrome-b and found great discordance between the genetic and morphological based phylogenies (Figure 2); this led to the separation of many taxa previously included in *lherminieri*/*assimilis* as separate species (unfortunately *bannermani* was not included). Austin et al. (2004) found that *lherminieri* clade was restricted to the North Atlantic, whereas the *bailloni* complex and *persicus* group were sister to each other and part of a subtropical/tropical Indo-Pacific clade which included *myrtae, newelli,* and *opisthomelas* (Figure 2).

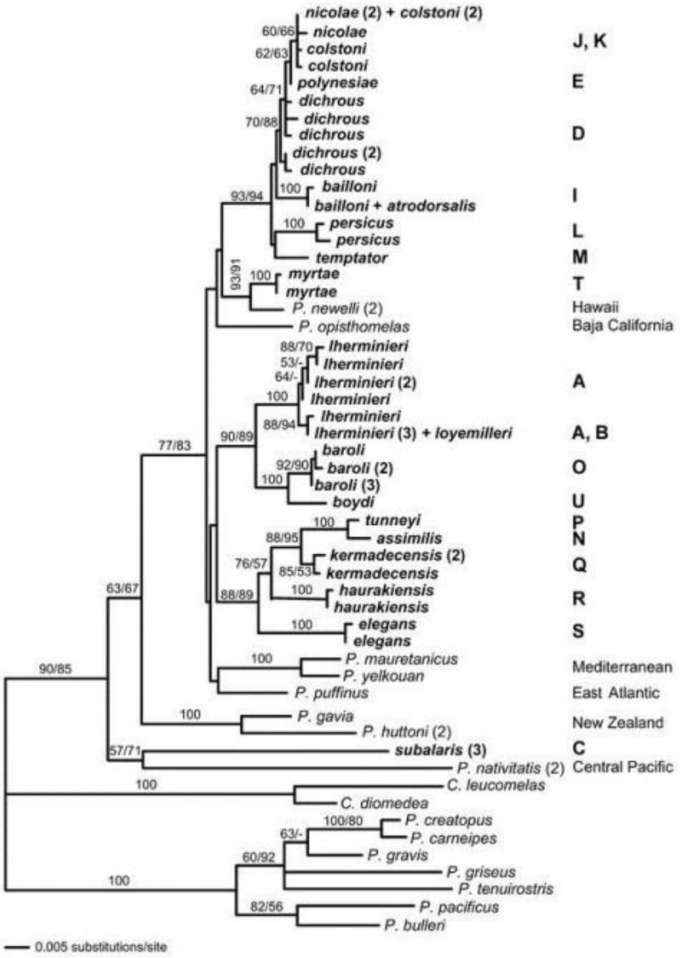

Fig. 2. Maximum-likelihood phylogenetic tree for *Puffinus* shearwaters based on 917 bp of mtDNA cytochrome-*b* gene sequence (-ln $L = 4248.65$). Numbers above and adjacent to branches are maximum-parsimony (MP) and neighbor-joining (NJ) bootstrap support values. Where only one value is given, MP and NJ support values were identical. Uppercase letters refer to breeding ranges shown in Figure 1. (From Austin *et al.* 2004)

Note that although the two groups were found to be sister, *nicolae/colstoni* breeds between the ranges of *persicus* and *temptator*. As *bannermani* was not included in earlier studies its position was subsequently debated, with some lumping it within the *bailloni* complex (Clements et al. 2016). Proposals have previously been voted on (in 2011 and 2013) for those taxa occurring in the NACC area (*subalaris* and *baroli*) and for extralimital *boydi* (2018), but a proposal has not been previously submitted for these extralimital taxa.

All taxa are morphologically similar, although some differences do exist (see Howell and Zufelt 2019); those in the *bailloni* complex show the most diversity in plumage. All are also similar in size, although some average differences exist (Table 1 from Pyle et al. 2011)

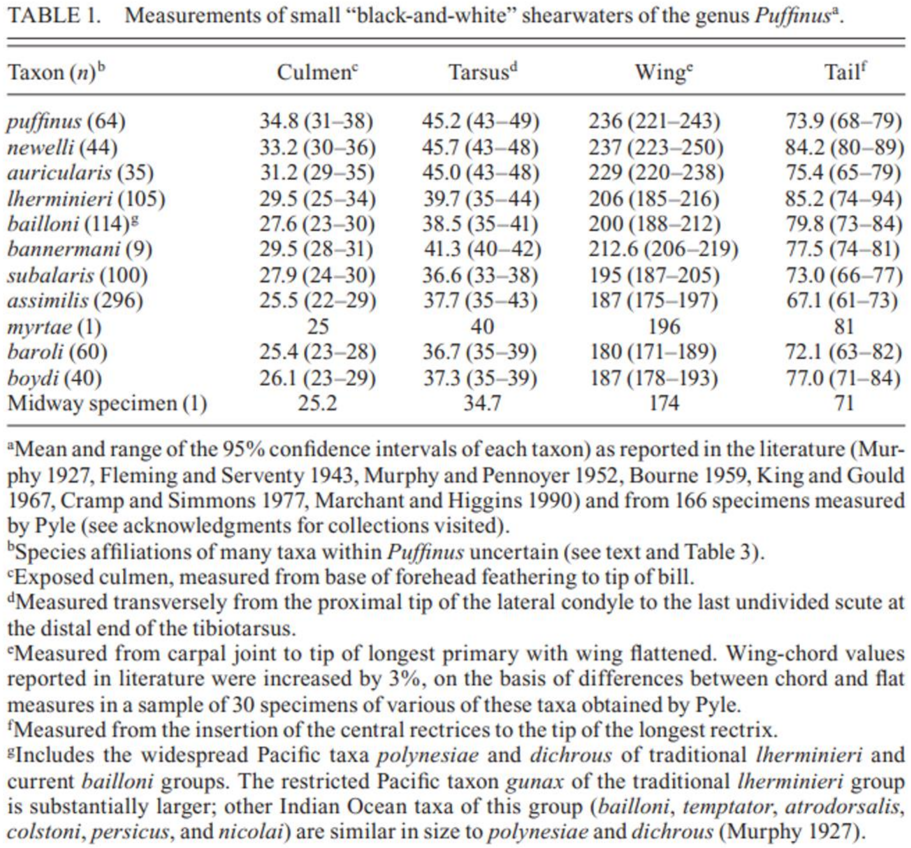

TABLE 1. Measurements of small "black-and-white" shearwaters of the genus *Puffinus*[a].

Taxon (*n*)[b]	Culmen[c]	Tarsus[d]	Wing[e]	Tail[f]
puffinus (64)	34.8 (31–38)	45.2 (43–49)	236 (221–243)	73.9 (68–79)
newelli (44)	33.2 (30–36)	45.7 (43–48)	237 (223–250)	84.2 (80–89)
auricularis (35)	31.2 (29–35)	45.0 (43–48)	229 (220–238)	75.4 (65–79)
lherminieri (105)	29.5 (25–34)	39.7 (35–44)	206 (185–216)	85.2 (74–94)
bailloni (114)[g]	27.6 (23–30)	38.5 (35–41)	200 (188–212)	79.8 (73–84)
bannermani (9)	29.5 (28–31)	41.3 (40–42)	212.6 (206–219)	77.5 (74–81)
subalaris (100)	27.9 (24–30)	36.6 (33–38)	195 (187–205)	73.0 (66–77)
assimilis (296)	25.5 (22–29)	37.7 (35–43)	187 (175–197)	67.1 (61–73)
myrtae (1)	25	40	196	81
baroli (60)	25.4 (23–28)	36.7 (35–39)	180 (171–189)	72.1 (63–82)
boydi (40)	26.1 (23–29)	37.3 (35–39)	187 (178–193)	77.0 (71–84)
Midway specimen (1)	25.2	34.7	174	71

[a] Mean and range of the 95% confidence intervals of each taxon) as reported in the literature (Murphy 1927, Fleming and Serventy 1943, Murphy and Pennoyer 1952, Bourne 1959, King and Gould 1967, Cramp and Simmons 1977, Marchant and Higgins 1990) and from 166 specimens measured by Pyle (see acknowledgments for collections visited).

[b] Species affiliations of many taxa within *Puffinus* uncertain (see text and Table 3).

[c] Exposed culmen, measured from base of forehead feathering to tip of bill.

[d] Measured transversely from the proximal tip of the lateral condyle to the last undivided scute at the distal end of the tibiotarsus.

[e] Measured from carpal joint to tip of longest primary with wing flattened. Wing-chord values reported in literature were increased by 3%, on the basis of differences between chord and flat measures in a sample of 30 specimens of various of these taxa obtained by Pyle.

[f] Measured from the insertion of the central rectrices to the tip of the longest rectrix.

[g] Includes the widespread Pacific taxa *polynesiae* and *dichrous* of traditional *lherminieri* and current *bailloni* groups. The restricted Pacific taxon *gunax* of the traditional *lherminieri* group is substantially larger; other Indian Ocean taxa of this group (*bailloni*, *temptator*, *atrodorsalis*, *colstoni*, *persicus*, and *nicolai*) are similar in size to *polynesiae* and *dichrous* (Murphy 1927).

From Pyle et al. 2011

No detailed studies have been published comparing vocalizations, although differences have been noted within taxa of *bailloni* complex and between *bailloni* and *P. p. temptator*; these, however, await a formal study to rule out sex and broader intra-taxonomic differences. No known or at least publicly available recordings of *bannermani* exist, whereas eBird and xeno-canto have only one recording of *persicus*, 2 of *lherminieri*, and 20+ recordings of *bailloni*, although these are spread across 3+ taxa.

New Information:

Further molecular studies using cyt-b (Pyle et al. 2011, Martínez-Gómez et al. 2015) have unsurprisingly found topologies similar to those of Austin et al. (2004), with a North Atlantic clade and an Indian/Pacific Ocean clade of small shearwaters. The *bailloni* complex and *persicus* group again were sister to each other, although these studies sampled more taxa and individuals. Kawakami et al. (2018) recovered the *bailloni* complex and *persicus* group as sisters, their relationship to other taxa was unresolved (Figure 3). A recent study that included

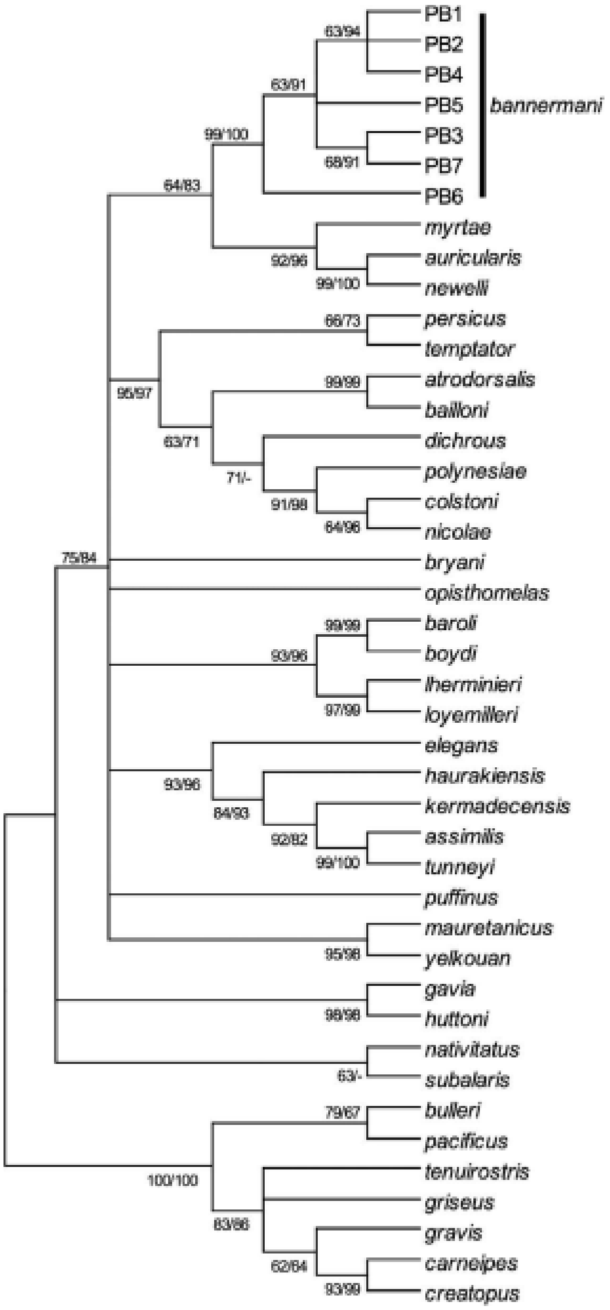

Fig. 2. The maximum likelihood (ML) consensus tree for 882 bp cytochrome *b* gene sequences from 43 *Puffinus* shearwaters. Branches correspond to partitions reproduced in <60% bootstrap replicates that are collapsed. Numbers above and adjacent to the branches are ML and maximum parsimony bootstrap support values. See Tables 1 and 2 for DDBJ/EMBL/GenBank Accession numbers.

Figure 3: From Kawakami et al. (2018)

three taxa of the *bailloni* complex but lacked *bannermani* and the *persicus* group, using a 75% complete matrix of UCE and PE-ddRAD loci, also recovered *bailloni* as part of the Indo-Pacific Clade (Ferrer Obiol et al. 2021).

In the only study to date that included *bannermani*, Kawakami et al. (2018) sequenced 917 bp of cyt-b and found that *bannermani* was sister to the *myrtae*/*newelli*/*auricularis* clade (Figure 3). They found 1.66% sequence divergence between *bannermani* and *myrtae*, which was greater than the divergence between other related species (e.g., 0.34% between *newelli* and *auricularis*, two species typically treated as valid (including by NACC).

(*Puffinus bailloni* has been proposed to consist of as many as five species (Howell and Zufelt 2019), but none of these occurs in the NACC area. As *P. bailloni* is extralimital and these splits are not currently recognized by global checklists, it would be premature for the NACC to split *bailloni*.)

Recommendation:

Based on differences on genetics, biogeography, and subtle morphological differences, I strongly recommend a **YES** to split these three extralimital species. This will also bring the NACC in line with world checklists and authorities on seabirds.

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Austin, J.J., V. Bretagnolle, and E. Pasquet. 2004. A global molecular phylogeny of the small *Puffinus* shearwaters and implications for systematics of the Little-Audubon's Shearwater complex. Auk 121:847–864.

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Kawakami, K., M. Eda, H. Izumi, K. Horikoshi, and H. Suzuki (2018). Phylogenetic position of endangered *Puffinus lherminieri bannermani*. Ornithological Science 17:11–18.

Martínez-Gómez, J. E., N. Matías-Ferrer, R. N. M. Sehgal, and P. Escalante (2015). Phylogenetic placement of the critically endangered Townsend's Shearwater (*Puffinus auricularis auricularis*): evidence for its conspecific status with Newell's Shearwater (*Puffinus a. newelli*) and a mismatch between genetic and phenotypic differentiation. Journal of Ornithology 156:1025–1034.

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Submitted By: David Vander Pluym, Louisiana State University

Date of Proposal: 21 August 2023

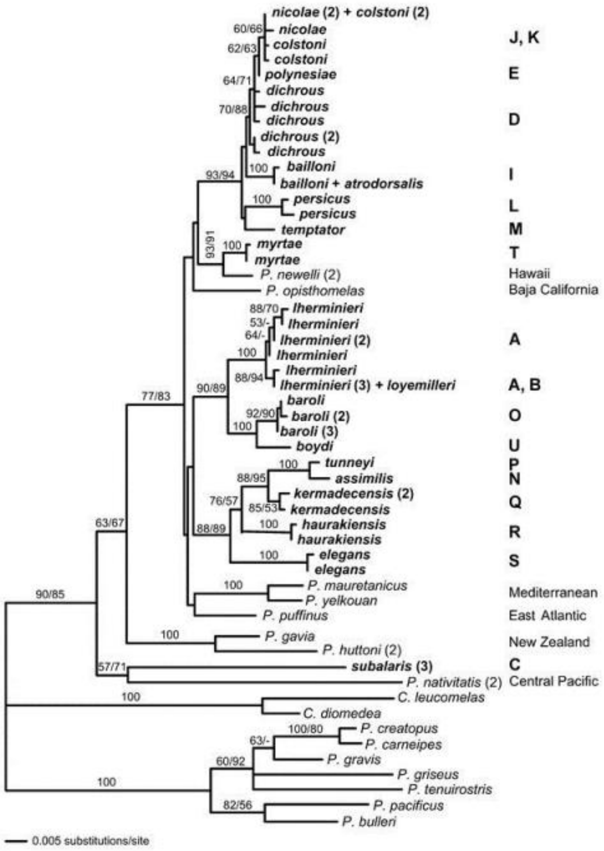
Treat extralimital *Puffinus boydi* as a separate species from Audubon's Shearwater *P. lherminieri*

Effect on NACC:

If accepted, this proposal would split an extralimital taxon to the NACC area (although fossil remains have been found on Bermuda; Olson 2010) and would result in changes to the distributional statement and notes for *P. lherminieri* (removing the Cape Verde Islands from the range). This would also bring the NACC checklist in line with the global treatment of these taxa.

Background: Species limits within the former *Puffinus lherminieri*/*assimilis* group have long been contentious, with *boydi* considered either to be with the *lherminieri* or the *assimilis* groups at different points. Austin et al. (2004) published a molecular phylogeny of the group (Figure 1), using 917 bp of

Figure 1



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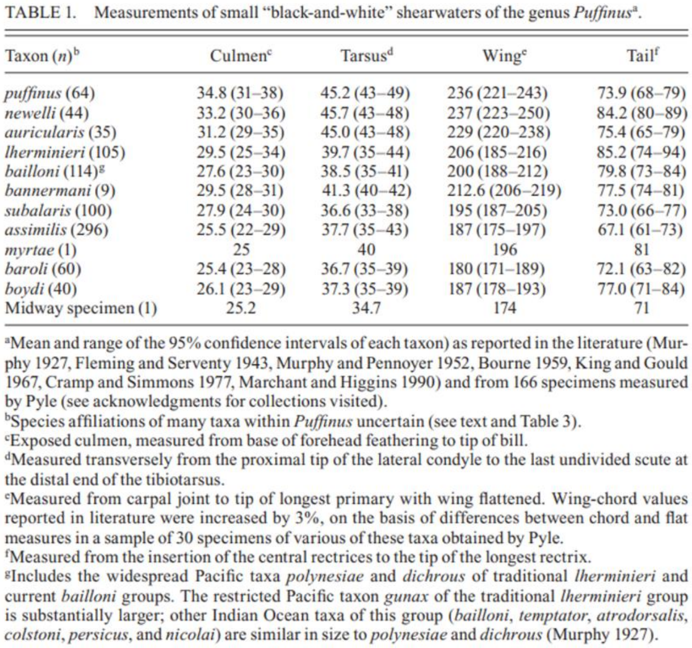
mtDNA cyt-b, that differed greatly from morphologically based ideas of relatedness, and which led to many taxa previously included in *lherminieri*/*assimilis* being split as separate species. Austin et al. (2004) found that *boydi* was part of a North Atlantic clade which included *lherminieri* (including *loyemilleri* sometimes subsumed into the taxon *lherminieri*), and *baroli*, and that *baroli* and *boydi* were sister taxa. In turn, this clade was sister to the subantarctic *assimilis* clade. All subsequent phylogenetic papers have found *lherminieri*/*baroli*/*boydi* to form a clade. A previous proposal to the NACC to split *boydi* from *lherminieri*, leaving these paraphyletic with respect to *baroli*. For more background information, including paleontological evidence that *boydi* occurred on Bermuda 400,000+ years ago, please see the proposal to split *baroli* (Proposal 2013-A-6, "Split Barolo Shearwater" https://americanornithology.org/wp-content/uploads/2020/02/2013-A.pdf), and previous submission to split *boydi* (Proposal 2018-C-5 "Split *Puffinus boydi*" https://americanornithology.org/wp-content/uploads/2020/02/2018-C-amended.pdf). These previous proposals also make the case for treating *baroli* as a separate monotypic species.

