AOU Classification Committee – North and Middle America
Proposal Set 2017-B

Recognize additional species in the *Aulacorhynchus "prasinus"* toucanet complex

Background:

The AOU (1998) presently considers there to be just one species of *Aulacorhynchus prasinus*, which ranges from Mexico to Guyana and Bolivia. This taxon's range combines the taxonomic oversight regions of both the North American and South American classification committees, so this proposal is designed to be submitted to both, with committee-structured voting sections at the end. This is easy to do biologically, because the taxa fall out fairly neatly split between North and South America. (The Panamanian blue-throated population breeding on Cerro Tacarcuna (subspecies *cognatus*) has (Hilty and Brown 1986) and has not been (Donegan et al. 2015) included in the Colombian avifauna.)

The AOU's first treatment of this group in Middle America began with the geographic expansion undertaken in the sixth edition of the Check-list (AOU 1983). The historic treatments of the genus are given in Table 1 (from Winker 2016). In brief, evidence of hybridization caused massive lumping into a broadly defined *prasinus* from Peters (1948) onward, with recent genetic evidence of divergence causing some authors to propose that the *prasinus* complex is made up of as many as seven species (Table 1). These recent proposals have not been widely accepted; I summed the situation up as follows (Winker 2016):

"Renewed interest in this complex (Navarro et al., 2001; Puebla-Olivares et al., 2008; Bonaccorso et al., 2011; Del Hoyo & Collar, 2014) is beginning to rectify the absence of data, but the ensuing taxonomic changes recommended have either been based on a different species concept (Bonaccorso et al., 2011) or have inadequately considered the hybridization and intergradation (e.g., Navarro et al., 2001; Puebla-Olivares et al., 2008; Del Hoyo & Collar, 2014) that have been integral to supporting the "post-Peters" taxonomy. These latter works have recommended elevation of numerous *A. prasinus* (*sensu lato*) taxa to species status (Table 1), but they did not address the reasons for lumping in the first place: evidence of hybridization. There has also been heavy reliance on a single molecular marker (mtDNA) for species delimitation in the *A. prasinus* complex (Puebla-Olivares et al., 2008; Bonaccorso et al., 2011). This is problematic because mtDNA can be misleading about species limits and relationships between populations due to gene-tree/species-tree mismatches and because genetic distance is not a reliable indicator of species limits (Avise & Wollenberg, 1997; Irwin, 2002; Funk & Omland, 2003; Degnan & Rosenberg, 2006; Cheviron & Brumfield, 2009; Galtier et al., 2009; Ribeiro, Lloyd & Bowie, 2011; Toews & Brelsford, 2012; Pavlova et al., 2013; Peters et al., 2014; Dolman & Joseph, 2015; Morales et al., 2015). Thus, species limits in the group remain uncertain (Table 1)."

There are six color-based groups in the *prasinus* complex, within which some have additional described subspecies. These major groups have been recognized through much of the history of the taxon (Table 1) and were reaffirmed by the analyses of del Hoyo and Collar (2014). The characters upon which they are based are given in Winker (2016: table 2) and can be seen in the accompanying Plate.

Figure 1. The six major, color-based taxonomic groups of the *Aulacorhynchus "prasinus"* species complex, from top to bottom: A) *wagleri*; B) *prasinus* (nominate *prasinus* and *warneri*, the full-bodied bird, are portrayed): C) *caeruleogularis*; D) *albivitta* (*griseigularis* and nominate *albivitta* are portrayed); E) *cyanolaemus* (yellow-tipped bill); and F) *atrogularis*.
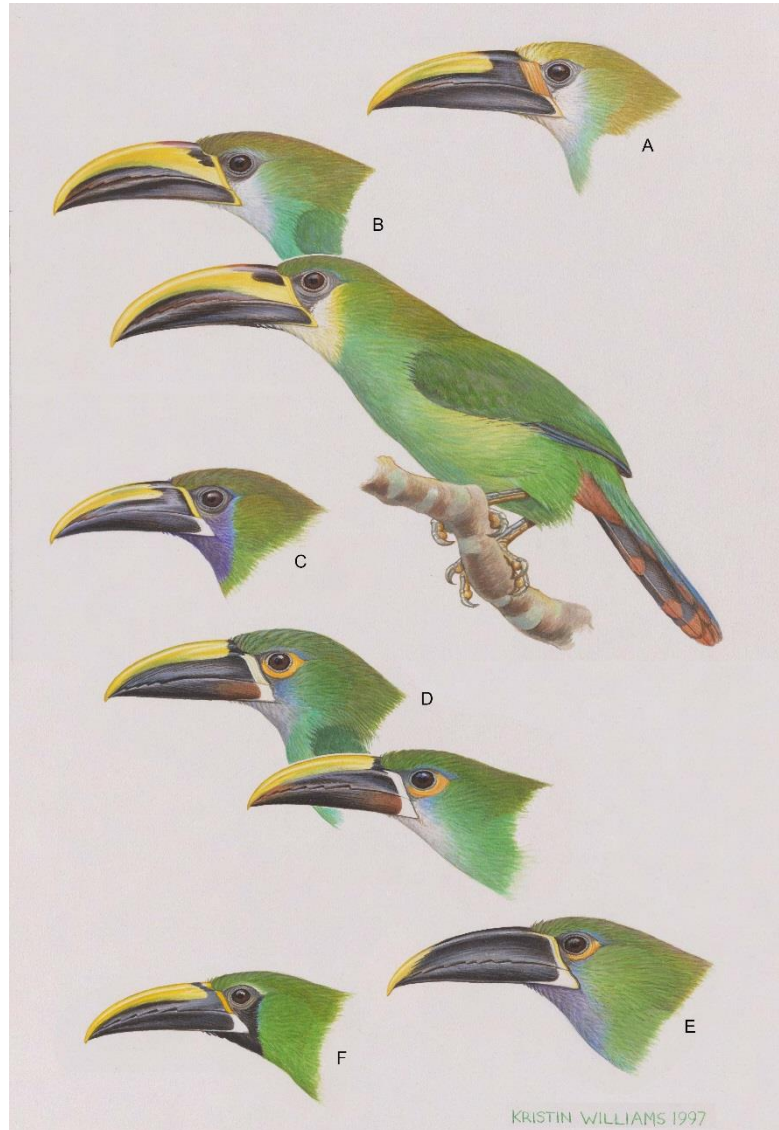
Table 1. Treatments of species-level diversity in the genus *Aulacorhynchus*. Taxa historically recognized only as subspecies are not included (see text for these taxa in "*prasinus*"). An X means the taxon was treated as a species, a dash indicates not available to be treated yet, and a blank indicates that the taxon was not considered.