New Information:

The small black and white shearwaters are all morphologically conserved, although *lherminieri* and *boydi* are extremely similar with no known ways to identify the two in the field, except potentially by size (Howell 2012; Howell and Zufelt 2019). Foot color differs between the two with *boydi* having grayish-blue legs and feet, including webbing, whereas *lherminieri* shows pink legs and feet, although some may show blue on the legs and toes while retaining pink webbing; it is unclear if this is related to age (Howell 2012). At-sea identification of *boydi* from *baroli* is more difficult than previously thought and is best done by using a combination of undertail covert, under-primary, and face patterns (Flood and van der Vliet 2019). In size, *boydi* is intermediate between *lherminieri* and *baroli* in most measurements (Ramos et al. 2020). Although it may overlap with both species, it more extensively overlaps with *baroli* in morphometrics (Table 1 from Pyle et al. 2011) and in skeletal measurements (Figure 2 from Olson 2010). The blue feet and small size were why it has sometimes been placed in the *assimilis* group.



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From Pyle et al. 2011

Figure 2 from Olson (2010)

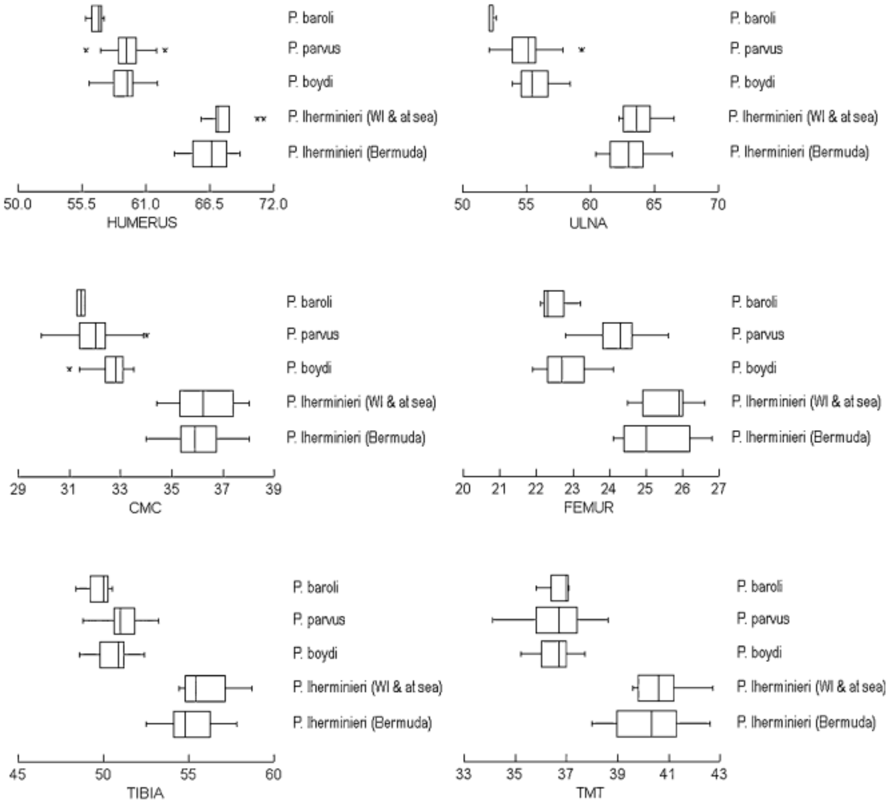

Figure 2. Bar and whisker diagrams of summary statistics of length measurements (mm) of six skeletal elements in five populations of small *Puffinus*. Birds from the West Indies (WI) and at sea were taken after the Bermuda population had been extirpated and hence did not originate in Bermuda. *Puffinus lherminieri* from Bermuda are identical in size with West Indian *lherminieri* and larger than all of the other populations. *Puffinus boydi* and *Puffinus parvus* are almost identical in size and are consistently smaller than *P. lherminieri*. The sample of *P. baroli* is insufficient but indicates a bird as small as *P. boydi* but with shorter wing elements. CMC, carpometacarpus; TMT, tarsometatarsus.

No detailed studies have been published comparing vocalizations. Mackin (2004) analyzed *lherminieri* individuals of known sex in burrows, and noted that birds in flight sounded similar. Robb et al. (2008) recorded provisionally sexed *boydi* in flight and thus, although having Mackin's recordings, was unable to compare the two, although they noted some differences in calls (shorter phrases and faster delivery in *boydi*). It should also be noted that whereas differences between *boydi* and *baroli* were found to be significant, Robb et al. (2008) wondered if individual birds could be safely assigned as there was some overlap in vocalizations. eBird and xeno-canto together have only two recordings of *lherminieri* and 13 of *boydi*; comparisons using publicly available data are thus not realistic.

Formerly thought to be largely sedentary around the Cabo Verde Islands where it is known to breed, *boydi* has now been found to have distinct breeding and non-breeding ranges and forages well away from its breeding islands in pelagic habitats. Tracking of 28 adults over 1-2 years found that during the breeding season, the majority foraged around or north of the Cabo Verde Islands towards the Canary Islands (one foraged to the south) and during the non-breeding season all but one migrated to an area over the mid-ocean ridge west and southwest of the Cabo Verde Islands off of northeastern South America (Zajková et al. 2017). Though *lherminieri*/*baroli*/*boydi* are largely non-overlapping spatially, *boydi* has some limited overlap with each of the others (Figure 3). The three taxa also share similar phenologies, ecological plasticity, and at-sea behavior (Ramos et al. 2020)

Away from breeding areas on the Cabo Verde Islands, *boydi* has been detected visiting other islands in the Atlantic Ocean, including visiting *baroli* colonies in the Canary Islands (Flood and van der Vliet 2019), St. Helena (Bourne and Loveridge 1978; but see Kirwan et al. 2020), and possibly Ascension Island (Robb et al. 2008). Conversely, *baroli* have been found visiting *boydi* colonies in the Cabo Verde Islands (Flood and van der Vliet 2019). In addition to Bermuda, *lherminieri* formerly occurred on and likely has recently visited Ascension Island (Bourne and Loveridge 1978, Bourne et al. 2003) and St. Helena (Olson 1975). Though breeding season differs between both populations and taxa among *lherminieri*/*baroli*/*boydi*, they all overlap to some extent (Ramos et al. 2020). The more widespread and seasonal movements of *boydi* with limited overlap with both *lherminieri* and *baroli* indicate that opportunities for movement between colonies exist.

Figure 3 from Ramos et al. (2020). *P. boydi* is in green.

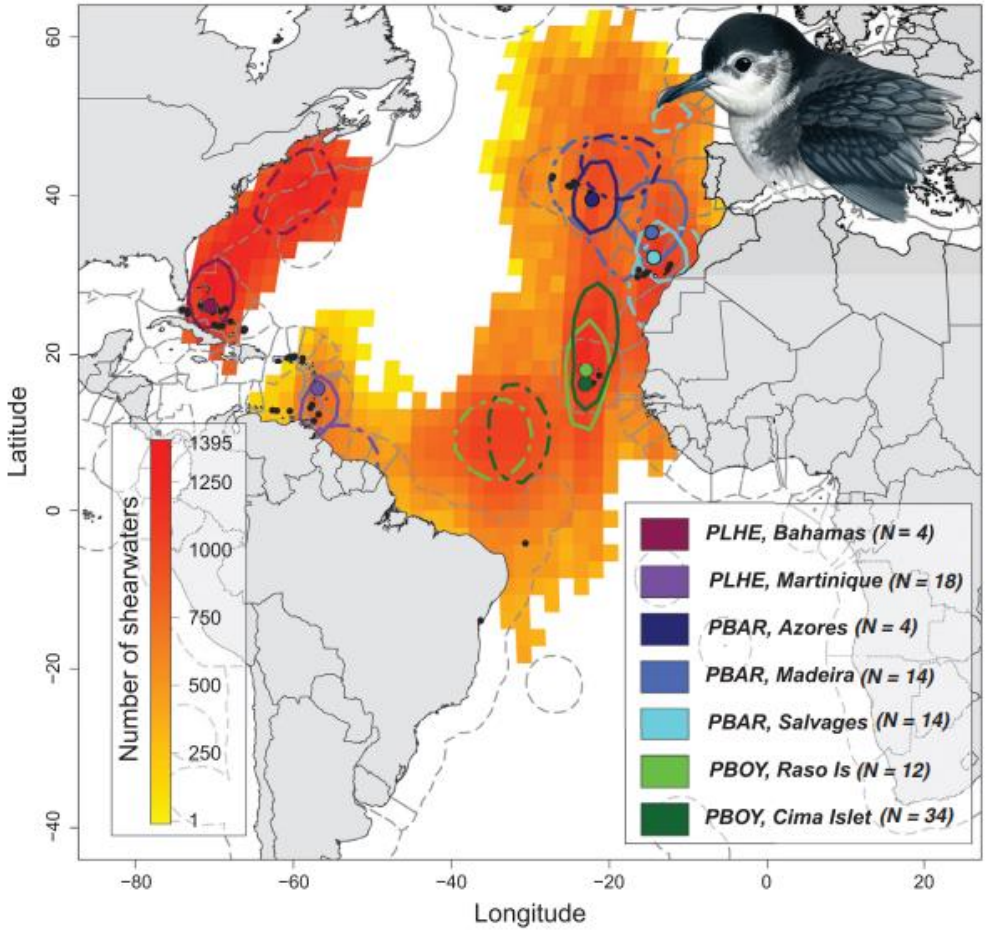

Figure 1. Distribution of seven colonies of little shearwaters that breed in the North Atlantic Ocean (*Puffinus assimilis–lherminieri* complex). Grid map shows the number of locations that fall in each 2 × 2° cell (units in birds/cell), corrected by the sampling effort on the population of origin (i.e. total number of positions from that colony site) and multiplied by the size of that population of origin (see Table 1). Additionally, specific kernel density distributions (50% UDs) are depicted in continuous lines for the breeding season and in dash-dotted lines for the non-breeding season for each of the sampled colonies (in purples for PLHE, in blues for PBAR, and in greens for PBOY). The number of tracks of each sampled colony is shown in brackets. Coloured circles show the location of the respective breeding colonies. Small, dark grey points show locations of colonies not sampled in this study. Exclusive Economic Zones (EEZs) are also shown in light grey dashed lines. The bird silhouette represents a PBAR, courtesy of Martí Franch.

Not surprisingly, results of further studies using mtDNA cyt-b have been similar to those of Austin et al. (2004), with a North Atlantic Clade (including *P. puffinus*) and *boydi* and *baroli* being closely related and sister to *lherminieri*. Although these studies had more taxa and sampled more individuals, they were unable to resolve the relationship of these three taxa with other *Puffinus* (Ramirez et al. 2010, Pyle et al. 2011, Kawakami et al. 2018).

Recent studies using a combination of mitochondrial and nuclear markers; a 75% complete matrix of UCE and PE-ddRAD loci (Ferrer Obiol et al. 2021), ddRAD (Ferrer Obiol et al. 2022, 2023), or six nuclear markers (Torres et al. 2021) all found a close sister relationship between *boydi* and *baroli* (Figures 4-7), with *lherminieri* being sister to these two taxa. Torres et al. (2021) investigated relationships of *boydi*, *baroli*, *lherminieri* and 3 taxa of the *bailloni* clade, and suggested that the Atlantic Ocean taxa diversified from the Indian Ocean rather than Pacific Ocean, with *boydi* being the ancestral population in the Atlantic, although studies including more taxa have found that *bailloni* is part of the Indo-Pacific clade and is not closely related to the North Atlantic clade (Austin et al. 2004, Ferrer Obiol et al. 2021, 2022). Ferrer Obiol et al. (2021 and 2022) found that all North Atlantic *Puffinus* formed a monophyletic clade with high support. Despite this, Torres et al. (2021) found patterns suggestive of hybridization, although they could not rule out incomplete lineage sorting, including one *baroli* showing both *baroli* and *nicolae* (*bailloni*) alleles at four nuclear markers. For divergence times, Torres et al. estimated that *lherminieri* and *boydi*/*baroli* separated around 1.38 My ago (0.78–2.04), and *baroli* and *boydi* approximately 0.85 My ago (0.44–1.32). Ferrer Obiol et al. (2023) found a similar divergence time with *lherminieri* (~1 mya), but a more recent (~120,000 years ago) split of *baroli* and *boydi*.

Figure 4: From Torres et al. (2021), *boydi* is in green, *baroli* in red.

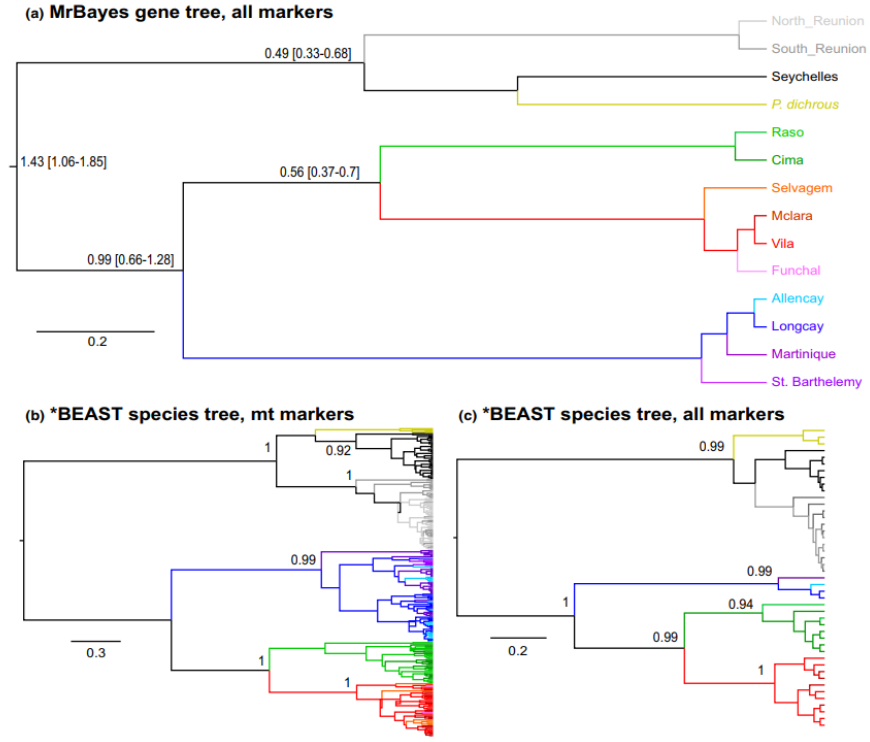

FIGURE 2 Gene trees and scenario of breeding site colonization. (a) Gene tree obtained by Bayesian inference for all markers, node bars correspond to the 95% confidence interval of the estimated divergence times. The scale corresponds to time before present in Million years (My). (b) Species tree obtained using *BEAST for all mitochondrial markers with dichrous haplotypes in yellow. (c) Species tree obtained using *BEAST for all mitochondrial and nuclear markers with dichrous sequences in yellow. In (b and c), only individuals sequenced for all mitochondrial markers and all markers respectively are shown. Only the posterior values >0.90 are shown

Figure 5: from Ferrer Obiol et al. (2022)

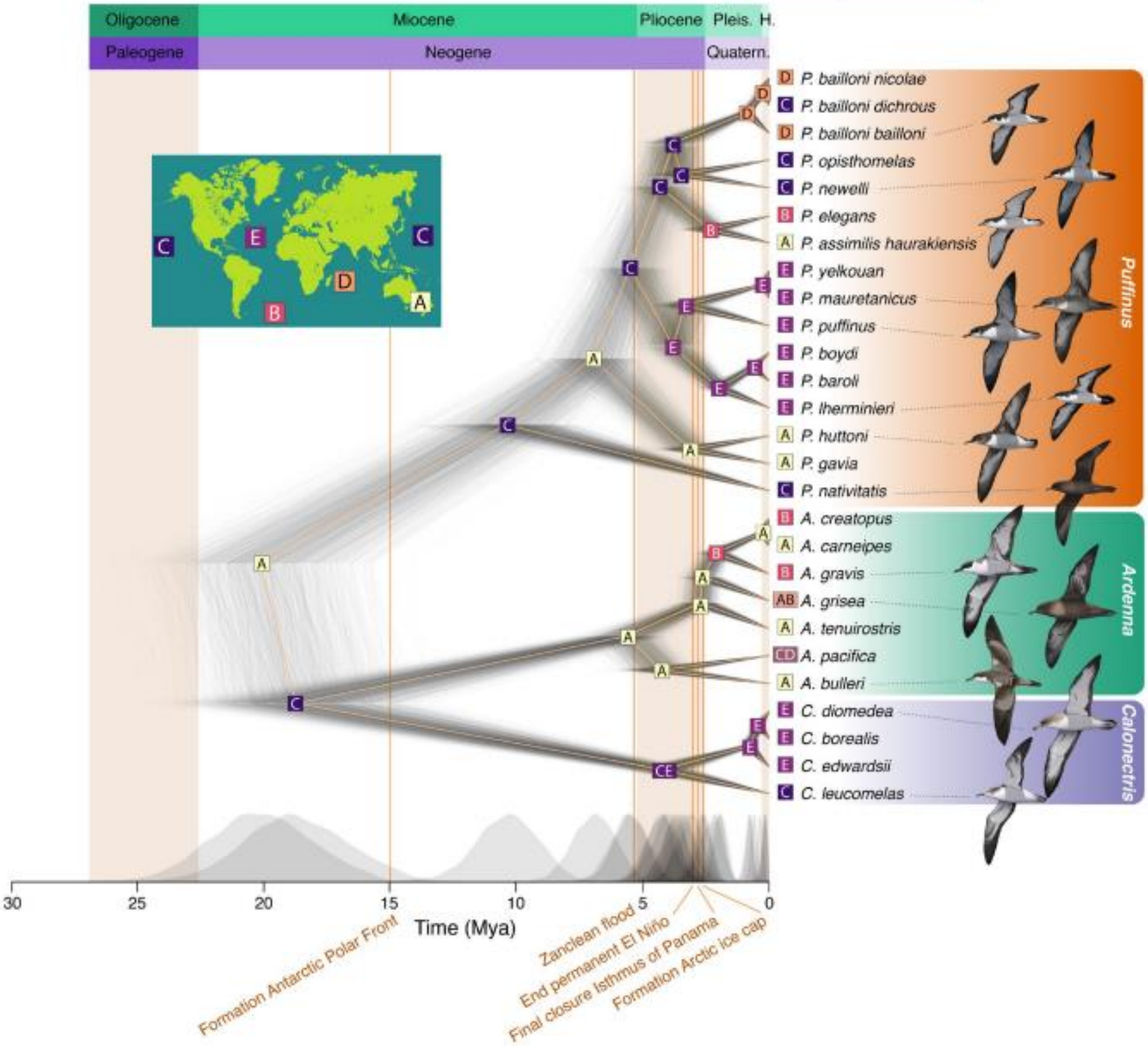

FIGURE 1 Time-calibrated species tree of the shearwaters using a constraint on the root age and a fixed topology. Geological periods and epochs are labelled above the tree. Posterior densities of divergence times are shown below the species tree. Note the diversification peak during the late Pliocene–early Pleistocene. Ancestral ranges were estimated under the DIVALIKE + *j* model using a dispersal matrix restricting dispersal between areas connected by main historical and present surface ocean currents in 'BioGeoBEARS' and are shown as boxes at nodes and tips coded according to the map (Inset; Southern Australia and New Zealand (A), Southern Ocean (B), North and Tropical Pacific Ocean (C), Tropical Indian Ocean (D), and North Atlantic Ocean and Mediterranean Sea (E)). Posterior estimates of divergence times are summarised in Table S2. Illustrations by Martí Franch are representative shearwater species depicted by their lineages

Figure 6: from Ferrer Obiol et al. (2021)

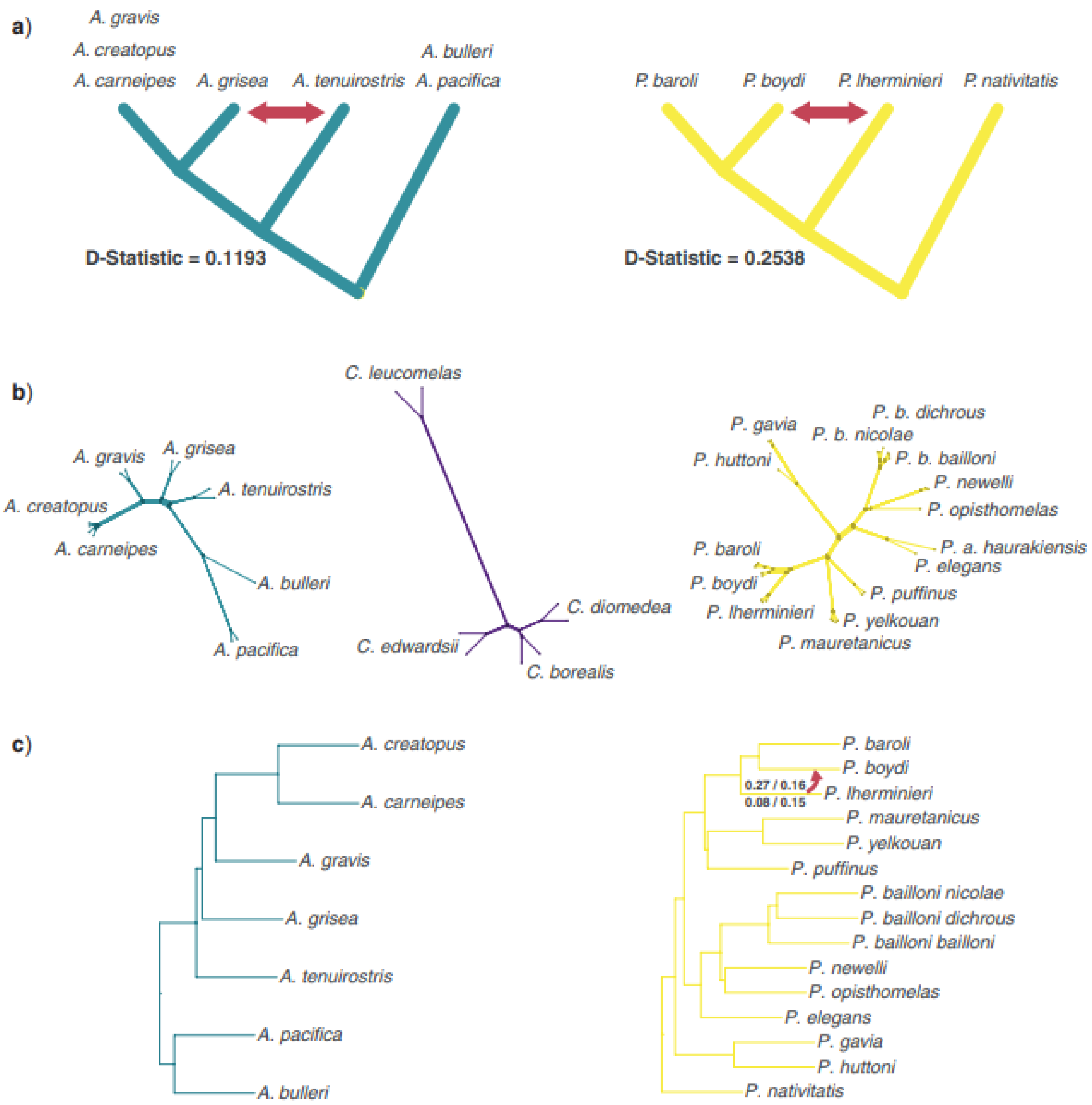

FIGURE 6. Introgression analyses in shearwaters. a) Gene-flow hypotheses obtained from D-statistic analyses (significant values) are shown with red arrows. Mean D-statistic values for the two cases are also shown. b) Neighbor-net networks for the three shearwater genera. c) Maximum pseudolikelihood SNaQ networks for *Ardenna* ($h = 0$) and *Puffinus* ($h = 1$). For the inferred hybridization event in *Puffinus*, optimized inheritance probabilities for the minor hybrid edge (γ) using PE-ddRAD/UCE gene trees (above) and PE-ddRAD SNPs/UCE SNPs (below) are shown.

Figure 7: From Ferrer Obiol et al. (2023)

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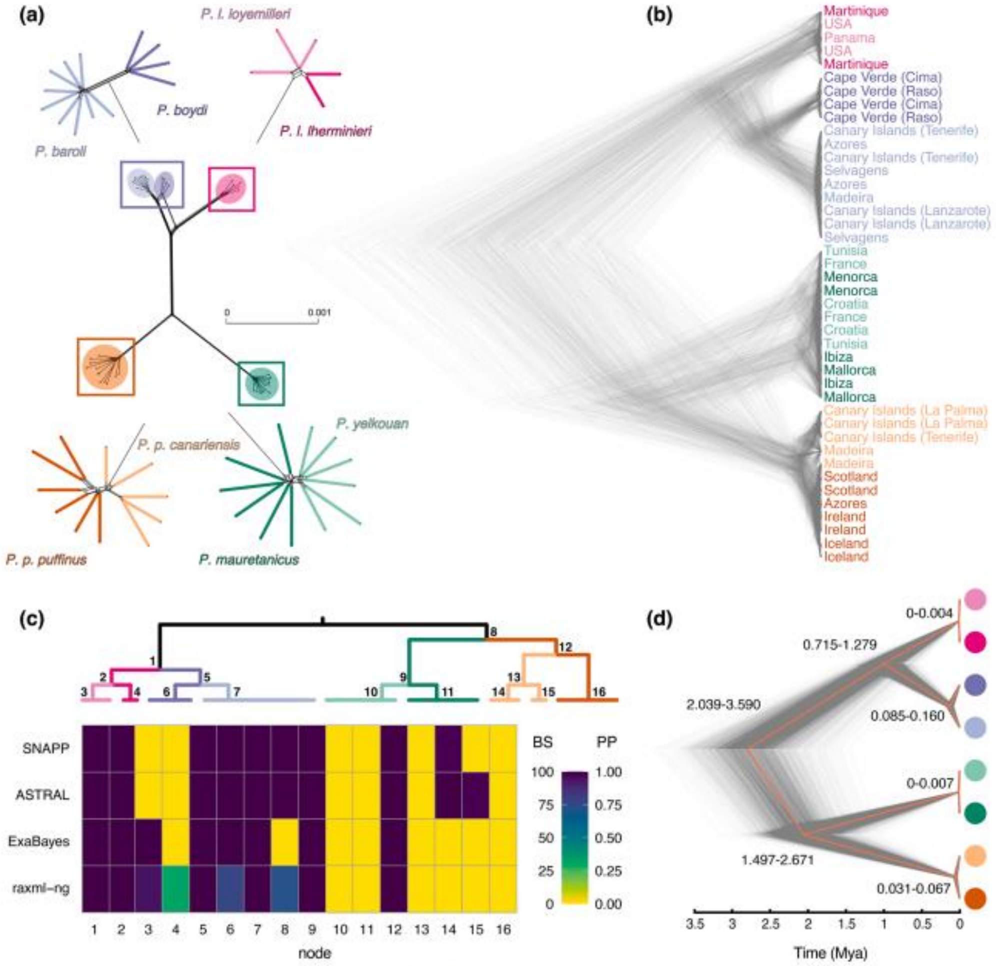

Fig. 4. Phylogenetic analyses of *Puffinus* shearwaters using 15,525 ddRAD loci. (a) Neighbour-net network. Squares represent regions of the network that are shown in more detail adjacently. Note that reticulation denotes non-tree-like areas. (b) Cloudogram of SNAPP trees from the posterior tree distribution showing topological and branch length variation. Tip labels represent sampling localities. (c) Heatmap summarising phylogenetic analyses using different methods. The nodes shown in the heatmap are those from the fineRADtructure dendrogram (shown above). Within *P. p. canariensis*, node 14 represents a monophyletic group containing all Canary Islands individuals and node 15 a monophyletic group containing all Madeiran individuals. Bootstrap support values or posterior probabilities are colour-coded as represented in the legend. (d) Time-calibrated SNAPP species tree (5403 transition sites). Individual trees shown in grey are samples from the posterior tree distribution and a maximum-clade-credibility summary tree is shown in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Although the phylogenetic analyses in Ferrer Obiol et al. (2021) showed full support for the sister relationship of *baroli* and *boydi*, 28% of gene trees supported a sister relationship of *boydi* and *lherminieri* and 18% supported a sister relationship of *baroli* and *lherminieri*. Their D-statistic tests found an excess of shared derived alleles between *boydi* and *lherminieri* (Figure 8). Despite the difficulties in determining ancestral hybridization from ancestral population structure and that incomplete lineage sorting could account for this, the candidate networks using PE-ddRAD data showed support for ancestral introgression, with *boydi* being the likely recipient of genetic material from *lherminieri*. They hypothesized this hybridization took place during the Pleistocene, a time when *boydi* occurred on Bermuda (Olson 2010) and the two may have had a higher degree of overlap. Ferrer Obiol et al. (2023) investigated population structure of the North Atlantic *Puffinus* shearwaters with their k=4 showing the most support (Figure 8).

Figure 7: From Ferrer Obiol et al. (2021)

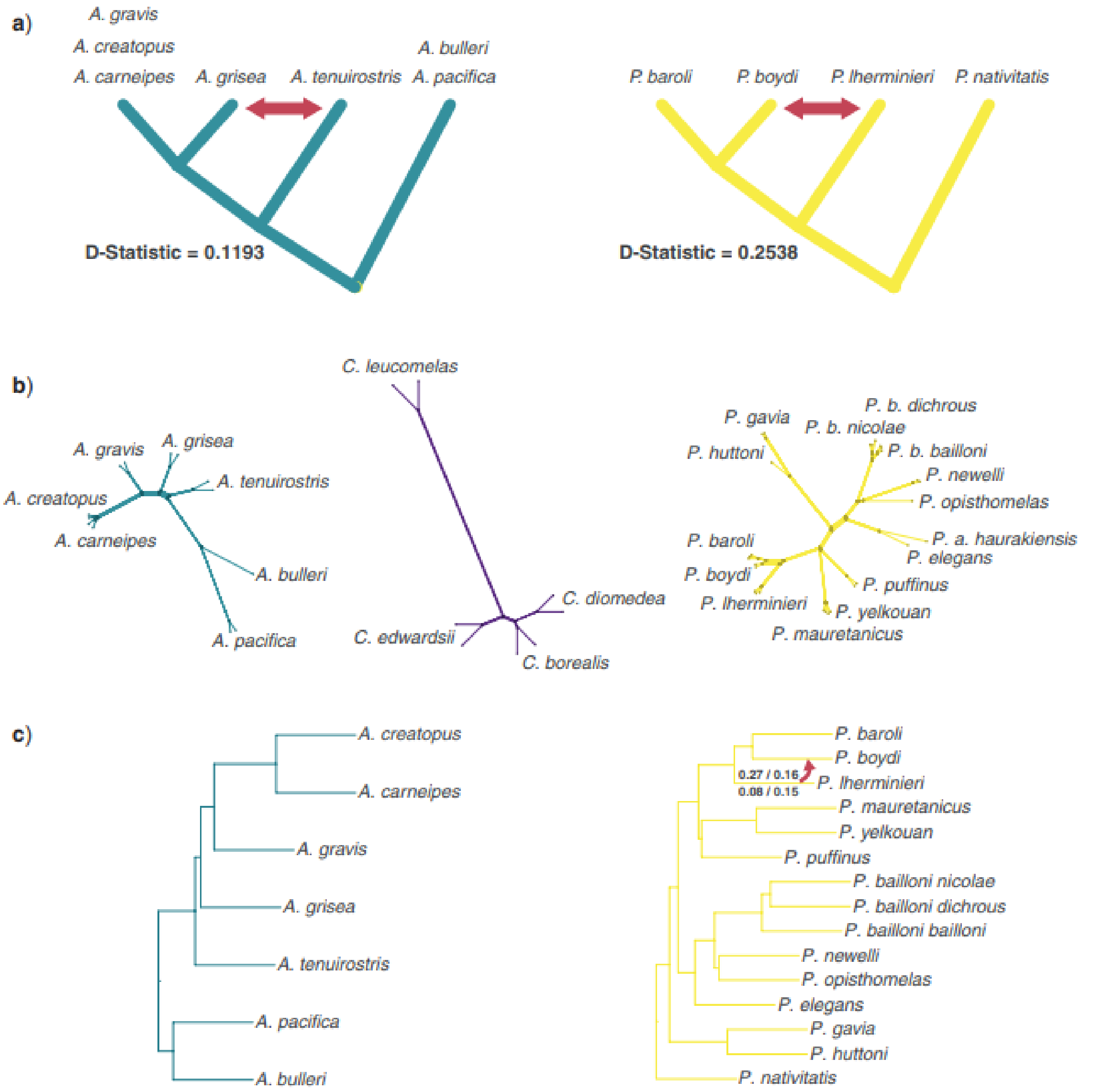

FIGURE 6. Introgression analyses in shearwaters. a) Gene-flow hypotheses obtained from D-statistic analyses (significant values) are shown with red arrows. Mean D-statistic values for the two cases are also shown. b) Neighbor-net networks for the three shearwater genera. c) Maximum pseudolikelihood SNaQ networks for *Ardenna* (h = 0) and *Puffinus* (h = 1). For the inferred hybridization event in *Puffinus*, optimized inheritance probabilities for the minor hybrid edge (γ) using PE-ddRAD/UCE gene trees (above) and PE-ddRAD SNPs/UCE SNPs (below) are shown.

Figure 8: from Ferrer Obiol et al. (2023) showing population structure of North Atlantic *Puffinus*

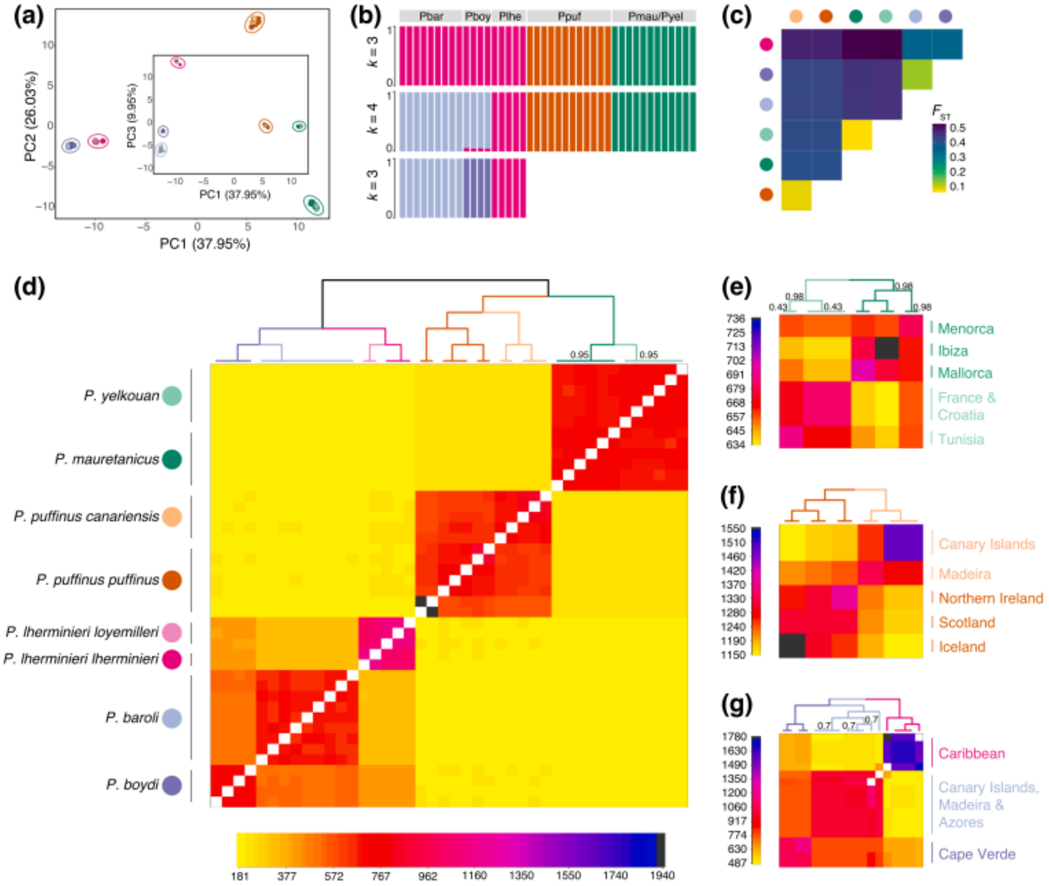

Fig. 2. Population structure of the eight recognised taxa of North Atlantic and Mediterranean *Puffinus* shearwaters. (a) Principal Components Analysis (PCA) showing PC1 (38 % variance) and PC2 (26 % variance). Inset shows PC1 versus PC3 (10 % of variance). (b) ADMIXTURE results for $K = 3$ and $K = 4$ which had the lowest cross-validation error and results for $K = 3$ for the small-sized taxa only. Facet labels above the plots represent: *P. baroli* (Pbar), *P. boydi* (Pboy), *P. lherminieri* (Plhe), *P. puffinus* (Ppuf), *P. mauretanicus* (Pmau) and *P. yelkouan* (Pyel). (c) Heatmap of pairwise F_{ST} estimates between *Puffinus* shearwater taxa. (d-g) Patterns of shared coancestry inferred from fineRADstructure. Each panel represents a heatmap showing coancestry coefficients between shearwater samples. Coancestry coefficients are colour coded from low (yellow) to high (blue-black) corresponding to the values in the legend. Atop each heatmap is a fineRADstructure clustering dendrogram based on the matrix of coancestry coefficients with branches coloured by taxon following the same colour code used next to the taxon labels on the left of the panel. Branch supports are shown for branches with posterior probabilities < 1. (d) Coancestry coefficients among all samples. (e) Average coancestry coefficients among all samples of *P. mauretanicus* and *P. yelkouan*, (f) *P. puffinus*, and (g) *P. lherminieri*, *P. boydi* and *P. baroli*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Despite the close relationship between *baroli* and *boydi* and the suggestion that the genetic differences are at a subspecies level (Ferrer Obiol et al. 2022), I have not included an option to move *boydi* to *baroli* due to subtle differences in vocalizations, morphology, lack of evidence of hybridization despite occurrences at each other's colonies, and unique haplotype groups (Ferrer Obiol et al. 2023).

Recommendation:

Based on differences in genetics and biogeography, and subtle morphological differences (size and foot color), I recommend a **YES** to split this extralimital species. This will also bring the NACC in agreement with world checklists and authorities on seabirds.

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Submitted By: David Vander Pluym, Louisiana State University

Date of Proposal: 3 September 2023

2023-A-6 N&MA Classification Committee pp. 17-18

Treat Cory's Shearwater as two species, *Calonectris diomedea* and *C. borealis*

Effect on NACC:

This proposal would add a new species (Scopoli's Shearwater) to the checklist and would result in changes to the distributional statement of Cory’s Shearwater. In addition, the scientific name *C. diomedea* would be transferred from Cory’s Shearwater to Scopoli’s Shearwater, and the species with the English name Cory’s Shearwater would henceforth be known as *C. borealis*.