	Sclater (1891)	S & G (1896)a B & C (1912)b	Cory (1919)	Peters (1948)	Sibley & Monroe (1990)	Short & Horne (2001)	Nav. et al. (2001)g P-O et al. (2008)g B. et al. (2011)g	Dickinson & Remsen (2013)i	del Hoyo & Collar (2014)	Winker (2016)
A. sulcatus	×	×	×	×	×	×	×	×	×	
A. erythrognathus	×	×	ssp. of *sulcatus*	ssp. of *sulcatus*		ssp. of *sulcatus*	ssp. of *sulcatus*	ssp. of *sulcatus*	ssp. of *sulcatus*	
A. calorhynchus	×	×	×	×	ssp. of *sulcatus*	ssp. of *sulcatus*	ssp. of *sulcatus*	ssp. of *sulcatus*	×	
A. derbianus	×	×	×	×	×	×	×	×	×	
A. whitelianus	×	×	×	ssp. of *derbianus*		ssp. of *derbianus*	×	×	×	
A. haematopygus	×	×	×	×	×	×	×	×	×	
A. coeruleicinctis	×	×	×	×	×	×	×	×	×	
A. huallagae	– c	– c	– c	×	×	×	×	×	×	
A. prasinus	×	×	×	×	×	×	×	×	×	×
A. wagleri	×	×	×	ssp. of *prasinus*		ssp. of *prasinus*	×	ssp. of *prasinus*	×	×
A. caeruleogularis	×	×	×	ssp. of *prasinus*	ssp. of *prasinus*	ssp. of *prasinus*	×	ssp. of *prasinus*	×	×
A. cognatus	– d	– d	ssp. of *caeruleogularis*	ssp. of *prasinus*		ssp. of *prasinus*	×	ssp. of *prasinus*	ssp. of *caeruleogularis*	ssp. of *caeruleogularis*
A. albivitta	×	×	×	ssp. of *prasinus*		ssp. of *prasinus*	×	ssp. of *prasinus*	×	×
A. griseigularis	– e	– e	– e	ssp. of *prasinus*		ssp. of *prasinus*	×	ssp. of *prasinus*	ssp. of *albivitta*	ssp. of *albivitta*
A. lautus	– f	×	×	ssp. of *prasinus*		ssp. of *prasinus*	× h	ssp. of *prasinus*	ssp. of *albivitta*	ssp. of *albivitta*
A. cyanolaemus	×	×	×	ssp. of *prasinus*		ssp. of *prasinus*	ssp. of *atrogularis*	ssp. of *prasinus*	×	ssp. of *atrogularis*
A. dimidiatus	×	×	×	ssp. of *prasinus*		ssp. of *prasinus*	ssp. of *atrogularis*	ssp. of *prasinus*	ssp. of *atrogularis*	ssp. of *atrogularis*
A. atrogularis	×	×	×	ssp. of *prasinus*		ssp. of *prasinus*	×	ssp. of *prasinus*	×	×

a – Salvin & Godman (1896) treated only Middle American *Aulacorhynchus*, which at the time were considered *Aulacorhamphus*.
b – Brabourne and Chubb (1912) treated South American members of the genus (then considered *Aulacorhamphus.*
c – *huallagae* was described by Carriker (1933).
d – *cognatus* was described as a subspecies by Nelson (1912).
e – *griseigularis* was described as a subspecies by Chapman (1915).

f – *lautus* was described by Bangs (1898).
g – Navarro et al. (2001), Puebla-Olivares et al. (2008), & Bonaccorso et al. (2011) together included most Middle American and South American *Aulacorhynchus* taxa.
h – though not included in either study.
i – Treatment matches the South American Classification Committee (Remsen et al. 2016).

New Information:

In Winker (2016) I tested the hypothesis that these are "cookie-cutter" (i.e., morphologically nearly identical) toucanets differing mostly in coloration. I also examined specimens carefully for phenotypic evidence of hybridization.
A couple of key factors were central to my treatment of the group. First, these birds move about considerably during the nonbreeding season, providing hypothetical opportunities for gene flow across zones of nearest approach. "For example, in south-central Mexico (Oaxaca), *A. prasinus* and *A. wagleri* breed within about 100 km of each other, a distance that *A. prasinus* individuals appear to move routinely away from their breeding areas, e.g., at the base of the Yucatan Peninsula (e.g., Land, 1970; Jones, 2003), which does not seem unusual for an arboreal frugivore (see also discussions in O'Neill & Gardner, 1974, and Navarro et al., 2001)." (Winker 2016). The hitherto unrecognized (although published by Puebla-Olivares et al. 2008) gene flow between *albivitta* and *atrogularis* in NE Ecuador indicates that this hypothesis has merit. Second, I considered that the likelihood of successful gene flow/reticulation between two lineages decreases with increased anagenesis or adaptive divergence, arguing as follows (Winker 2016):

 "Effective lineage reticulation requires that hybrid offspring have equal or greater fitness than offspring of pure parental forms. Also, gene flow must occur frequently enough to overcome the differentiating selective factors likely to be operating on largely allopatric populations (and this relationship is nonlinear; see Winker, 2010 for discussion). The more differences there are between populations in morphology, the more differences there are likely to be in selective factors operating on these populations and the more difficult effective gene flow is likely to be between populations; at larger scales this results in the general correlation between morphological difference and reproductive isolation (Mayr, 1963; Price, 2008)."