Background:

Cory's Shearwater was formerly a polytypic species comprised of three well-recognized subspecies: *diomedea*, *borealis*, and *edwardsii, the latter* now generally treated as a separate species. Both *borealis, which breeds* mainly on eastern North Atlantic islands, and *diomedea,* which breeds mainly on islands in the Mediterranean Sea, occur regularly off our Atlantic coast north to the southern mid-Atlantic region, but nearly all records off New England and Atlantic Canada are of *borealis*. Both taxa occur and have been documented in the Gulf of Mexico. The few documented sightings from the northeast Pacific all involve *borealis.* The Cape Verde Shearwater (*C. edwardsii*) occurs in North America as an accidental with perhaps as few as a single solid record.

New Information:

The arguments below largely follow Sangster et al. (2012), who split these species on the BOU list. The split has now been recognized by most global references (e.g., Dickinson and Remsen 2013, del Hoyo and Collar 2014, and Gill and Donsker 2017).

This split is well-supported under traditional BSC arguments. Although the two taxa have largely separate breeding ranges, *borealis* breeds in at least two colonies in the Mediterranean Sea (Almeria; Gomez-Diaz et al. 2006; Chafarinas Islands, Navarro et al. 2009) and a few pairs of *diomedea* have bred along the Bay of Biscay coast in western France (Mays et al. 2006). The Chafarinas Islands hold 10,000 breeding pairs of Cory's Shearwaters, and based on morphometric data from 82 birds (*diomedea* is smaller) 78% are *diomedea* and 22% are *borealis* (Gomez-Diaz et al. 2009, Navarro et al. 2009). The two forms on the Chafarinas Islands differ in feeding ecology and foraging areas during both chick-rearing and winter periods (Navarro et al. 2009). Subspecies *borealis has been reported* elsewhere in the breeding colonies of nominate *diomedea,* but these records are thought to have involved non-breeding birds (Lo Valvo and Massa 1998, Thibault and Bretagnolle 1998, Martinez-Abrain et al. 2002). Despite intensive monitoring of Atlantic and Mediterranean breeding colonies, reports of interbreeding between *borealis* and *diomedea* are limited to one record of a mixed pair raising a young bird in the Collumbretes Islands in 2011 (Martinez-Abrain et al. 2002), two birds showing phenotypic characters of one taxon and a genotype of the other taxon (Gomez-Dias et al. 2009), and one record of a male *borealis* or hybrid breeding with a female with characters intermediate, or atypical, of *diomedea* on Gireglia Island in 1993, 1994, and 1995 (Thibault and Bretagnolle 1998).

Duet calls of *borealis* have three brief syllables whereas most (97%-98%) of *diomedea* have two longer syllables (Bretagnolle and Lequette 1990, Thibault and Bretagnolle 1998, see also Robb et al. 2008). Of about 400 male calls of *borealis* and *diomedea* examined, none was detected from one taxon showing call characters of the other (Thibault and Bretagnolle 1998). Playback studies have documented differential responses to recordings of *borealis* and *diomedea* (Bretagnolle and Lequette 1990). *Calonectris edwardsii* gives calls like nominate *diomedea* but higher pitched.

Studies of the mitochondrial DNA of *borealis* and *diomedea, as well as former conspecific edwardsi* (Gomez-Diaz et al. 2006, 2009), indicated that individuals of these three taxa each formed monophyletic groups, and that *diomedea and edwardsi* were more closely related to each other than either was to *borealis*, as might have been expected from the vocalizations.

More recently, Zidat et al. (2017) analyzed nuclear genotypic (microsatellites) and phenotypic (chemical profiles of uropygial secretions) characters of birds of both species from the Chafarinas Islands, where they are sympatric, and compared their results to data from birds from Selvagem (*borealis* only) and Linosa *(diomedea only).* They found (a) that there were consistent interspecific differences in both the genotypic and phenotypic characters, and (b) that these differences were maintained in sympatry. They concluded that *borealis* and *diomedea are reproductively isolated,* supporting their separation as distinct species. Moreover, the chemical differences observed between species may well serve as cues to mate choice and species recognition.

NACC considered this proposal in 2018 but rejected it 7-3 based on unpublished data suggesting high levels of morphologically intermediate specimens. Five-and-a-half years later, these data are still unpublished, and the one global list (Clements/eBird) that has not yet adopted the separation of *C. borealis* from *C. diomedea* will be adopting it soon (the split was previously adopted by Howard & Moore, IOC, and HBW-Birdlife). In our view, this committee should rely on the many published papers that indicate separate species status and follow the various global lists in their treatment of these species, which occur in our area only as non-breeders. The presence of apparently intermediate non-breeding birds may eventually suggest a different view of species status, but we strongly suggest that the NACC follow standard operating procedure and rely on the currently published data, rather than continuing to wait for publication of additional data that may or may not provide a different perspective on this issue.

Recommendation:

We recommend that *borealis* be split from *diomedea, which would result in* two monotypic species. Given the slightly overlapping ranges and almost no evidence of hybridization on islands where both occur (assortative mating), the evidence for the split is compelling and is buttressed by differences in vocalizations and other characters.

English names: Although AOS guidelines indicate that we should create English names for both daughter species that differ from that of the parental species (Cory’s Shearwater), unless there are compelling reasons not to, we suggest retaining the English names already in general usage for these Old World species. Cory's Shearwater would be retained for the eastern Atlantic breeding species, although the scientific name of Cory's would change to *borealis*, and the name Scopoli's Shearwater would be used for the Mediterranean Sea breeding nominate *diomedea.*

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Submitted by: Jon Dunn and Terry Chesser

Date of Proposal: 28 August 2023

Treat Jamaican Petrel *Pterodroma caribbaea* as a separate species from Black-capped Petrel *Pterodroma hasitata*

Background and Analysis:

***Taxonomy*:** The Jamaican Petrel *Pterodroma caribbaea* was described by Carte in 1886. In the first edition of the first volume of Peters' *Birds of the World* (1931) it was retained at species level. Murphy (1936) was the first to consider *caribbaea* a "dark morph" of the Black-capped Petrel (*P. hasitata*). He cited various old records (pre-1800) from breeding colonies in Guadeloupe that referred to abundant dark petrels, while others mentioned black-and-white petrels (see Murphy 1936, Collar et al. 1992). Murphy reasoned that populations of *hasitata* had both dark and pied forms, which had shifted in occurrence over time. The few extant specimens from Guadeloupe, however, are all black and white *hasitata* types. Murphy's one-species treatment was followed in the second edition of Peters' *Birds of the World* (Mayr and Cottrell 1979) and by others (e.g., Bond 1947, 1956; Collar et al. 1992). In the sixth and seventh edition of the AOU checklist (AOU 1983, 1998), *caribbaea* was considered a "dark form" of *hasitata* restricted to Jamaica. At present, the Howard and Moore (Dickinson and Remsen 2013) and Clements (Clements et al. 2022) lists consider *caribbaea* a subspecies of *hasitata*. The first volume of HBW (del Hoyo et al. 1992) treated *caribbaea* as a subspecies of *hasitata*. Confusion on whether to consider *caribbaea* a color morph of *hasitata*, a subspecies of *hasitata*, or a distinct species has muddied the taxonomy in recent decades.

Imber (1991) questioned regarding *caribbaea* as a color morph; he found that it was smaller than *hasitata* (Table 1) and posited that it was more closely related to *P. feae*. He added that since Jamacia had only dark forms it should be considered a separate species, whereas if it was a morph of *hasitata* both forms should be present there. He also found that, contra Murphy (1936), the underwing pattern of *hasitata* and *caribbaea* differed, whereas Murphy had claimed that co-occurring dark and light morphs of other petrel and shearwater species (*P. neglecta*, *Ardenna pacifica*) have the same underwing pattern. The feather lice of *P. caribbaea* also differ from those of *hasitata* (Zonfrillo 1993): two lice taxa (*Austromenopon* and *Trabeculus*) are found on *hasitata* and not *caribbaea*, and the lice species found on *caribbaea* is also found on *P. feae* but not *hasitata*. The revised HBW edition (Del Hoyo and Collar 2014) split *caribbaea* split from *hasitata*, and Raffaele et al. (1998), Howell (2012), and IOC (Gill et al 2023) also treated *caribbaea* as a separate species. Confounding the taxonomy, two color morphs (Figure 1) of *P. hasitata* are known from both breeding and non-breeding grounds. They differ in the amount of black in the face, morphometrics, and in timing of molt and breeding (Howell and Patteson 2008, Manly 2013). Howell (2012) speculated that these may be cryptic species.

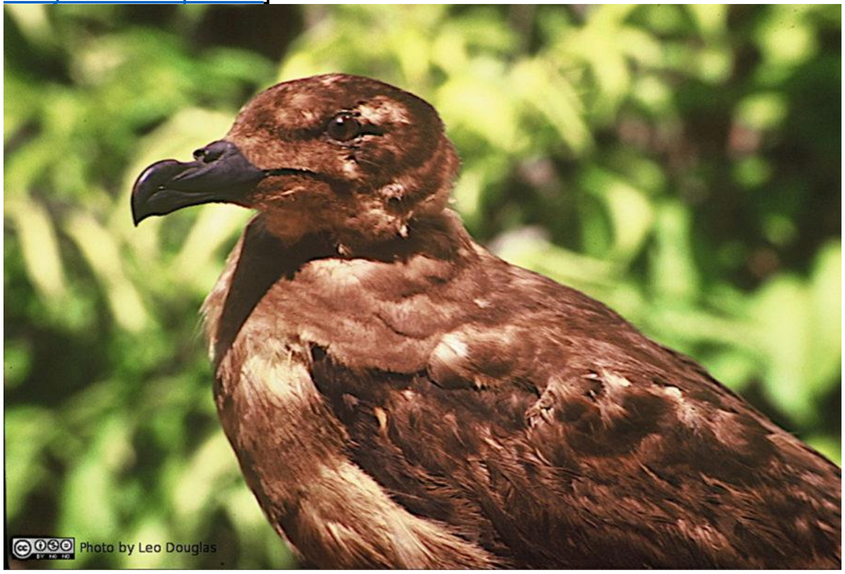
Table 1. Dimensions (mm) of Jamaican Petrels, Cape Verde Petrels *P. feae,* and Black-capped Petrels *P. hasitata* [from Imber 1991, Table 2]

	P. feae		*P. caribbaea*		*P. hasitata*	
	Range	Mean (N)	Range	Mean (N)	Range	Mean (N)
CULMEN	26-30	28.4 (30)	29.0-31.8	29.9 (10)	30.5-35.2	32.5 (9)
WING	258-274	268 (29)	267-285	278 (7)	280-295	290 (9)
TAIL	108-115	113.1 (17)	113.5-123.5	120.1 (10)	118-140	127.2 (9)
TARSUS	32-38	35.0 (20)	34.4-36.9	35.9 (10)	35.5-39.0	37.5 (10)
MID-TOE+CLAW	41-47	45.0 (23)	49.0-52.5	50.8 (10)	51.1-57.0	54.4 (9)

Pterodroma caribbaea (Figure 2) differs from *P. hasitata* in being smaller (Imber 1991), and in having overall sooty brown plumage, with a pale buffy gray band across the upper tail coverts (Howell 2012). Some birds are paler and grayer with a ghosting of a black cap (Howell and Patteson (2008).

Figure 1. Dark morph (top, UF53138) and light morph (bottom, UF49030) of *Pterodroma hasitata*.

Figure 2. Study skin of the Jamaican Petrel from the American Museum of Natural History. The species was last seen and collected in 1879; however, nocturnal petrels are notoriously difficult to find, so it could still survive in remote areas of the Blue and John Crow Mountains of Jamaica. (Photo by Leo Douglas) [from https://www.birdscaribbean.org/2020/09/looking-for-and-finding-the-jamaican-petrel/]



Status**:** The Jamaican Petrel is generally considered to be extinct. It formerly bred above 1600 m in burrows in the Blue Mountains (type locality) and John Crow Mountains of Jamacia. It is thought to have declined rapidly after introduced mammalian predators (mongooses, dogs, cats) were brought to Jamaica. It has not been recorded with certainty since 1890. Its at-sea distribution is unknown, and all 26 existing specimens were taken from breeding grounds in Jamaica from 1869-1879 (Imber 1991). Reports of dark petrels on Guadeloupe before 1800 (see above) may refer to *caribbaea*, but without any material for comparison, it could just as easily have been a different taxon. Some (Collar et al 1992, Douglas 2000) offer hope that *caribbaea* may still be extant, and that the lack of records since the 1890s result from rarity, nocturnal habitats during breeding season, and difficult to access breeding grounds, as has been found in other *Pterodroma* species.

Recommendation:

Aside from anecdotal historical accounts, there is no concrete evidence that breeding petrels on Guadeloupe may have had co-occurring dark and light morphs or that *P. hasitata* has a dark morph. The occurrence of dark and light morphs in other species of *Pterodroma* (e.g., *P. neglecta, P. arminjoniana*) is completely different than the situation with *hasitata* and *caribbaea*: the dark and light morphs are found in the same breeding colonies, not on separate islands, and have similar morphometrics. The scale of plumage differences between *hasitata* and *caribbaea* is much greater than that between many closely related species within the large genus *Pterodroma*. In addition, the morphometrics and feather lice argue for a long period of geographic and temporal isolation, and that *hasitata* and *caribbaea* should be considered separate species. Given that the two morphs of *hasitata* on Hispaniola may be reproductively isolated (Manly 2013), reproductive isolation between *hasitata* and *caribbaea*, which are much more different in plumage than the two *hasitata* color morphs, seems very likely.

English names:

I recommend that *Pterodroma hasitata* and *caribbaea* maintain their widely used English names Black-capped Petrel, and Jamaican Petrel, respectively. All recent literature that considers these separate species uses these two names. In the much older literature, the name Blue Mountain Duck was used for *caribbaea*, but that name is no longer accurate or descriptive.

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Submitted by: Andrew W. Kratter**,** Florida Museum of Natural History

Date of Proposal: 1 September 2023

Treat *Coccyzus bahamensis* as a separate species from Great Lizard-Cuckoo *C. merlini*

Introduction:

The Great Lizard-Cuckoo is distributed on the Cuban archipelago and on the three larger islands in the northern half of the Bahamas: Andros, New Providence, Eleuthera (as well as the smaller Harbour Island). This species is a very large cuckoo that occupies various types of forest and scrub, and is characterized by red facial skin around the eye, a long bill, white or gray breast, rufous belly, olive-brown plumage above, and a long tail. The diet includes lizards, frogs, snakes, young birds, and insects (Kirwan et al. 2021).

Although currently placed in the genus *Coccyzus*, *C. bahamensis* was previously (as in AOU 1983, 1998) placed in *Saurothera*, one of two genera of West Indian cuckoos merged into *Coccyzus* (the other was *Hyetornis*) based on phylogenetic data (Sorenson and Payne 2005). Ridgway (1916) and Cory (1919) included five species in *Saurothera*, using English names that refer to the islands on which the species or subspecies occur:

1. *S. bahamensis* (two subspecies: *bahamensis* Bahaman Lizard-Cuckoo and *andria* Andros Island Cuckoo)
2. *S. merlini* (two subspecies: *merlini* Cuban Lizard-Cuckoo and *decolor* Isle of Pines Cuckoo)
3. *S. vieilloti* (monotypic) - Porto Rican Lizard-Cuckoo
4. *S. vetula* (monotypic) - Jamaican Lizard-Cuckoo
5. *S. dominicencis* (monotypic) - Haitian Lizard-Cuckoo

Peters (1940) merged *S. bahamensis* and *S. merlini* into a single species (and also merged *S. vieilloti* and *S. dominicensis* into *S. vetula*), recognizing four subspecies in *S. merlini*:

S. m. merlini - Cuba
S. m. decolor - Isle of Pines
S. m. bahamensis - Bahama Islands: New Providence, Eleuthera
S. m. andria - Bahama Islands: Andros

Although the lump of *vieilloti*, *dominicensis*, and *vetula* has not been widely followed (if at all), almost all sources over the past century, some published prior to Peters (e.g., Bond 1936), have treated *merlini* and *bahamensis* as subspecies of a single species, thus treating the former *Saurothera* as a four-species group. These include Bond's subsequent field guides and annotated checklists of West Indian birds, Wolters (1975), AOU (1983, 1998), Sibley and Monroe (1990), Raffaele et al. (1998, 2003), Sorenson and Payne (2005), Erritzøe et al. (2012), Howard and Moore, IOC, and eBird/Clements. *Coccyzus merlini* is now typically considered to consist of four subspecies (*C. m. merlini*, *C. m. bahamensis*, *C. m. decolor*, and *C. m. santamariae*, the latter a subspecies from the islands of north-central Cuba described in 1971); subspecies *andria* is generally not recognized.

Kirwan et al. (2021) described the four subspecies as follows:

C. m. merlini – "Sexes alike. An olive-brown crown, nape, and upperparts, with rufous primaries, a long, graduated gray tail with a black subterminal band and broad white tips, except the central rectrices, which are all gray (the tail appears barred on its underside). Below, throat whitish, breast and cheeks pale gray, and the belly and undertail coverts are rufous."

C. m decolor – "considered to be more grayish brown above, with a bill shorter than that of the nominate, and the central rectrices are gray and unmarked."

C. m. santamariae – "considered to have paler upperparts and a longer bill, but overall smaller-bodied compared to the nominate.", In the estimation of Kirkconnell et al. (2020), it is only weakly separated from *decolor*, with its principal distinguishing characters showing some approach to Bahaman *C. m. bahamensis*.

C. m. bahamensis – "Compared to the three Cuban subspecies, *C. m. bahamensis* is smaller (shorter-winged), grayer above, has the belly washed buff, and central rectrices with a subterminal black band."

Below are photos showing, from left to right, male and female specimens of *merlini*, *decolor*, and *bahamensis* from the USNM collection (which lacks *santamariae*). As noted by Kirkconnell et al. (2020), subspecies *decolor*, being smaller and paler than nominate *merlini*, approaches *bahamensis* in these characters.

Kirwan et al. (2021) provided comparative measurements of overall length, which show the similarity of *decolor* to *bahamensis* rather than to *merlini*:

“Overall length ca. 48-54 cm (nominate, Cuba); ca. 42-49 cm (*decolor*, Isle of Pines; 41-50 cm (*bahamensis*, northern Bahamas).”

Ridgway’s (1916) measurements also show *decolor* as either as intermediate or as more similar to *bahamensis*:

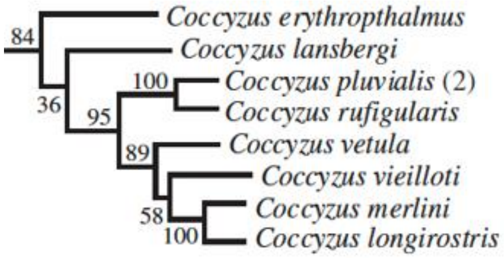
	wing length	tail length	culmen length
bahamensis male	149-167 (155)	246-265 (257)	48-53 (51)
bahamensis female	154-164 (159)	250-280 (268)	50-57 (55)
decolor male	160-172 (167)	247-278 (265)	47-53 (51)
decolor female	155-178 (168)	234-270 (264)	47-52 (50)
merlini male	165-185 (174)	272-327 (303)	50-55 (52)
merlini female	170-187 (177)	295-331 (307)	51-60 (54)

The reason the status of *bahamensis* has arisen is because Birdlife treats *bahamensis* as a separate species, based on the following rationale: "Hitherto treated as [a] subspecies of *C. merlini*, but differs in absence of rufous wing panel, since outer vanes of primaries are concolorous with wing and all upperparts, although inner vanes are rufous and show up in flight (3); black tip of upper tail (2); and (by comparison with *decolor* from I of Pines, which most closely resembles *bahamensis* in lacking rufous tone to upperparts) purer grey on breast and paler rufous on lower underparts (2)."

New Information:

There's very little new information, but here we review the available data on genetics, voice, and the tip of the tail.

Genetics: Sorenson and Payne (2005) sampled the four recognized species of *Saurothera* and the two species of *Hyetornis* (*pluvialis* and *rufigularis*) for their phylogeny of the Cuculidae. These two endemic West Indian genera were sister groups and, as noted above, were embedded within *Coccyzus*, prompting the transfer of all species of *Saurothera* and *Hyetornis* to *Coccyzus*. The single individual of *C. merlini* was sister to their sample of *C. longirostris* (Hispaniolan Lizard-Cuckoo), making the *C. vetula* of Peters (1940) paraphyletic. No genetic studies appear to have sampled within *C. merlini*, so there are no data on intraspecific variation.



Vocalizations: These cuckoos give a variety of calls, including long calls, groans, chuckles, and screeches. Kirwan et al. (2021) described the long call of as follows:

> The principal vocalization is a throaty *ka-ka-ka-ka-ka-ka-kau-kau-ko-ko* lasting a total of ca. 9 seconds at a rate of ca. 12 notes/second, with the second part gradually increasing in volume and increasing slightly in the speed of delivery before finally slowing again in terminus, which is overall louder, longer, and faster than the main call of the partially sympatric Mangrove Cuckoo (*Coccyzus minor*); peak amplitude is reached at ca. 2.0 kHz, with most energy concentrated below this, which is lower-pitched than other lizard-cuckoos (former genus *Saurothera*).

Here are examples including long calls from *C. m. merlini*: https://xeno-canto.org/66837
and from *C. m. bahamensis*: https://macaulaylibrary.org/asset/8300

Kirwan et al. (2021) also stated that no detailed comparisons have been made between the Cuban subspecies and *bahamensis*, and noted that "Bahamian populations are generally believed to sound similar to those on Cuba, giving a fairly loud, methodically paced *ack, ack, ack* in apparent agitation, and croaking single or double-noted *ka* or *tacoo* calls, delivered at a fairly even pace." Recordings on xeno-canto and Macaulay Library sound very similar to our ears, and JLD, who has field experience with this species on Cuba, Andros, and New Providence, has never considered separate species to be involved.

Tips of rectrices: Although the differing language is a bit confusing, we think that both Birdlife and Kirwan et al. (2021) refer to a black tip on the central rectrices of *bahamensis* versus the plain gray central rectrices of *merlini*. However, quite a few USNM specimens of *merlini* have black coloration at the tip of their central rectrices, so this does not appear to be a diagnostic character. Below is a photo comparing the upper side of the tails of three USNM specimens of *merlini* (on the left) and three of *bahamensis* (on the right) – note that the central rectrices of the *merlini* have been pulled a bit to the side so that the black coloration is more visible:

And here's a comparison showing the similarity of black tips on the underside of the tail of two of these specimens, *bahamensis* on the top (with the splayed tail) and *merlini* on the bottom (with the longer central rectrices sticking out from beneath the other rectrices):

Recommendation:

We recommend a NO vote on treating *bahamensis* as a separate species from Great Lizard-Cuckoo *C. merlini*. The Birdlife split is based principally on two characters, the extent of rufous in the wing and the black tip to the tail. On their own, these don't convince us that this is a species-level split, especially considering that rufous coloration is present, just not as extensive, in the wing of *bahamensis*, making this a difference of degree, and that the tails of at least some *merlini* also show black tips. The additional characters used to distinguish *bahamensis* from the Cuban subspecies *decolor*, such as paler rufous on the underparts, appear to indicate the intermediacy of *decolor* between *merlini* and *bahamensis*, and may show overlap between *decolor* and *bahamensis*, as is present in the morphometrics. As for other data, we currently lack any analysis of vocalizations, which seem very similar, or of intraspecific genetic variation. A dedicated study of *bahamensis* relative to *C. merlini* would be ideal, including song and genetic data in addition to more formal analyses of morphology and color.

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Submitted by: Blanca Hernández, Terry Chesser, and Jon L. Dunn

Date of proposal: 4 September 2023

2024-A-9 N&MA Classification Committee pp. 249-250

Treat *Piaya mexicana* and *P.* “*circe*” as separate species from Squirrel Cuckoo *P. cayana*

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. Similar proposals to split *Piaya cayana* are being considered concurrently by both SACC and WGAC.

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 a 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 Isthmus 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.

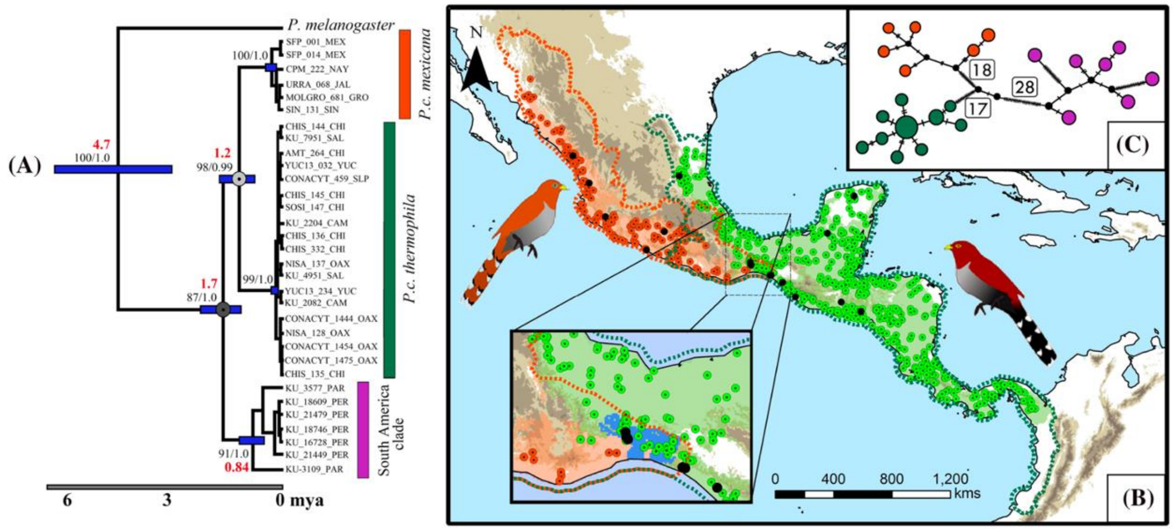
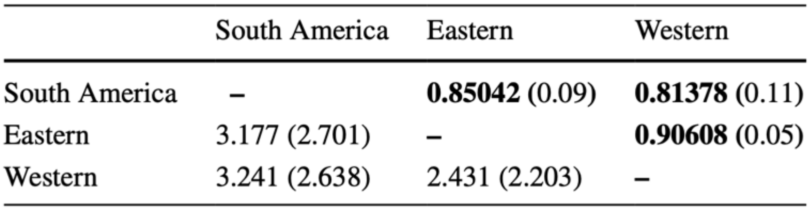


Fig. 1 Geographic distribution and phylogenetics of the Squirrel cuckoo *Piaya cayana* (**A**) mDNA Bayesian phylogenetic tree based on a ND2 (1041 bp) and a fragment of Cytb (622 bp) concatenated dataset. Numbers above branches indicate divergence time (in red), and bootstrap/posterior probability values (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 distribution (*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

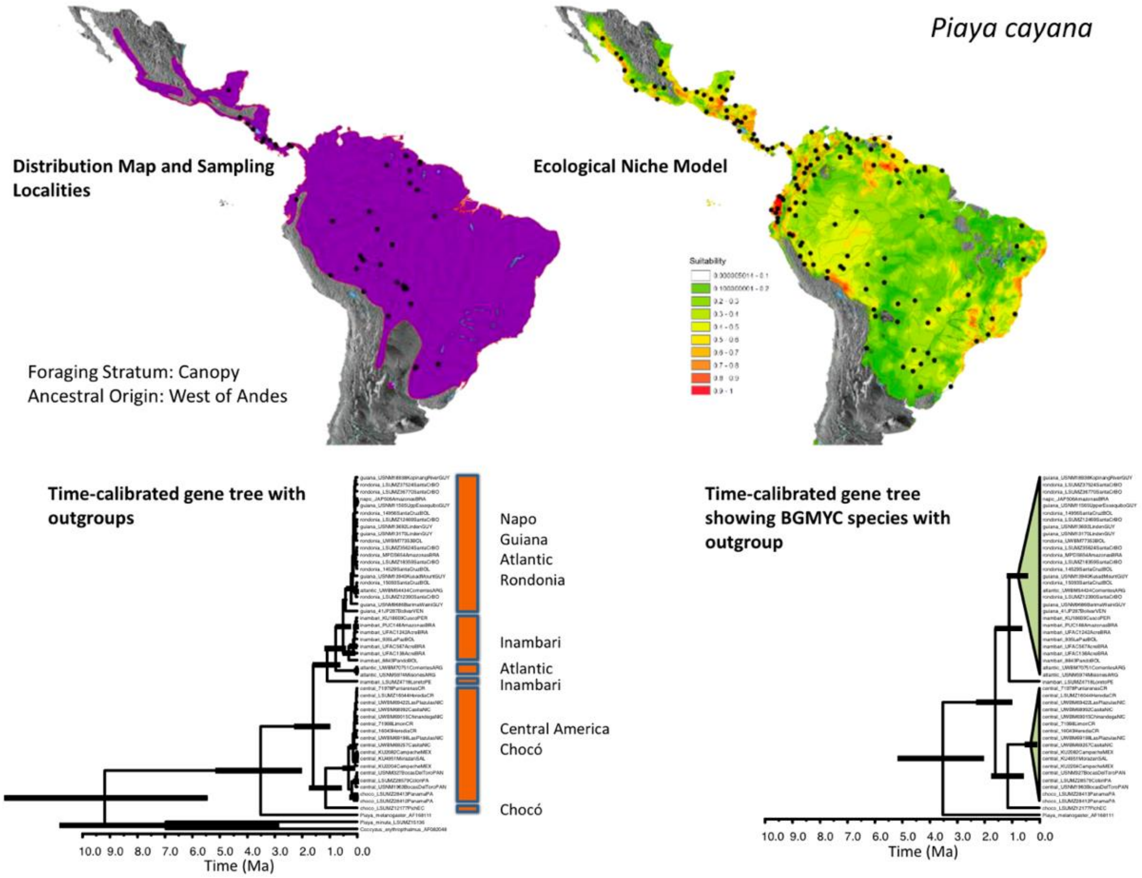
Table 1 Genetic differentiation for *P. cayana*.



	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.



Supplementary Figure 14 | Range map, ENM, time-calibrated gene trees and delimited species for *Piaya cayana*. Range map (natureserv.org) showing approximate geographic distribution of each lineage with sampling localities as black circles (upper left). Ecological niche model (ENM) indicating areas with suitable climatic conditions from 0 (clear) to 1.0 (red); locality records used to construct the ENM appear as black circles (upper right). Time-calibrated gene tree showing geographic clades (bottom left). Time-calibrated gene tree with 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.

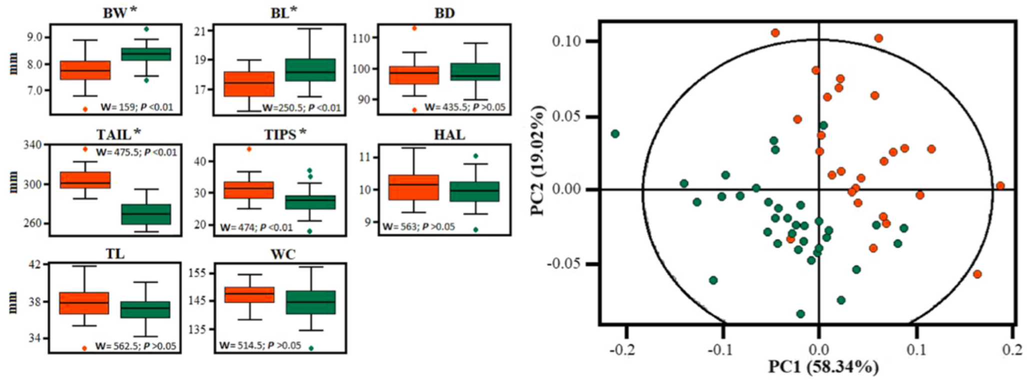


Fig. 2 Morphometrics for the two Mesoamerican lineages. Orange color depicts mean and samples for the Western lineage (*P. mexicana*); green color indicates mean and samples for the Eastern lineage (*P. c. thermophila*). Mann–Whitney *U* test boxplots for comparison of the means for the different characters.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

Squirrel Cuckoo (West Mexico)

Piaya cayana mexicana

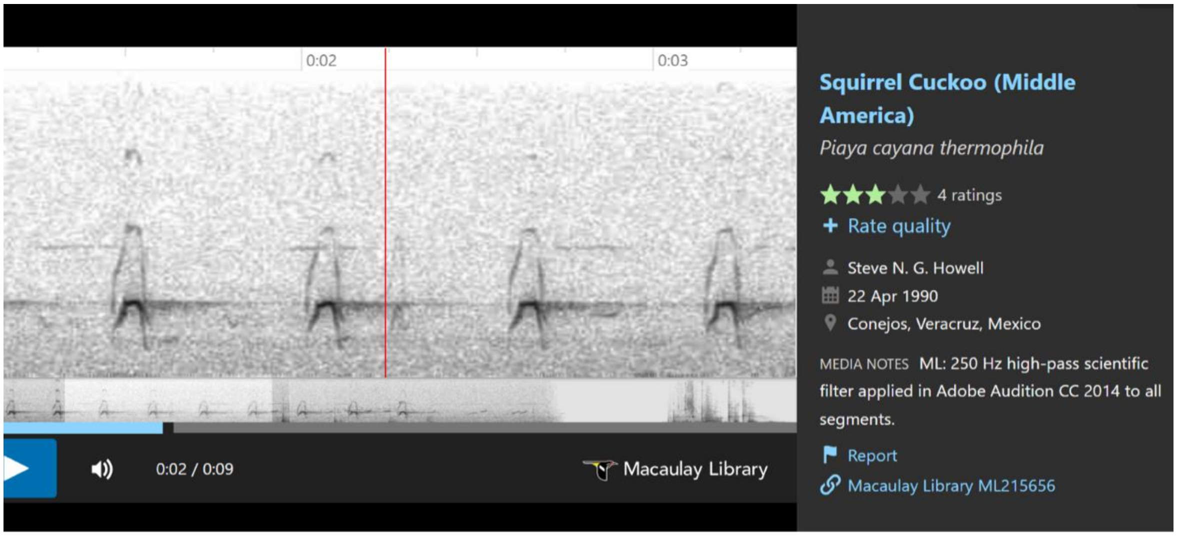
Geoffrey A. Keller

29 Apr 2000

Mazatlan, Panuco Road, Sinaloa, Mexico

SOUNDS Song

Macaulay Library ML524301



Squirrel Cuckoo (Middle America)
Piaya cayana thermophila
4 ratings
Steve N. G. Howell
22 Apr 1990
Conejos, Veracruz, Mexico
MEDIA NOTES ML: 250 Hz high-pass scientific filter applied in Adobe Audition CC 2014 to all segments.
Macaulay Library ML215656

Squirrel Cuckoo *Piaya cayana*
3 ratings
Martin Manassero
25 Sep 2021
Establecimiento Ramonita II, de los Moreira, General Obligado, Santa Fe, Argentina
eBird checklist S95311985
Macaulay Library ML373492111

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*.

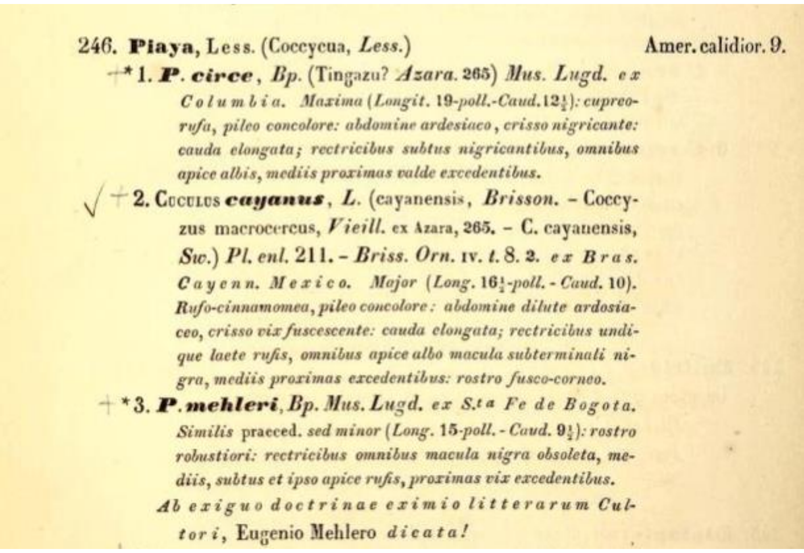
Chapman (1917) noted that *mesura* is "distinguished chiefly by the comparative blackness of all but the central tail-feathers, seen from below, a character that at once separates it from the other Colombian forms". This character is apparent in the photo of *mesura* in proposal 2022-B-11, especially 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 in 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 https://macaulaylibrary.org/asset/586198261. 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: https://macaulaylibrary.org/asset/217105071. 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 https://macaulaylibrary.org/asset/518051361 versus https://macaulaylibrary.org/asset/600766311.

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:



246. **Piaya**, Less. (Coccycua, *Less.*) Amer. calidior. 9.

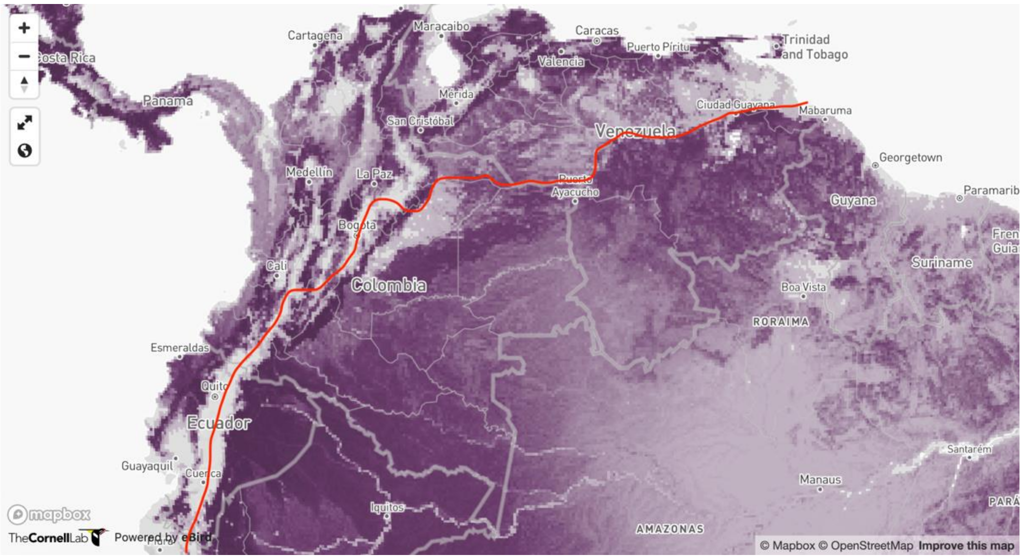
+*1. **P. circe**, *Bp.* (Tingazu? *Azara.* 265) *Mus. Lugd. ex Columbia. Maxima* (*Longit.* 19-*poll.-Caud.* 12½): *cupreo-rufa, pileo concolore: abdomine ardesiaco, crisso nigricante: cauda elongata; rectricibus subtus nigricantibus, omnibus apice albis, mediis proximas valde excedentibus.*

√ + 2. Cuculus ***cayanus***, *L.* (cayanensis, *Brisson.* – Coccyzus macrocercus, *Vieill.* ex Azara, 265. – C. cayanensis, *Sw.*) *Pl. enl.* 211. – *Briss. Orn.* IV. *t.* 8. 2. *ex Bras. Cayenn. Mexico. Major* (*Long.* 16½-*poll.* - *Caud.* 10). *Rufo-cinnamomea, pileo concolore: abdomine dilute ardosiaceo, crisso vix fuscescente: cauda elongata; rectricibus undique laete rufis, omnibus apice albo macula subterminali nigra, mediis proximas excedentibus: rostro fusco-corneo.*

+ *3. **P. mehleri**, *Bp. Mus. Lugd. ex S.ta Fe de Bogota. Similis* praeced. *sed minor* (*Long.* 15-*poll.* - *Caud.* 9½): *rostro robustiori: rectricibus omnibus macula nigra obsoleta, mediis, subtus et ipso apice rufis, proximas vix excedentibus.*

Ab exiguo doctrinae eximio litterarum Cultori, Eugenio Mehlero *dicata!*

To provide a better visualization of where these taxa come into contact in Colombia, below is the eBird abundance map (https://science.ebird.org/en/status-and-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* Allen, 1900 (type locality Santa Marta, Colombia), as a synonym, apparently overlooking *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.