Another important factor that I considered that did not seem to have been adequately addressed before is that named subspecies in this group do not represent equivalent levels of divergence. Historically, it seemed that commonly observed intergradation between named forms within the major color-based groups (among the more minor forms) led to observations that hybridization was common, but this seemed to cloud a thorough understanding of the full distribution of hybridization in the whole group—i.e., it's not just where birds hybridize, but where they don't and what phenotypic characteristics accompany these phenomena. I focused on the major groups and made pairwise comparisons between them.

My results (from 578 specimens) showed multiple and complex morphometric relationships between pairwise comparisons of neighboring forms. These differences were different between the sexes and the differences were different between populations, and only a small percentage of the variation observed could be explained by geography (in females only, latitude and longitude explained $\leq$ 6% of variation). **As it turned out, degrees of morphometric differentiation were highly correlated with genetic distance (R^2 = 0.67), as predicted by the processes of anagenesis and speciation (Winker 2016: figure 5)**.
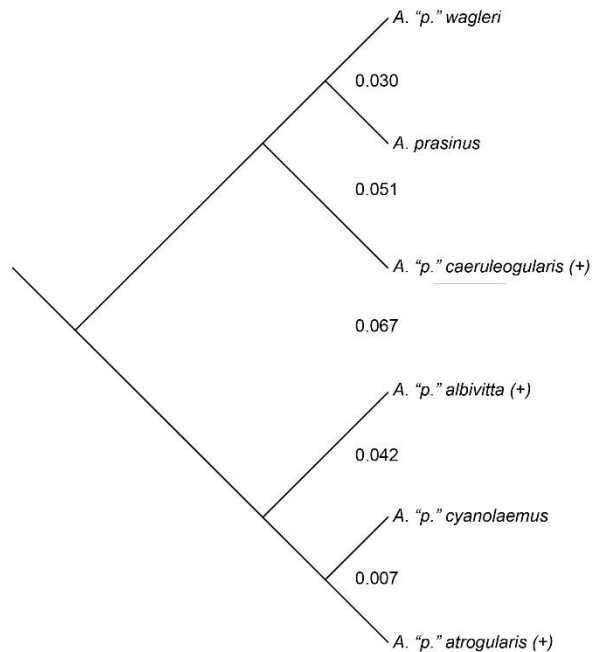

Figure 2. The mtDNA topology of the relationships among the six major subspecific groups, following Puebla-Olivares et al. (2008). Taxa labeled with a "(+)" are non-monophyletic in mtDNA. Values between the major subspecific groups are the between-group mean genetic distances between them.

Neither geography nor phenotypic plasticity is likely to explain the degree of differences found. "Concordant shifts in suites of mensural and other morphological characters are precisely what we would predict to occur between individuals representing genetically disjunct, locally adapted gene pools. Consequently, this evidence suggests that this is what they are, and at these levels of morphological differentiation (morphometrics, coloration, and pattern) we would usually consider these groups to be full biological species." But that conclusion does not include consideration of hybridization.

Evidence of hybridization between members of the six color-based groups occurs phenotypically between *cyanolaemus* and *atrogularis*, and (genetic evidence only) between *atrogularis* and *albivitta*. The frequency of gene flow was loosely inferred by using phenotypic evidence of hybridization as a surrogate. Gene flow appears to be substantial between the two most closely related taxa (0.7% divergence), *cyanolaemus* and *atrogularis*, and rare (zero phenotypic evidence) between *albivitta* and *atrogularis* (4.2% divergence; genetic data of Puebla-Olivares et al. 2008). There is no evidence for Haldane's rule occurring (genetic incompatibilities so extreme as to result in higher levels of mortality in hybrids of the heterogametic sex—females in this case). There was no evidence of hybridization among the North American forms (3-5.1% divergence), nor between North and South American forms (6.7% divergent).

"Hybridization per se is not sufficient evidence for conspecificity, and in this group I find the lack of hybrids at most zones of potential crossing of major subspecific groups to be more compelling in the determination of species limits than its clear and seemingly

routine presence at one—particularly in light of the repeated evidence of varying suites of morphological characters changing abruptly across these zones. However, I do consider that the apparent frequency of hybridization between *A. atrogularis cyanolaemus* and *A. a. atrogularis* warrants a conservative approach to their separation at the species level, and thus I do not recommend doing so without more evidence. In short, morphologically there is no evidence for hybridization between five of the major subspecific groups, despite likely opportunity, especially in northern Middle America. This is coupled with pronounced morphometric differences between these groups, suggesting group-specific ecological adaptation in addition to whatever social selection factors have likely caused the rather dramatic head and bill color differences." (Winker 2016). In other words, I doubt these taxa exist in total allopatry, and the genetic evidence between *albivitta* and *atrogularis* would seem to support this supposition, yet intergroup hybrids seem to be rare except between the two most closely related forms, *cyanolaemus* and *atrogularis*.

Voice is an important reproductive isolating mechanism (RIM) in at least some *Aulacorhynchus*, (Schwartz 1972, Haffer 1974). However, I think it would be a mistake to consider it the only or even the most important one, despite its utility in some cases. In Winker (2016) I did not discuss RIMs, but the treatment relied more on the likelihood of postzygotic RIMs (increasing evidence of morphological divergence making successful hybrids and reticulation less likely) than on prezygotic ones (of which voice could be an important one). From a subjective view, vocal divergence does not seem to be evolving as quickly in the *prasinus* complex as it has among other *Aulacorhynchus* species in South America. The South American radiation of the species *haematopygus, whitelianus, derbianus*, and *sulcatus* likely began after that of the *prasinus* clade (~4.5 Mya vs. ~5.2 Mya; Bonaccorso et al. 2013, figure inserted here). But (subjectively) in the former group vocal divergence has been more rapid (Schwartz 1972).
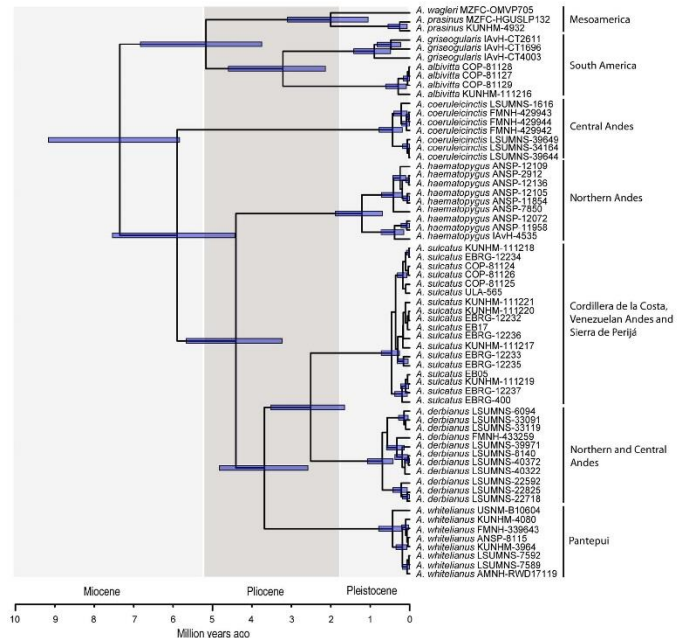

Figure 4. BEAST analysis showing the timeframe estimated for the evolutionary history of species in the genus *Aulacorhynchus*. Bars at each node indicate the highest posterior density (HPD) interval.
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Donegan et al. (2015) relied exclusively on voice in maintaining all *prasinus* taxa as one species, mostly reiterating prior work (though providing more sonograms) of Haffer (1974) and Short and Horne (2001), which downplayed phenotypic differences (not adequately explored, in my view) and relied rather heavily on voice. Inadequate attention has been paid to the fact that the vocally similar taxa hybridizing to a degree to be considered conspecific (e.g., *cyanolaemus-atrogularis* and *sulcatus-calorhynchus*; Schwartz 1972) are among the most closely related in the genus (Puebla-Olivares 2008, Bonaccorso et al. 2011: fig. 2, inserted at right). And, again, there are additional quite striking morphological characters changing besides bill and throat colors. In addition to the mensural characteristics

Fig. 2 Bayesian 50% majority rule consensus tree estimated from combined analysis of ND2 and *cytb*. Bayesian posterior probabilities, maximum likelihood, and maximum parsimony bootstrap values are indicated whenever nodes were recovered with less than 1.00 Bayesian posterior probability or 100% bootstrap support.

found in Winker (2016), there are characters like eye-skin color changes and the basal upper mandible encrustations in adult *wagleri* that increase the likelihood of other RIMs being present in the absence of vocal differences. So, despite vocal similarities among *prasinus* taxa, I consider the steadily increasing morphological differences with increasing genetic distance (Winker 2016: fig. 5) and the absence of phenotypic evidence of hybridization across most zones of closest approach to warrant species-level splits.
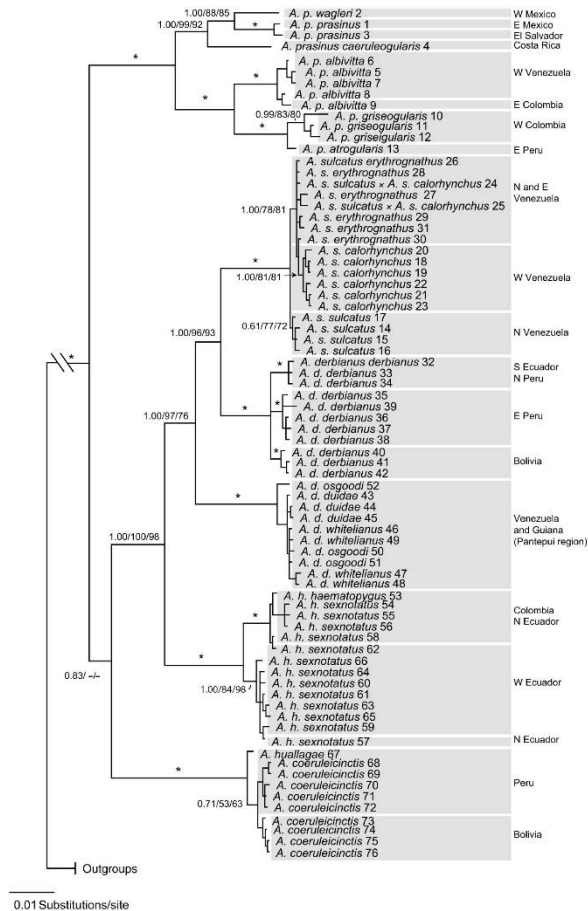
More work is needed in this group. Voice, for example, although notably similar throughout the *prasinus* complex's range (Haffer 1974, Donegan et al. 2015), does show some likely pace differences between *wagleri* and *prasinus* (Winker 2016). Also, given the current evidence it seems likely that population genetic studies will show low rates of historic gene flow across more of the zones of closest contact.
"Using the biological species concept, I suggest that consideration of all of the available evidence indicates that we should recognize five species in the A. "*prasinus*" complex (*A. wagleri, prasinus, caeruleogularis, albivitta*, and *atrogularis*), each with any associated named subspecies (Appendix)."