Please vote on the following issues:

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 SACC voting on this, given that *cayana* only occurs in the SACC area)

Recommendation:

This is clearly a borderline case with suboptimal data (and a potential nomenclatural issue), but we tentatively recommend a **YES** on both A and B.

The split of *mexicana* would be based on the mitochondrial genetic differences, consistent plumage differences, morphometric differences, possible sharper call notes, and narrow contact zone with *thermophila*. This is the treatment recommended by Sánchez-González et al. (2023). This contact zone does appear to be narrow and occurs across a sharp ecotone, albeit with a few intermediates. However, there are still no formal analyses of vocal or plumage data. The vocal information mentioned above does seem to indicate a sharper, higher-pitched call note in *mexicana*, but it is unknown whether these differences are diagnosable, if they're affected by the level of agitation of the bird, or if they're relevant in playback trials. The plumage differences between *mexicana* and *thermophila* are readily apparent visually (especially the rufous undertail of *mexicana*), but the overall pale rufous plumage coloration is repeated in other taxa such as *mehleri* and *pallescens*. The morphometric data from Sánchez-González et al. (2023) for *mexicana* vs. *thermophila* do show average differences between the two groups, but with overlap. The data show that the longer tail of *mexicana* is closer to being diagnostic versus *thermophila* than are other characters (i.e., less overlap in the box plots). However, splitting *mexicana* from *cayana*, and not splitting *thermophila*, would render *cayana* paraphyletic for the mitochondrial gene tree. This may not be an issue, given gene tree / species tree issues, but nuclear DNA data would be preferable. There are also little data on gene flow across the contact zone. If the *Nm* values in Sánchez-González et al. (2023) are reliable (which we posit that they are not), there is little gene flow across the contact zone (*Nm* = 0.05). In short, there appear to be diagnosable differences across a small contact zone, but it is not clear whether these differences correspond to biological species.

In contrast, as noted above, there are still many unanswered questions regarding the contact zone between the "*circe*" and *cayana* groups. Most importantly, there are no genetic samples from potential contact zones in Venezuela, Colombia, or Ecuador. However, given the available data, splitting "*circe*" and *mexicana* would maintain monophyly for the mitochondrial gene tree and split two clades that are 1.2 – 1.7 million years divergent. The data from Smith et al. (2014) suggest that there is a mitochondrial clade in northern Peru that is distinct from the rest of South America, and whether this clade is the same as the one found in Colombia is unknown. We think that the critical data are from the very abrupt turnover between taxa with red orbital rings and those with greenish-yellow orbital rings. Analyses of these contact zones do seem critical to determining species limits, but we think the data at hand tip the scales towards valid species. However, the sonograms of the *thermophila* and *cayana* groups shown above look fairly similar to us. There is also still the issue of the extensive plumage variation within the *cayana* group even if the "*circe*" group is split, with pale bellied and pale rufous taxa (e.g., *pallescens*) and dark-vented (e.g., *macroura*) taxa that at least superficially resemble the Middle American and northern South American taxa.

The nomenclatural issue of *circe* and *mehleri* is problematic. As stated above, because *circe* and *mehleri* were published simultaneously, a first reviser action would likely be necessary to determine which species name would apply if this northern group were split from *P. cayana*. We think it is worth considering this novel species treatment given the available data, but it may be worth waiting until for a publication to sort out the nomenclatural issues before implementing the split.

The way that the voting options are structured, there are a few other possible voting solutions. The first is a YES on A and a NO on B, which would render *P. cayana* paraphyletic in the mitochondrial gene trees but would split the taxon restricted to North America and leave the South American split up to SACC. The other option would be a NO on A and a YES on B, which would prioritize the deeper split in the mitochondrial gene tree and the more obvious difference in orbital ring color (the blue-gray orbital ring of *mexicana* is somewhat more similar to the greenish-yellow of *thermophila*). Note that if this latter option is adopted then the species would be *P. mexicana* (Swainson, 1827), which has priority over *circe* Bonaparte, 1850.

Note also that the WGAC is considering splitting just *thermophila* and *nigricrissa* from the remainder of the South American taxa. We do not consider this a viable solution to this taxonomic problem, and are not including it as a voting option.

If any splits are adopted, an English name proposal should be drafted to address the new names, preferably in coordination with the SACC. We tentatively recommend Mexican Squirrel-Cuckoo for *mexicana*, following Chapman (1917). Although a bit of a mouthful, Chapman (1917) used Central American Squirrel-Cuckoo for *thermophila* (although *nigricrissa* occurs in South America), but this name would not be appropriate for the more widespread *P. circe*. One option, though not ideal, could be Northern Squirrel-Cuckoo for *circe* and Southern Squirrel-Cuckoo for *cayana*. South American Squirrel-Cuckoo could also work for *cayana*.

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Date of proposal: 5 September 2023

Treat *Stelgidopteryx ridgwayi* as a separate species from Northern Rough-winged Swallow *S. serripennis*

The current AOS Checklist (1998) treats *Stelgidopteryx ridgwayi* as conspecific with the Northern Rough-winged Swallow *S. serripennis*. This proposal, if accepted, would elevate *S. ridgwayi* to species status.

Background:

Ridgway's Rough-winged Swallow *Stelgidopteryx ridgwayi* was described by Nelson (1901) based on a specimen taken from Chichén Itzá, Yucatán, Mexico. Most taxonomic authorities consider *ridgwayi* conspecific with Northern Rough-winged Swallow *S. serripennis* (Dickinson and Remsen 2013, Clements et al. 2022, Gill et al. 2023). Clements taxonomy currently recognizes six subspecies of *S. serripennis*:

S. s. serripennis Audubon, 1838 (type locality: Charleston, South Carolina), breeds from se Alaska, s Canada to wc, sc, se USA; non-breeding range to c Panama

S. s. psammochroa Griscom, 1929 (type locality: near Oposura, Sonora), breeds from sw USA to sw Mexico; non-breeding range to Panama

S. s. fulvipennis Sclater, PL, 1860 (type locality: Jalapa, Veracruz), breeds from c Mexico to Costa Rica

S. s. burleighi Phillips, AR, 1986 (type locality: Gallon Jug, Orange Walk District, Belize), breeds in s Yucatán Peninsula (se Mexico), Belize

S. s. ridgwayi Nelson, 1901 (type locality: Chichén Itzá, Yucatán), breeds in n Yucatán Peninsula (se Mexico)

S. s. stuarti Brodkorb, 1942 (type locality: Finca Panzamala, Alta Verapaz, Guatemala), breeds from s Veracruz, Oaxaca, and Chiapas (se Mexico) s to n Guatemala and Belize

When *S. ridgwayi* is considered a separate species, it contains subspecies *ridgwayi*, *stuarti*, and sometimes *burleighi*. Phillips (1986) stated that the distribution of *S. ridgwayi* "[c]ertainly overlaps *S. serripennis* widely in Chiapas and Belize (if not throughout its range), even in breeding season," but see below regarding specifics.

Nelson (1901) described *ridgwayi* as distinct from *serripennis* based on whitish supraloral spots and darker plumage. Ridgway (1904) treated *ridgwayi* as a species, but Hellmayr (1934) considered *ridgwayi* conspecific with *serripennis*. Phillips (1986) treated *ridgwayi* (with *stuarti*) as distinct from *serripennis* based on the plumage features described by Nelson (1901) but did not provide sample sizes of the comparative material he examined. In addition, Phillips (1986) stated that *ridgwayi* nests in caves and ruins, although again providing no details, as opposed to holes along embankments like other members of the genus. Sibley and Ahlquist (1990) and Howell and Webb (1995) adopted Phillips's taxonomic treatment, whereas the AOU (1989, 1998) rejected the proposed split on the grounds of insufficient data. Although a main topic of Phillips (1994) was the AOU's rejection of the proposed split of *S. ridgwayi*, Phillips did not provide the additional data on distribution, sympatry, or morphology that would have bolstered his case. Johnson (1994) explained in some detail the AOU's rationale for not accepting *S. ridgwayi*:

> With respect to "*S. ridgway*i," the CLC unanimously agreed that Phillips' (1986) information was inadequate to support a taxonomic change (a judgment which by no means ruled out the possibility that "*S. ridgwayi*" is actually a species). Instead of careful lists and maps of certain nesting localities documented by specimens in reproductive condition, Phillips offered brief, highly generalized statements of breeding occurrence which are so riddled with uncertainty as to be essentially useless to anyone seeking areas of possible contact between "*S. ridgwayi*" and *S. serripennis*. Motzorongo, Veracruz (for "*S. ridgwayi*") is the only precise nesting locality provided for either species. Thus, documentation of supposed sympatry is lacking.
>
> Furthermore, Phillips (1986) offered no quantitative appraisal of geographic variation, either of morphology (stated, without documentation, to be invariant) or color, of any taxon in *Stelgidopteryx*. For depth of furca ("longest minus central rectrices"), the only morphologic feature by which *S. ridgwayi* is said to show "little or no overlap" with other forms of *S. serripennis*, Phillips (1994:770) only gives extreme measurements in a key. He provides no sample sizes, sample means, standard deviations, or standard errors to enable interpretation of significance. The possibility of geographic variation in depth of furca is not mentioned let alone explored. Regarding voice, Phillips (1994:771) states that "This is apparently less important for species recognition in swallows than in flycatchers; that of *S. ridgwayi* is apparently unrecorded." Thus, Phillips obtained no tape recordings of vocalizations of these potential sibling species of swallows and, therefore, his account lacks audiospectrograms, data relevant to possible reproductive isolation. He described no fieldwork indicating familiarity with these swallow taxa in their natural setting. One searches in vain in Phillips' work for either data or analysis reflecting a modern treatment of variation that could support the recognition of *ridgwayi* as a distinct species, whatever its true biologic status.
>
> In seeking the most complete information possible as a basis for sound taxonomic decisions, the Checklist Committee routinely encourages further study and such is definitely needed in *Stelgidopteryx*. Proper data on breeding distribution, possible sympatry, morphologic variation, vocalizations, and genetic variation should be sought in southern Mexico.

Navarro-Sigüenza and Peterson (2004), working within a PSC/ESC framework, also treated *ridgwayi* as a separate species from *serripennis* following the treatment of Phillips (1986). They used an operational criterion of diagnosability based principally on phenotypic differences reported in Phillips (1986) and their comparison of museum specimens, concluding that *serripennis* has lighter plumage, no supraloral spots, creamy white undertail coverts, and a shallow tail cleft whereas *ridgwayi* has darker overall coloration, pale forehead spots, and blackish distal undertail coverts.

Most global taxonomic authorities (e.g., Howard and Moore, IOC, and Clements/eBird) treat *ridgwayi* and *serripennis* as conspecific, Birdlife split them based on the following rationale:

> [*ridgwayi* u]sually considered conspecific with *S. serripennis*, but differs in its whitish frontal lores (2); broad black tips on undertail-coverts (2); darker upperparts (1); pale collar-line behind ear-coverts (ns1); darker, more extensive grey-brown on flanks (ns1); deeper tail fork (at least 1); wider-frequency excited calls (at least 1) (Boesman 2016); unclear whether breeding sympatry is also involved. Treatment as separate species supported by phylogenetic studies (Babin 2005, Navarro-Sigüenza & Peterson 2004).

New Information:

Key information on distribution and possible sympatry is still lacking, and the diagnosability of some of the morphological characters (e.g., tips to undertail coverts) has been disputed, but new, largely unpublished information is available on genetics and vocalizations.

Genetics

Two unpublished theses have sampled both *S. serripennis* and *ridgwayi*. Babin (2005) sequenced 54 samples for mtDNA (cytochrome-b) and nuclear DNA (five microsatellite loci) to clarify relationships within *Stelgidopteryx*, including two samples from the *ridgwayi* group (both individuals of subspecies *ridgwayi* were from Yucatán, Mexico). The closest geographic locations to the Yucatán samples were the central and southern USA (Kansas, California, Texas, Louisiana) and Costa Rica, far away from the putative contact zone between *serripennis* and *ridgwayi*.

The mtDNA phylogeny from Babin (2005) recovered *S. serripennis* as sister to the South American species, *S. ruficollis*, with strong support (Fig. 1). The *ridgwayi* samples were recovered as sister to *serripennis* group, albeit with weak support (PP=63). Moreover, the *serripennis* group included three *ruficollis* samples from Costa Rica and Panama, likely related to incomplete lineage sorting rather than hybridization (see Babin 2005). Nuclear microsatellite loci showed private alleles in *ridgwayi* and differences in allelic frequency, but N=2 limited the ability to draw any concrete conclusions.

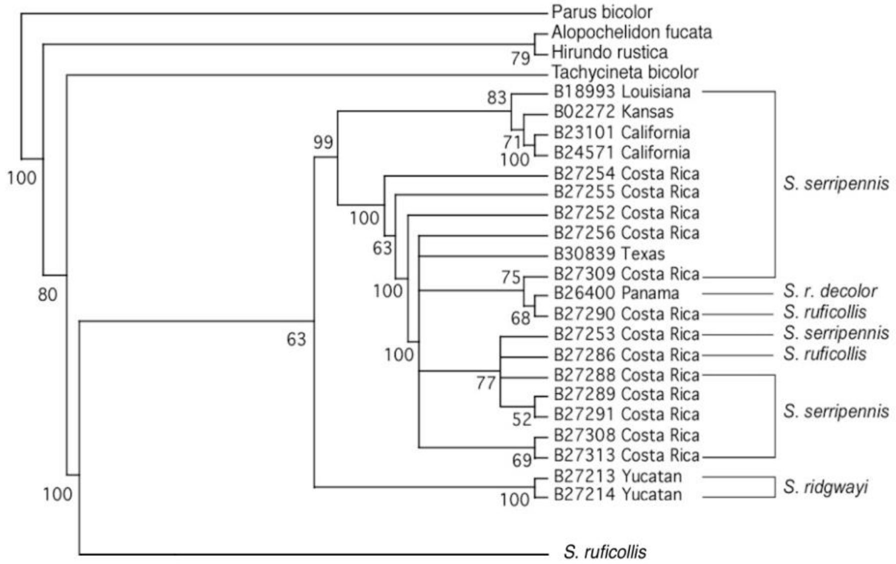

Figure 1. mtDNA phylogeny modified from Babin (2005). Support values represent posterior probabilities.

Based on thousands of genome-wide UCE markers, Brown (2019) reconstructed a species-level phylogeny of the Hirundinidae. Six samples from the genus *Stelgidopteryx* were included: four *S. serripennis* and two *S. ruficollis*, including the same two *ridgwayi* samples from Babin (2005). Concatenated and coalescent species tree analyses indicated that *ruficollis* is sister to a clade consisting of *serripennis* and *ridgwayi*, which were reciprocally monophyletic, with strong support (Fig 2). However, reciprocal monophyly was based on very small sample sizes and in this context could be consistent with either species or subspecies rank because sampling did not take into account the opportunity for gene flow.

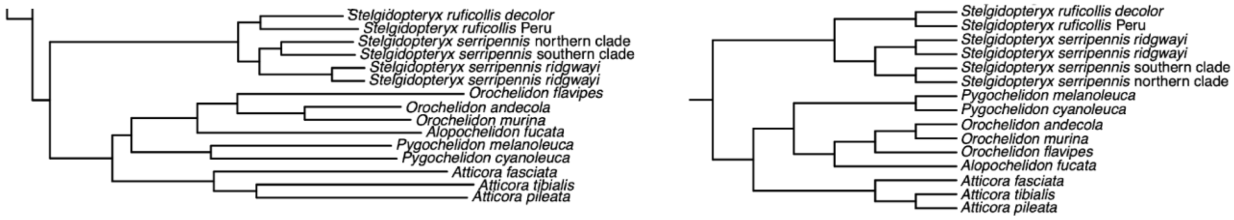

Figure 2. Concatenated Maximum Likelihood phylogeny (left) and coalescent species tree (right) based on 4453 UCEs from Brown (2019). Both methods recovered identical topologies within *Stelgidopteryx* with 100% bootstrap support.

Apart from the small sample sizes, lack of geographic coverage, and lack of peer review, the genetic analyses are hampered by the lack of sampling of *stuarti*, one of the two subspecies of *S. ridgwayi*, and of *burleighi*, described as the darkest subspecies of *S. serripennis* (i.e., most like *ridgwayi*) and the subspecies that purportedly occurs closest to the range of *S. ridgwayi*, in the southern Yucatán Peninsula in Belize and northern Guatemala.

Vocalizations

Howell and Webb (1995) described the voice of *ridgwayi* as a hard buzzy call, harder than *serripennis*.

Boesman (2016) compared and analyzed vocalizations of *S. serripennis* using recordings from xeno-canto (XC) and Macaulay Library (ML) available at the time. However, the exercise was seriously limited because only two possible recordings of *stuarti* and no recordings of *ridgwayi* were available. Both recordings of possible *stuarti* were from Tikal, Petén, Guatemala, from March 2009; Boesman assumed that these were *stuarti* but noted that he couldn't be certain because they might be wintering individuals from northern races of *serripennis* (note that they might also be resident *burleighi* based on distribution, if the range information on *burleighi* is correct).

Boesman divided vocalizations into excited calls, songs, and flight calls, although he wasn't always clear as to the identification. One spectrogram of songs or excited calls (?) of *stuarti* (Fig. 3) showed narrower-frequency calls than the typical call of nominate (Fig 4).

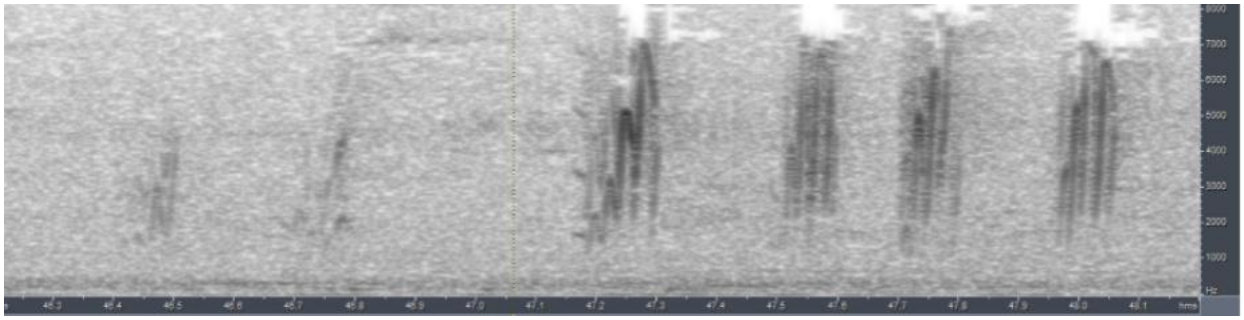

Figure 3. Song or excited call of *S. serripennis stuarti* (?), Petén, Guatemala, 18 March 2009. ML139404.