South American forms, where all of the hybridization thus far recognized (between the

major color-based groups) occurs, remain the least certain, and future work may change the perceptions outlined here.

Recommendation:

Unsurprisingly, I recommend voting Yes on all of A-G below (A, B, E, F, and G for NACC, and C, D, E, F, and G for SACC).

For now, I will include in the proposal an up or down vote on the English names given in the Appendix of Winker (2016). Should either of those two votes fail while the split votes pass (NACC or SACC), we will need to further address those issues.

NACC: (More NACC below...)

A) A yes vote would recognize all three major Middle American forms (*prasinus*, *wagleri*, and *caeruleogularis*) as full biological species.

B) Should the vote on A pass, we need to adopt English names for these taxa. A yes vote here would accept the English names for these taxa proposed in Winker (2016), i.e., Northern Emerald Toucanet (*A. prasinus*), Wagler's Toucanet (*A. wagleri*), and Blue-throated Toucanet (*A. caeruleogularis*). The only change from historic usage is in adding "Northern" to the first. Different historic treatments are given below in Table 2.

SACC:

C) A yes vote would recognize two South American forms (*albivitta* and *atrogularis*) as full biological species.

D) Should the vote on C pass, we need to adopt English names for these taxa. A yes vote here would accept the English names for these taxa proposed by Winker (2016), i.e., Southern Emerald Toucanet (*A. albivitta*) and Black-throated Toucanet (*A. atrogularis*). The first gets around throat-color problems both within the group and with the fact that the white color of the nominate form's throat matches that of *prasinus* sensu stricto. The second, however, does not, in that the subspecies *cyanolaemus* has a blue throat. Different historic treatments are given below in Table 2.

NACC and SACC:

E) Should the "A" and/or "C" votes above fail and we do not agree to recognize three and/or two species in each clade, respectively, it occurs to me that we should at least split the group into the two major clades, *prasinus* (North America) and *albivitta* (South America). Their nearest-approach neighbors in Panama and Colombia are phenotypically and genetically the most divergent, and they've been apart for a long time: an estimated ~1.7 Mya (using the 2% rule on the mtDNA data of Puebla-Olivares et al. 2008) or ~5.2 Mya from Bonaccorso et al. (2013). For a visual, see C and D in the accompanying Plate (Fig. 1 in the proposal) and the specimen photograph inserted

below (Fig. 2). A yes vote here would, if the A and/or C votes above fail, recognize just two species in the *prasinus* complex, whose English names might be...

F) Northern Emerald Toucanet (*A. prasinus*) and Southern Emerald Toucanet (*A. albivitta*). A yes vote here would accept these names should we only agree to split the complex into two species.

G) Finally, I propose that we adopt the sequence of taxa given in Winker (2016: appendix, copied below), which follows both geography (N-S) and taxonomy and can be taxonomically adjusted to accommodate the votes above.

Table 2. English names for *prasinus* taxa.

	Cory 1919 (names all subspp.)	HBW 2014	Winker 2016
A. prasinus	Emerald, Southern Emerald	Emerald Toucanet	Northern Emerald Toucanet
A. wagleri	Wagler's Toucanet	Wagler's Toucanet	Wagler's Toucanet
A. caeruleogularis	Blue-throated, Goldman's Bl-thr.	Blue-throated	Blue-throated Toucanet
A. albivitta	White-throated, Grayish-blue-throated, Plumbeous-throated	Grayish-throated	Southern Emerald Toucanet
A. griseigularis			
A. lautus	Santa Marta Toucanet		(subsp. of *albivitta*)
A. cyanolaemus	Gray-throated Toucanet	Black-billed	(subsp. of *atrogularis*)
A. dimidiatus	Ridgway's Toucanet		(subsp. of *atrogularis*)
A. atrogularis	Black-throated	Black-throated	Black-throated Toucanet

Figure 2 (only in proposal). Typical males of *caeruleogularis* (LSU 104668) and *A. albivitta lautus* (LSU 90407), the most proximal North and South American forms.

Appendix (from Winker 2016)

Suggested taxonomy.—Because I have examined all of the described taxa in the complex, this revision includes subspecies (although quantitative analyses were not undertaken below the level of the six major groups). Given below are species, subspecies, authors of original descriptions, type localities, and notes pertaining to each species. Distribution is not included, because I did not examine all existing specimens and can add little of substance to distributions set forth by the authors cited herein. The species sequence given follows the relationships in the mtDNA tree of Puebla-Olivares et al. (2008) but with the two major clades flipped to better accommodate the group's geographic distribution (as I have also done in Fig. 4).

Genus *Aulacorhynchus* (green toucanets), subgenus *Ramphoxanthus*
Aulacorhynchus wagleri (Sturm *in* Gould 1841:pl. 16 (heft 2, pl. 6)). Wagler's Toucanet. no type loc. [= Guerrero and Oaxaca, Mexico].

Aulacorhynchus prasinus (Gould 1833). Northern Emerald Toucanet.
   A. p. prasinus (Gould 1833). Mexico [= Valle Real, Oaxaca].
   A. p. warneri Winker (2000). Volcán San Martín, Sierra de Los Tuxtlas, Veracruz, Mexico.
   A. p. virescens Ridgway (1912:88). Chasniguas, Honduras.
   A. p. volcanius Dickey and van Rossem (1930:53). Volcán de San Miguel, Dept. San Miguel, El Salvador.
Notes: *A. p. stenorhabdus* (Dickey and van Rossem 1930:52) and *A. p. chiapensis* (Brodkorb 1940) are considered synonyms of *A. p. virescens*; variation among them appears to be clinal (see also Monroe 1968). Wetmore (1941, notes in USNM) considered *chiapensis* as "doubtfully separable," but recognized *stenorhabdus*. See notes under *A. albivitta* regarding the English common name.

Aulacorhynchus caeruleogularis (Gould 1854:45). Blue-throated Toucanet.
   A. c. caeruleogularis (Gould 1854:45). Veragua [, Panama] [= Boquete, Chiriquí; Wetmore 1968:508].
   A. c. cognatus (Nelson 1912:4). Mount Pirri (at 5,000 feet altitude) head of Rio Limon, eastern Panama.
Notes: *A. c. maxillaris* (Griscom 1924:2) is considered a synonym of *A. c. caeruleogularis* (cf. Wetmore 1968:509). See Wetmore (1968) for citation of the name *caeruleogularis* appearing first in the Zoologist in 1853; no description appears there, however, the reference being a report of what occurred at two meetings in February 1853 ("D.W.M." 1853). Olson (1997) provided more notes on these occurrences in relation to Gould.

Aulacorhynchus albivitta (Boissonneau 1840:70). Southern Emerald Toucanet.
   A. a. lautus (Bangs 1898:173). San Miguel [, Sierra Nevada de Santa Marta], Colombia.
   A. a. griseigularis Chapman (1915:639). Santa Elena (alt. 9000 ft.), Cen. Andes, Antioquia, Col.
   A. a. phaeolaemus Gould (1874:184). Concordia, in Columbia [sic], and Merida, in Venezuela [= Concordia, Antioquia, western Colombia; Hellmayr 1911:1213].
   A. a. albivitta (Boissonneau 1840:70). Santa-Fé de Bogota [, Colombia].
Notes: Chapman (1917) inexplicably omitted the occurrence of the species (endemic subsp. *lautus*) in the Santa Marta region. More detailed study is needed to resolve problems in the status, relationship, distributions, and nomenclature of *phaeolaemus* and *griseigularis* (see Chapman 1917, Haffer 1974). The English name for this species given by Cory (1919:377), White-throated Toucanet, is only appropriate for the subspecies *albivitta*, and thus is more appropriate at the species level for *A. prasinus* (*sensu stricto*, though not used there). The other subspecies of *albivitta* are all grayish or grayish-blue on the throat. Del Hoyo and Collar (2014) suggested Grayish-throated, but this overlooks both white-throated birds and those with blue in the throats.

Accordingly, I have suggested more fitting English names for this species and *A. prasinus*.

Aulacorhynchus atrogularis (Sturm *in* Gould 1841:heft 2, pl.2 & text). Black-throated Toucanet.
   A. a. cyanolaemus (Gould 1866:24). Loxa [=Loja] in Ecuador.
   A. a. atrogularis (Sturm *in* Gould 1841:heft 2, pl.2 & text). Andes of Peru [=Chunchamayo, central Peru; Cory 1919:380).
   A. a. dimidiatus (Ridgway 1886:93). No loc.; suggested by O'Neill and Gardner (1974:703) to be along the eastern foothills of the Andes of central southern Peru.
Note: Recognition of *A. a. dimidiatus* follows O'Neill and Gardner (1974). *A. a. cyanolaemus* is blue-throated (Fig. 1).

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Submitted by: Kevin Winker

Date of Proposal: 23 November 2016

Treat the subspecies (A) *spectabilis* and (B) *viridiceps* as separate species from *Eugenes fulgens* (Magnificent Hummingbird)

Background:

Currently, we recognized a single species in the hummingbird genus *Eugenes*: Magnificent Hummingbird, *E. fulgens*, with the two subspecies recognized in AOU (1998), as groups (the *fulgens* group, from SW USA to n-c. Nicaragua, and the *spectabilis* group in the mountains of Costa Rica and w. Panama).

The two groups were treated as separate species ("Rivoli's Hummingbird" and "Admirable Hummingbird") by Ridgway (1911), Cory (1918), but Peters (1945) treated them as conspecific without comment. This treatment was followed by all subsequent authors, including Dickinson & Remsen (2013), who noted that the two subspecies might merit treatment as separate species, citing Powers (1999) species account in Schuchmann's HBW chapter and Renner and Schuchmann (2004).

New Information:

Renner and Schuchmann (2004) illustrated and quantified the plumage and morphological differences between the two subspecies, and concluded: "Taxonomy. Both taxa of *Eugenes fulgens* show distinct plumage patterns and no evidence of intergradation, indicating that there is no genetic exchange between the population patches of *E. f. fulgens* and *E. f. spectabilis*. Therefore, the taxa should be treated as species, because of their clear disjunct distribution."