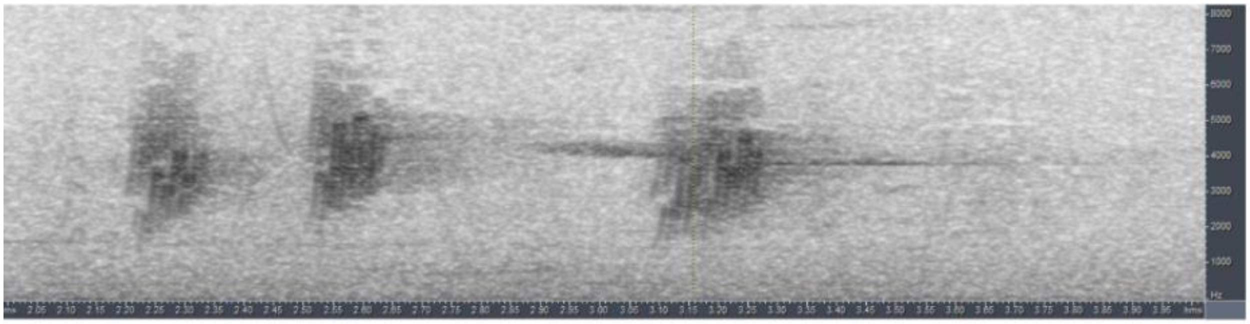

Figure 4. Song or excited call (?) of *S. serripennis*, Francisco Morazán, Honduras, 1 May 2013. XC132005.

However, other songs or excited calls are much more similar (Figs. 5, 6):

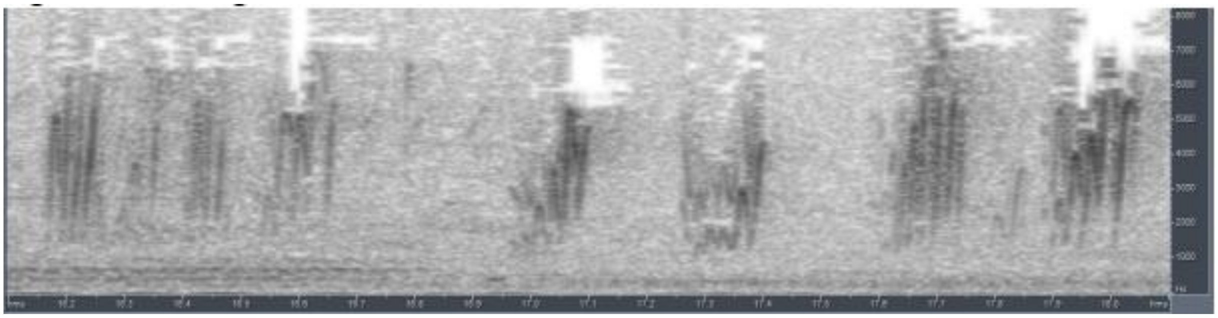

Figure 5. Flight call and song or excited call of *S. serripennis stuarti* (?).

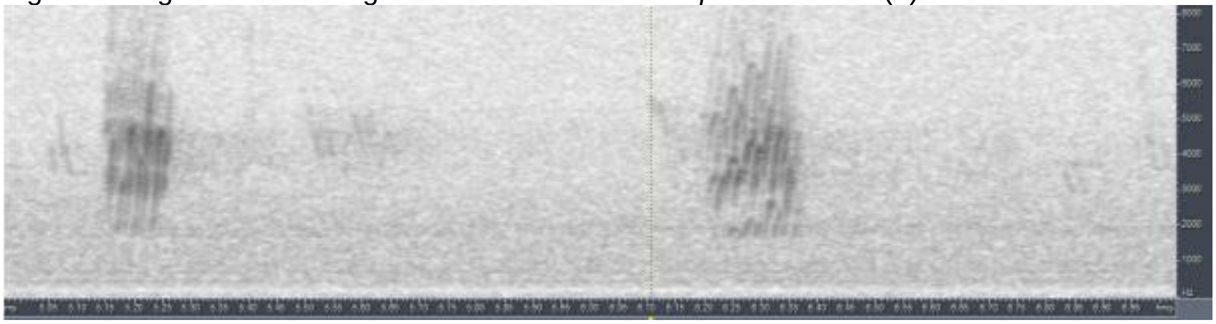

Fig. 6. Song or excited call of *S. serripennis* (non-*stuarti*).

According to Boesman, flight calls of *stuarti* were very similar to those of the other subspecies of *S. serripennis*, but potentially lower-pitched. Due to the small sample sizes, Boesman (2016) suggested obtaining more recordings to confirm vocal differences.

A few additional recordings are now available on xeno-canto and Macaulay Library, and trying to sort them out illustrates the confusion surrounding these birds. Recordings need to be parsed with attention to date (so that potential migrants or wintering birds can be excluded) and geographic location (so that resident birds are correctly placed into subspecies, to the extent that their distributions are known), and homologies of vocalizations must be carefully established among the 3-4 call and song types.

Xeno-canto contains three recordings that are not also in Macaulay, all from Tulum, Quintana Roo, Mexico, and so presumably subspecies *ridgwayi*. The first is listed as a flight call (from May), which resembles those for both taxa in Boesman (2016), and the other two are listed as songs (from December); however, the songs are twitterings, a fourth type of vocalization not analyzed by Boesman. The Macaulay Library contains seven recordings identified as *ridgwayi/stuarti*. Two of these, one of which is shared with xeno-canto, are from Las Cuevas Research Station in Cayo, Belize, and contain calls of birds flying to and from nests in the caves in May. Interestingly, these calls actually appear to be most similar to the wider-frequency calls of *serripennis* from Honduras in Fig. 4:

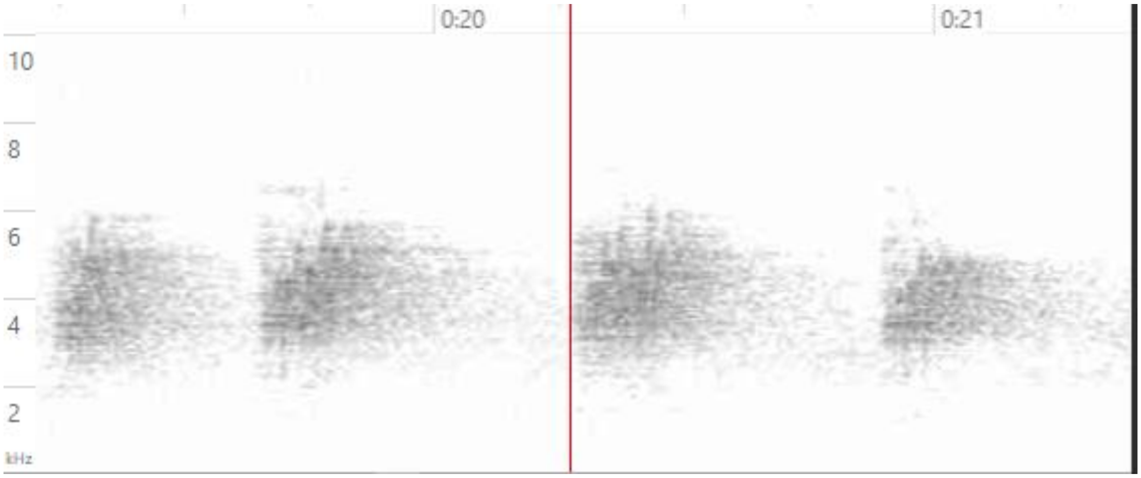

Fig. 7. https://xeno-canto.org/657782 (ML341875541) from Las Cuevas Research Station, Cayo, Belize, and identified as *ridgwayi/stuarti*. This appears to correspond to the “song or excited call (?)” of Boesman, as above.

We don’t know the basis for the identification, but both *burleighi* and *stuarti* are thought to occur in Belize. That these are birds nesting in caves would suggest that they would be *stuarti* (if Phillips is correct regarding the nesting), but the calls suggest that the distinctions of Boesman may not hold under even slightly larger sample sizes. Another recording, from Santa Elena in the northern Yucatán in December, may also be of wider frequency, although the identification is complicated by the possibility that these are wintering northern birds. Other recordings may include both narrow and wide frequency calls, such as one from Frontera Corazal, Petén, Guatemala, and another from Black Rock Lodge, Cayo Belize, in March. Two other recordings are also from Black Rock Lodge, the commentary for one of which (ML146665771) notes that the birds, specifically identified as *ridgwayi*, perched on a road and were then “checking out holes as potential nesting sites.” These recordings appear to be of narrow frequency calls, but birds using holes for nest sites would suggest that either the identification is wrong or that

Phillips's (1986) statement on nesting is incorrect. On the face of it we don't see that the new recordings bolster the case for splitting *ridgwayi*; instead, they seem to muddy the waters and highlight the need for a detailed study of breeding birds of known subspecies with particular attention to comparing homologous vocalizations.

Morphology and plumage coloration

Babin (2005) measured wing chord, tarsus length, bill length, and tail length from 215 museum specimens representing all subspecies. PCA based on these characters did not distinguish variation within *S*. *serripennis* (including *ridgwayi*). Likewise, the PCA did not separate *S*. *serripennis* from *S*. *ruficollis* groups (Fig. 8).

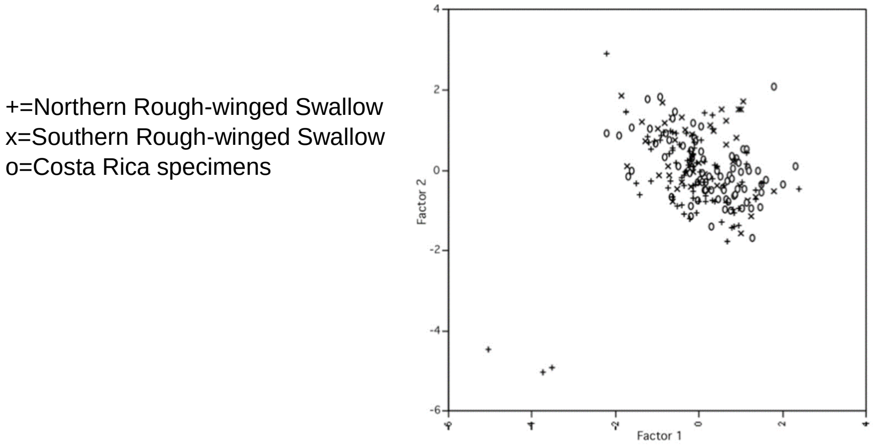

Figure 8. PCA plot based on morphological characters. Modified from Babin (2005).

Babin (2005) also analyzed plumage color variation via spectral reflectance of over 100 museum specimens, including all nominal taxa. Colorimetry analysis included three body regions: belly (3 *ridgwayi*), chin (1 *ridgwayi*), and undertail coverts (6 *ridgwayi*). The multivariate analysis of the plumage characters showed a clear separation between *S. serripennis* and *S. ruficollis*, although there was no evidence for differences within species (Fig. 9). However, Babin (2005) did not include the diagnostic traits, pale loral spots and dark flanks, for *ridgwayi* (and *stuarti*).

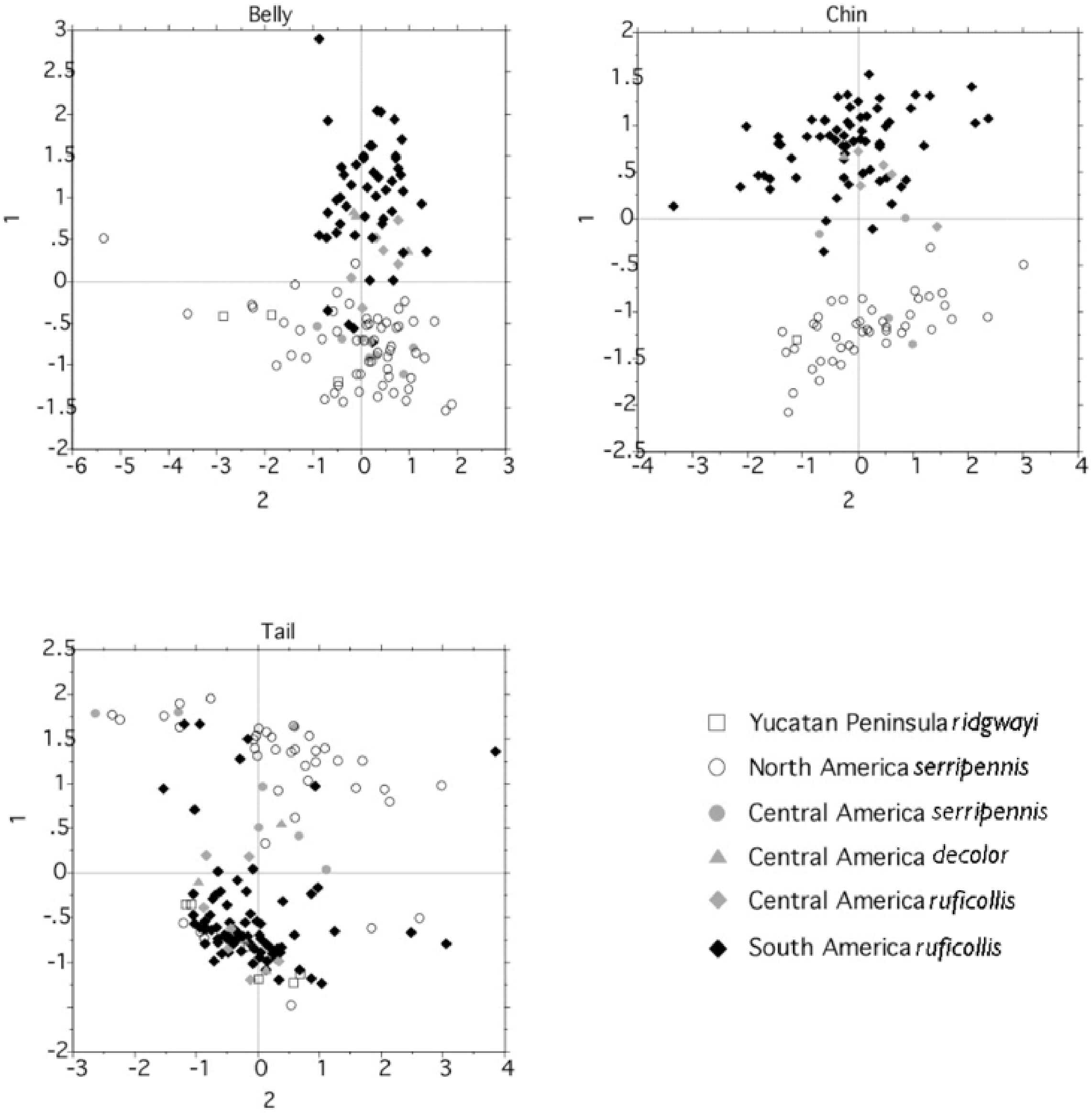

Figure 9. PCA plots based on plumage characters from Babin (2005).

Recommendation:

There are potential species-level differences. The HBW-Birdlife (2022) checklist treats *S. ridgwayi* as a separate species based on differences in appearance, vocalizations (although based on very small sample sizes and only for *stuarti*), and phylogenetic data (although based on small sample sizes and only for *ridgwayi*, and which don't distinguish species from subspecies). We recommend a **NO** on splitting *S. ridgwayi* from *S. serripennis* based on data deficiencies and the lack of published studies. First, there is little to no information on breeding range overlap with *serripennis*, and some of the recordings call into question the purported distinctive nesting habits of *ridgwayi*. If sympatric breeding or diagnostic nest-site differences were present, these are good arguments for treating *ridgwayi* as a separate species. Second, population-level genetic sampling is needed where the ranges of these forms come into contact, including samples of *burleighi* and of both subspecies of *ridgwayi*, as well as better geographic coverage of *S. serripennis*. Lastly, although there maybe differences in voice, more recordings are needed before any conclusions are drawn. More sampling is desirable, especially within the breeding season, as northern *serripennis* individuals overlap with *ridgwayi* during the winter and migration (and swallows are known to migrate early).

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Submitted by: Nicholas Vinciguerra, Museum of Southwestern Biology, Rosa Alicia Jiménez, Universidad de San Carlos de Guatemala, and Terry Chesser

Date of proposal: 5 September 2023

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

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, with extensive variation in various aspects of their plumage, 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 within 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, 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 (*L. 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 (*L. argentatus*), as currently recognized by the AOS, consists 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 Alaska. 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 them as conspecific with European populations (Coues 1873), an arrangement followed by all versions of the AOU/AOS Check-List (1886 through 1998). However, there has been a growing tendency 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 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, although most now place them both with *smithsonianus* (Dickinson and Remsen 2013, del Hoyo and Collar 2015, Clements et al. 2022). However, *vegae* and *mongolicus* have both been treated as separate species, and *mongolicus* has 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 *L. smithsonianus* and *L. vegae*, while placing *mongolicus* in *L. cachinnans*. The IOC World Bird List (Gill et al. 2023), as well as Harrison et al. (2021), has split Herring Gull into three species, with a monotypic *smithsonianus*, placing both of the Asian taxa together under Vega Gull (*L. vegae*, with subspecies *vegae* and *mongolicus*).

New Information:

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 distinct species (an approach followed by all current global authorities). While *argentatus*/*argenteus* shows evidence of only limited interbreeding with *fuscus* and *michahellis*, it appears that it hybridizes more frequently with *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 as *smithsonianus*, 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*, although Fring et al. (1958) did note that *argentatus/argenteus* did not respond to recordings of *smithsonianus*, suggesting some degree of isolation.

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 in turn derived from an ancestral refugium in central Asia, whereas *argentatus/argenteus* was derived from an ancestral refugium in the northeastern Atlantic. In addition, *mongolicus* appears to represent a separate colonization event 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 Black-backed 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 (*Larus californicus*), whereas nominate *argentatus* formed a clade with Glaucous

Gulls from Europe (North American Glaucous Gulls fell out in a different part of the phylogeny, more on that later; Fig. 1). In addition, *vegae* was found in this study to be more closely related to Lesser Black-backed Gull (*Larus fuscus*) and Caspian Gull (*L. cachinnans*), although this study included *mongolicus* with Caspian Gull, and so that close relationship may in part be due to the grouping of *mongolicus* with *vegae* (samples of *cachinnans* were not separated based on subspecies ID, so it is not possible to determine which *cachinnans* samples in the study are the ones that are closest to *vegae*).