Thus, this is essentially a PSC argument that could be applied to any two disjunct taxa. Lack of phenotypic evidence for gene flow between two disjunct, sedentary taxa only confirms that … they are disjunct, sedentary taxa, nothing more. Yes, northernmost populations of *fulgens* are migratory, but there is no evidence for migration in the bulk of the range of nominate *fulgens*. Schuchmann, who is highly knowledgeable concerning phenotypic variation in hummingbirds, could/should have extended the argument for ranking both populations as separate subspecies by pointing out that the differences between them are (or aren't?) within the rank of differences between parapatric or sympatric hummingbird species or even between allopatric taxa that are (or aren't?) currently treated at the species level, but did not.

Populations of *E. fulgens* sensu stricto south of the Isthmus of Tehuantepec were treated as a separate subspecies, *E. f. viridiceps*, by Peters (1945), but not by Ridgway (1911) or Schuchmann (1999 HBW). Boucard's OD of *viridiceps* indicated that it was less blackish than nominate *fulgens* … thus varying in the direction of *spectabilis*. Although Peters (1945) gave no reason for his treatment of *spectabilis* as conspecific with *fulgens*, I strongly suspect that he viewed *viridiceps* as somewhat intermediate, right or wrong, between the two, and thus used this as justification for the lump. Although Renner and Schuchmann (2004) found no characters supporting recognition

of *viridiceps*, this was based on only two specimens from Guatemala: "The two male specimens from Guatemala (F 91 and F 92, Fig. 1) show no plumage variation in comparison to the individuals from the northern taxon *E. f. fulgens.*" They also found that these two specimens are closer in measurements to nominate *fulgens* than to *spectabilis*.

Zamudio-Beltrán and Hernández-Baños (2015) sequenced nuclear (*BFib*, *ODC*, *MUSK*) and mitochondrial (*ND2, ND4, CR*) DNA of 16 individuals fairly evenly distributed among the three populations. They found that 5 individuals of *spectabilis* were sister to all other individuals (BPP > 0.95), but that nominate *fulgens* and *viridiceps* were somewhat admixed.

Then, they analyzed the data using *Beast and Bayesian species delimitation and found that three groups were strongly supported (BBP = 1.00) corresponding to the three taxa. From this they concluded that the three taxa should be treated as three separate species. They followed previous authors in regarding *viridiceps* as undiagnosable by plumage, and thus used the techniques above as the sole basis for assigning species rank.

Analysis and Recommendation:

Despite two new studies, I'm not sure much progress has been made. Renner & Schuchmann's conclusion that *viridiceps* is not diagnosable is based on N=2 specimens, and no data were actually presented. Perhaps the unpublished MS thesis by Tovilla-Sierra cited by Zamudio-Beltrán and Hernández-Baños (2015) quantifies plumage variation sufficiently to confirm this, but the wording in the latter is not clear about this. Anyway, at this point I conclude that there are no published data concerning phenotypic diagnosability of *viridiceps*. So, I looked at specimens here at LSU, and although did not see any convincing differences, I do think I see a tendency for the black ventral area of *viridiceps* to be slightly reduced in the lower belly relative to that of nominate *fulgens* (but a larger N with better specimens is needed; perhaps Boucard (and Peters?) were on to something.

Concerning the genetic data, I will leave it to those familiar with these species delimitation techniques to explicate the contradictory results between those analyses and those in Fig. 1 below. Regardless, assuming that the plumage differences have a genetic basis, then we already know that nominate *fulgens* must differ genetically from *spectabilis*. Likewise, just from biogeography, it is expected that those two would differ genetically at the loci sampled even if there were no plumage differences. So, I'm not sure what the published genetic data contribute except to reaffirm these predictions. With respect to *viridiceps*, assuming this presumably sedentary population is isolated from both of the other taxa, then some degree of genetic differentiation is expected also. Zamudio-Beltrán and Hernández-Baños's (2015) results confirm this.
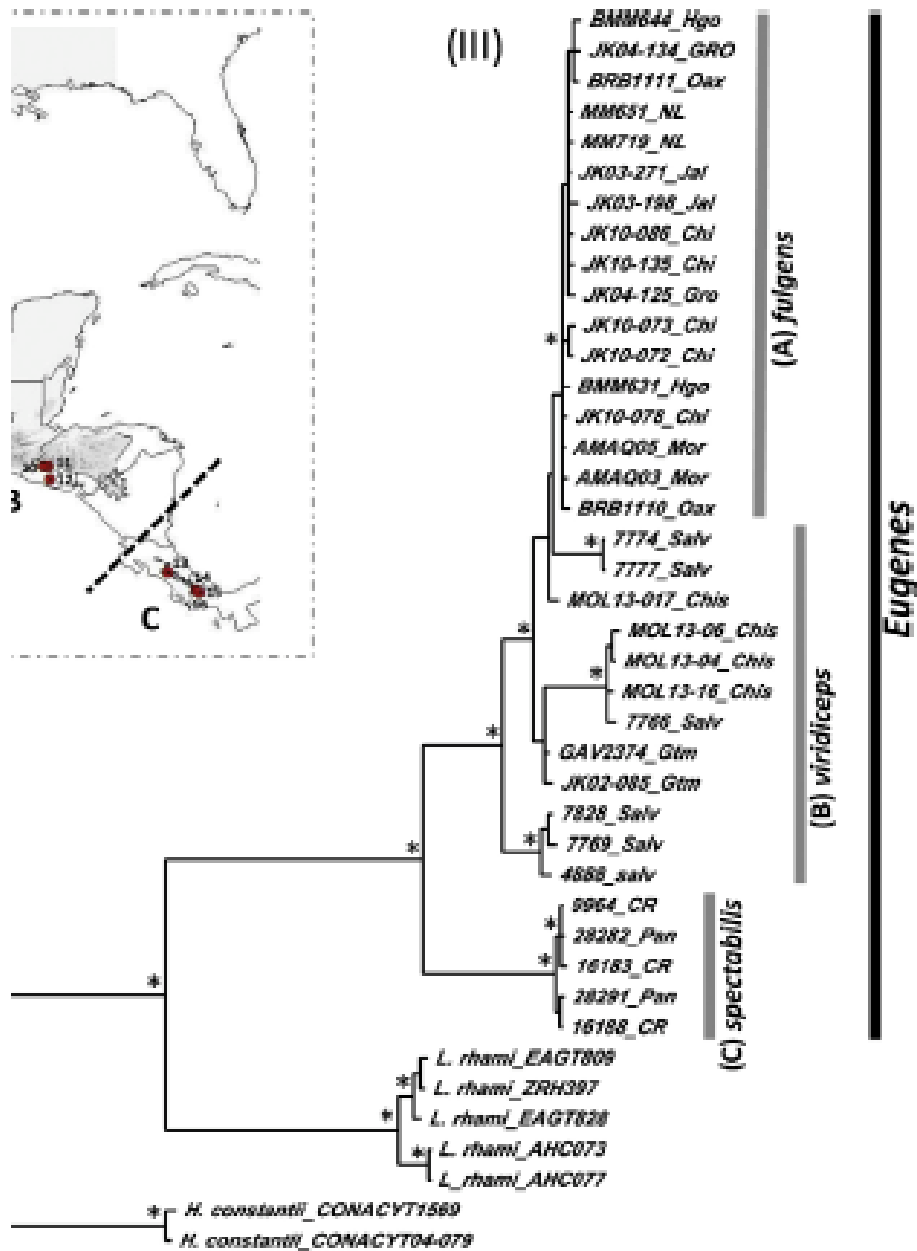
Fig. 1c = "Phylogenetic Bayesian Inference reconstruction from 34 individuals from *Eugenes fulgens* complex using mitochondrial and nuclear markers (ND2, ND4, RC, BFib, MUSK, and ODC). Posterior probabilities P > 0.95 are shown (*). Above right is represented the main different groups recovered on the phylogenetic reconstruction according to their geographic distribution and the subspecies proposed (A: *fulgens*, B: *viridiceps* [sic], C: *spectabilis*)." [Note that the *MPE* editorial staff, as is typical, let the authors down on English wording (and typos).]