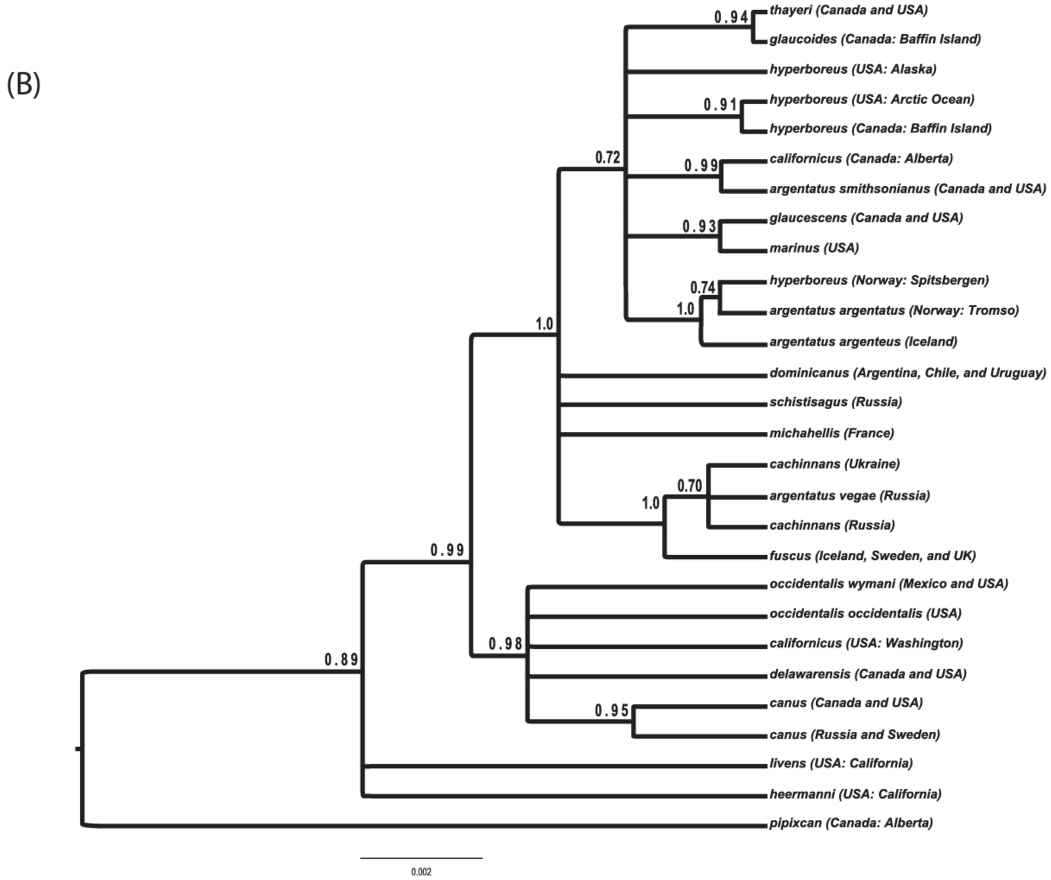

Figure 1. From Sonthagen et al. (2016), showing the phylogeny of gulls based on sequence of mtDNA control-region and six nuclear introns constructed using BEAST.

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*) in Leibers et al. (2004). They also included samples of other members of the Herring Gull complex, including North American *smithsonianus* (however, *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.

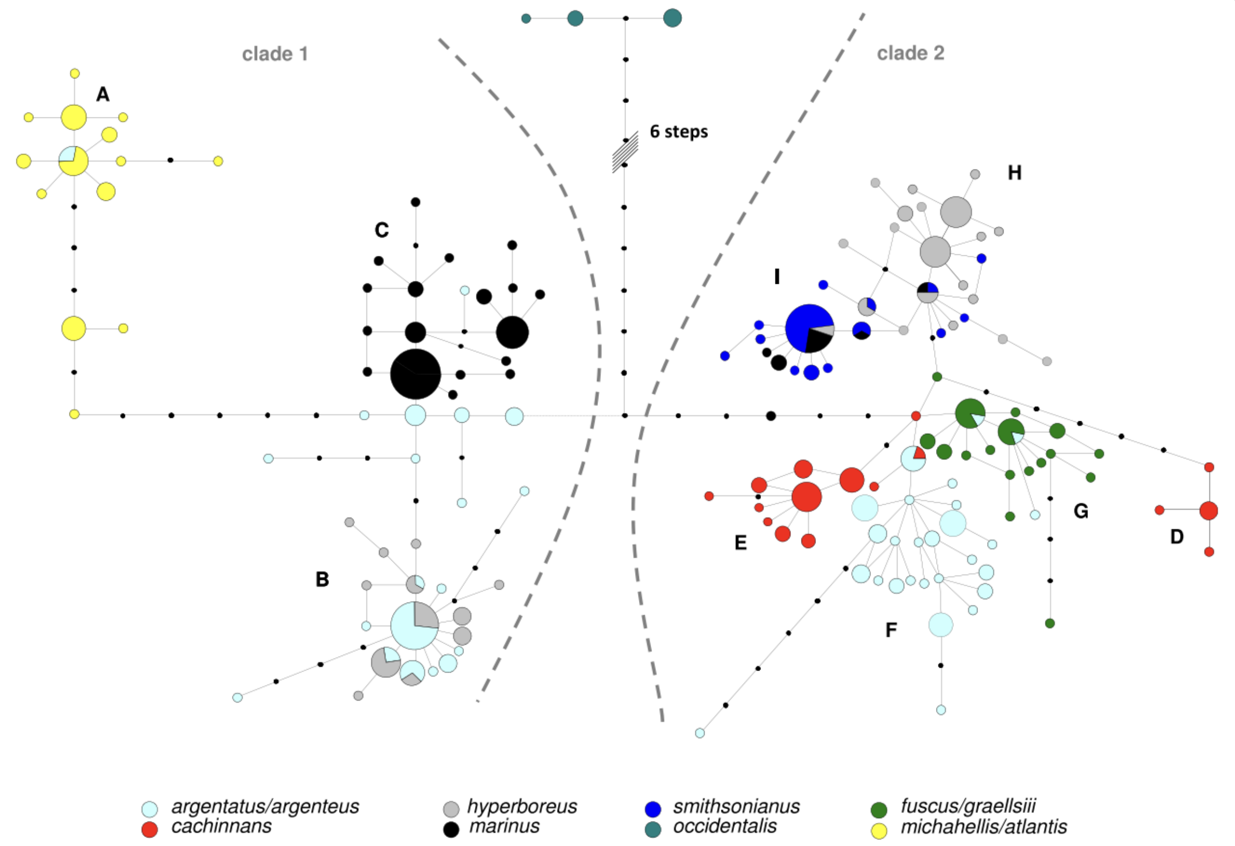

Figure 2 Median-joining network of mtDNA haplotypes among herring gull taxa. Median-joining network of 368 concatenated *cytB* and *HVR1* mtDNA sequence haplotypes (see Additional file 2) of all gull taxa included in this study. Distinct haplotype groups are labelled A-I. The network was rooted by the inclusion of previously published [8]*occidentalis* sequences. The network shows three biphyletic taxa of which individuals either carry clade 1 or clade 2 haplotypes: The European herring gull (*argentatus/argenteus* - pale blue) in haplogroup B, F and G; the glaucous gull (*hyperboreus* - grey) in group B, H and I; and the black-backed gull (*marinus* - black) in haplogroup C, I and H.

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, they sequenced 2,145 loci across the four species. In their study, Glaucous-winged Gull was consistently distinct and separate from the other three species, and will not be further discussed here. Considering *smithsonianus*, *hyperboreus*, and *argentatus/argenteus*, they found that *smithsonianus* and *hyperboreus* were consistently recovered as distinct, 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 (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. In an analysis of migration rates, migration rates from *smithsonianus* into *hyperboreus* were significantly greater than 0, and that was the only pairwise comparison in the study that was significantly greater than 0; the author also notes 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 speculates 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* was identified in the analyses from Iceland.

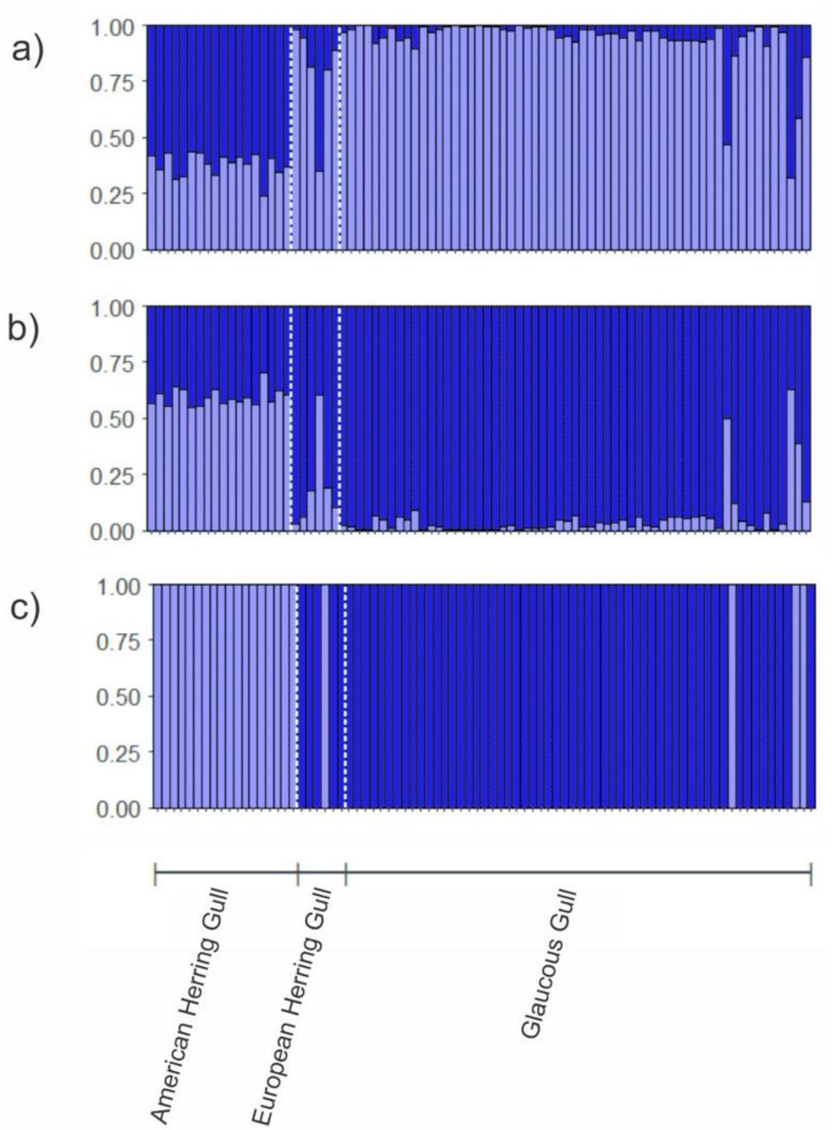

Figure 3. From Linklater (2021). STRUCTURE plots using ddRAD loci, where (a) shows the admixture model, (b) shows the admixture model and species as prior population information, and (c) shows only species as the prior population information. Notable is that *smithsonianus* is distinct from *argentatus/argenteus*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

Recommendation:

Gull taxonomy, especially among the Herring Gull complex, is 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. 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 (where North America was likely 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* are 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 his study, but again found that *smithsonianus* was genetically more distinct from *argentatus/argenteus* than *argentatus/argenteus* was from *hyperboreus*. Although no thorough study has been done, there is also behavioral evidence for the recognition of *smithsonianus* as a separate species from *argentatus/argenteus*: in a study investigating response to vocalizations of different European and North American taxa, Frings et al. (1958) found that *argentatus/argenteus* did not respond to the feeding calls of *smithsonianus*. Unfortunately, courtship vocalizations were not included in the study, nor were the reciprocal comparisons made in North America. 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: juvenile and first-year *smithsonianus* are darker overall than *argentatus/argenteus*, with *argentatus/argenteus* having a distinct pale rump, pale bases to the tail feathers, broader pale edging to wing coverts, and less uniformly dark plumage on the underparts (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 2015) and the Howard and Moore Checklist (Dickinson and Remsen 2013) place *vegae* and *mongolicus* together with *smithsonianus* (Arctic Herring Gull and American Herring Gull, respectively), whereas the IOC World Bird List (Gill et al. 2023) and Harrison et al. (2021) further split the group, recognizing a monotypic *smithsonianus* (American Herring Gull) and Vega Herring Gull (containing nominate *vegae* and *mongolicus*). There appears to be evidence for both 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, Sonthagen 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 Sonthagen et al. (2016) included *mongolicus* in their definition of *L. cachinnans*, and did not separate the two in their analyses, so it could be 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).

Although the status of *vegae/mongolicus* is messy and not as clear as *smithsonianus* relative to *argentatus/argenteus*, given the available evidence, I recommend splitting Herring Gull into 2 additional species: a monotypic *L. smithsonianus*, *L. vegae* (with subspecies *vegae* and *mongolicus*), and *L. argentatus* (with subspecies *argentatus* and *argenteus*). While this is my recommendation, I am presenting three voting options for this proposal:

A) A 3-way split that is the recommendation of this proposal, with the recognition of . *smithsonianus*, *L. vegae*, and *L. argentatus* (as adopted by Gill et al. 2023 and Harrison et al. 2021).
B) 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 (2015) and Dickinson and Remsen (2013).
C) No change, retaining *smithsonianus*, *vegae*, and *mongolicus* as subspecies of *L. argentatus*.

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

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

Date of Proposal: 5 September 2023

Transfer *Coccothraustes abeillei* and *C. vespertinus* to *Hesperiphona*

Background:

The genus *Coccothraustes* currently includes three species that share stocky bodies and thick, conical bills: two North American species (Evening Grosbeak *C. vespertinus* and Hooded Grosbeak *C. abeillei*) and one European species (Hawfinch *C. coccothraustes*). These species have long been thought to constitute a clade of closely related species (e.g., Coccothrausteae; Ridgway 1901) based on similarities in osteological characters (Sushkin 1925). The North American taxa were maintained in a separate genus, *Hesperiphona,* in the 2nd through 5th editions of the AOS Checklist, but were later transferred to *Coccothraustes* in the 6th edition without comment (American Ornithologists Union 1983), presumably following the treatment of Mayr and Short (1970) in the Peters Check-list series.

HBW-Birdlife and the IOC both place *vespertinus* and *abeillei* in *Hesperiphona*, which is also followed by other authorities (e.g., Dickinson and van Remsen 2003). HBW-Birdlife cites molecular evidence from Zuccon et al. (2012) in support of the change, whereas IOC does not offer any rationale. Here, I review the findings of Zuccon et al. (2012) on phylogenetic relationships of the Carduelinae in an attempt to bring our global genus-level taxonomies into alignment.

New Information:

The phylogeny in Zuccon et al. (2012; Fig. 1) is based on two mitochondrial gene regions (ND2 and ND3) and three nuclear loci: intron 2 of myoglobin gene, introns 6 and 7 of the ornithine decarboxylase (ODC) gene, and intron 11 of GAPDH. Zuccon et al. (2012) partitioned the

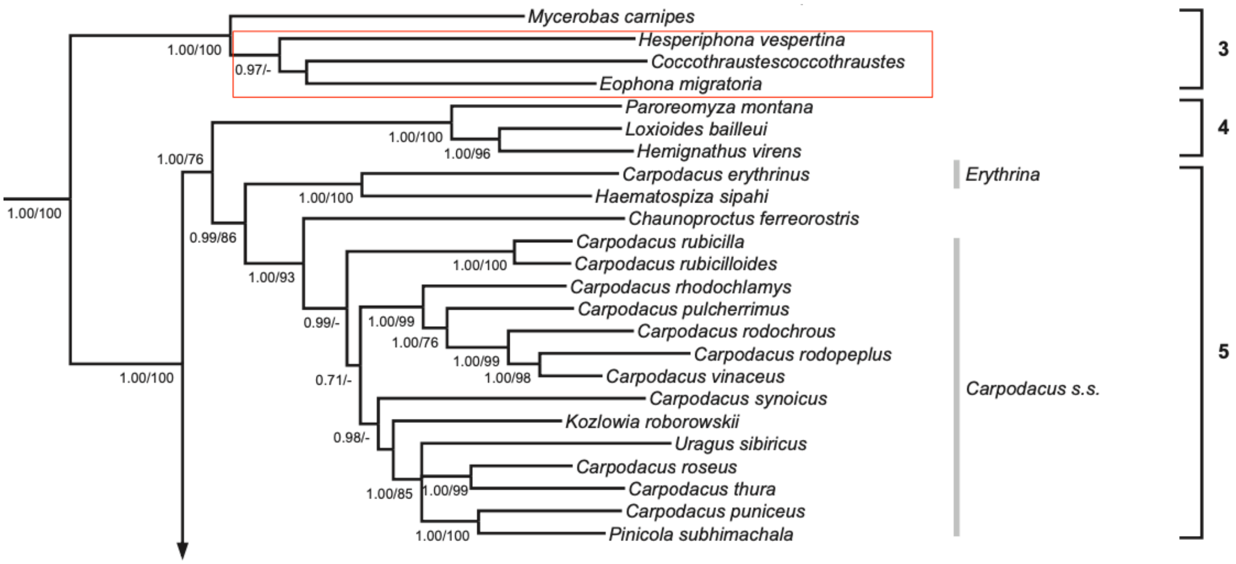

Figure 1: Majority rule consensus tree from Bayesian analysis of concatenated data set. Support values are posterior probability / bootstrap support. If numbers are not shown, then the posterior probability or bootstrap support values are lower than 0.70 or 70%, respectively.

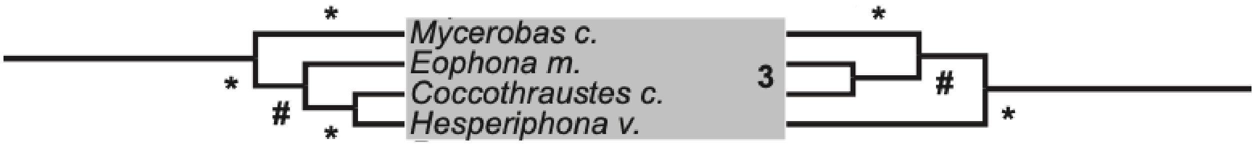

Figure 2: Comparison of the topologies obtained from the mixed-model Bayesian analysis of the concatenated mitochondrial on the left and nuclear genes on the right. Nodes with posterior probability equal to or higher than 0.95 have an asterisk (*) next to them, whereas nodes with posterior probability equal to or higher than 0.90 have a # next to them.

dataset via a mixed-model approach with each gene or gene region in its own partition. They then performed Bayesian inference with MrBayes and maximum likelihood searches via RAxML. Zuccon et al. (2012) sampled *vespertina* and *coccothraustes* but did not include *abeillei*.

As seen in the figures above, there is some evidence that *Hesperiphona* and *Coccothraustes* may not form a monophyletic lineage. In the concatenated data set, *Coccothraustes* is more closely related to *Eophona* than it is to *Hesperiphona*. However, this topology is not corroborated by strongly supported nodes: the node that unites *Coccothraustes* and *Eophona* to the exclusion of *Hesperiphona* has <0.70 PP and <70 BS. This low nodal support appears to be a product of mitonuclear discordance. Specifically, the mtDNA data set (Fig. 2 on the left side) strongly supports *Hesperiphona* and *Coccothraustes* as sister species, whereas *Eophona* is strongly supported as the sister taxon of *Hesperiphona* + *Coccothraustes*. In contrast, the nuDNA data (Fig. 2 on the right side) has reconstructed *Coccothraustes* and *Eophona* as sister taxa, while *Hesperiphona* is sister to *Mycerobas* + *Eophona* + *Coccothraustes*. Thus, there is mitonuclear discordance in this data set, which may be the result of incomplete lineage sorting, sex-biased dispersal, asymmetrical introgression, natural selection, or other evolutionary processes (Toews and Brelsford 2012).

Zuccon et al. (2012) noted this discrepancy between the concatenated Bayesian tree, the mtDNA tree, and the nuDNA tree in their discussion. The authors used *Hesperiphona* to refer to the North American taxa *vespertinus* and *abeillei*, but did not explicitly provide a rationale for recognizing *Hesperiphona* as separate from *Coccothraustes*.

Recommendation:

The decision to lump *vespertina* and *abeillei* into *Coccothraustes* was made without any accompanying rationale in the 6th edition of the AOS checklist. More recently, most other global taxonomies have transferred *vespertina* and *abeillei* into *Hesperiphona*, leaving *Coccothraustes coccothraustes* as the sole species in the genus *Coccothraustes*. The molecular phylogenies currently available to us are inconclusive in terms of the relationships among these taxa. Some may see changing *Coccothraustes* to a monotypic genus as a downside to recognizing *Hesperiphona*, because we then lose information on its closest relatives. However, assuming that the New World species *vespertina* and *abeillei* are sisters, as they have consistently been considered, transferring them to *Hesperiphona* presents a stable solution moving forward regardless of how the relationships among *Coccothraustes, Hesperiphona*, *Eophona*, and *Mycerobas* are resolved, and brings the NACC taxonomy in line with other global authorities.

I therefore recommend a YES vote to transfer *vespertina* and *abeillei* to *Hesperiphona*.

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