As for the relevance of all this to species limits, I don't see much. It's been known for more than a century that the allopatric taxa, *fulgens* (with or without *viridiceps*) and *spectabilis* are diagnosable taxa. Whether to rank them as species or subspecies is the standard problem for the BSC when dealing with allopatric taxa. The currently available data provide no answers in my opinion. What is needed, again in my opinion, are data

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on voice and display to assess whether these taxa have diverged to the point associated with lack of gene flow in parapatric and sympatric hummingbird species. Barring that, a comparative analysis of degree of plumage divergence in related parapatric hummingbird species and subspecies would also get at the question of whether these taxa have diverged to the point associated with species-level differences in hummingbirds.

Although Renner & Schuchmann didn't do it, a case can be made that these two taxa differ as much as any two allotaxa ranked as separate species. They differ notably in gorget color (see below), which would be unusual for taxa ranked as subspecies. They differ substantially in body coloration, and the depth of the fork in the tail. The combination of all these character differences is not consistent with their ranking as subspecies in a comparative context – think, for example, of the subtle differences between Rufous and Allen's hummingbirds.

Here are ventral views of some specimens of nominate *fulgens* (bottom) and *spectabilis* (top); you can see the blackish underparts of nominate *fulgens* vs. the greenish underparts of *spectabilis:*

Here are additional ventral views of some specimens of nominate *fulgens* (right) and *spectabilis* (left); again, you can see the blackish underparts of nominate *fulgens* vs. the greenish underparts of *spectabilis*, and the differences in gorget color:

Here are dorsal views of some specimens of nominate *fulgens* (right) and *spectabilis* (left); you can see the greater extent of blackish on the upperparts of nominate *fulgens*, and the slight difference in hindcrown color:

Although the newly published data don't add much, in my opinion, I think a case can be made to return to Ridgway's classification over that of Peters. The long track record of reversal of Peters' lumps to restore Ridgway's species limits is extensive. Add to that that Schuchmann, an experienced hummingbird taxonomist, also favored a reversal of the Peters lump.

This proposal separates the two taxa for voting:

(A) Elevate subspecies *spectabilis* to species rank. I tentatively recommend a YES on this one, not because of the new data, which in my view add very little, but because Peters' lump was never justified for these two strongly differentiated (by hummingbird standards) taxa.

(B) Elevate subspecies viridiceps to species rank. I strongly recommend a NO. This is probably isn't even a valid subspecies, much less species. That there is genetic structure among the populations within the fragmented range of *spectabilis sensu lato* differ is expected; given that this taxon consists of populations isolated in several montane areas, any result other than this would have been surprising.

English Names:

If A passes, then we need two new names for the daughter species of Magnificent Hummingbird. "Rivoli's Hummingbird" would be the obvious choice for *fulgens*; in use since Ridgway, it was the name used by the AOU until the 1983 AOUCL. A separate proposal would be needed, in my opinion, for the English name of *spectabilis*. The options would be to (1) retain Magnificent Hummingbird solely for *spectabilis*, which would create perpetual confusion; (2) revert to Ridgway's "Admirable Hummingbird," which sounds very odd to me (and for which I cannot figure out the derivation other than a loose translation of *spectabilis*); or (3) concoct a novel name.

Literature Cited:

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Submitted by: Van Remsen

Date of Proposal: 26 November 2016

Elevate *Turdus rufopalliatus graysoni* to species rank

Background:

Turdus rufopalliatus (Rufous-backed Robin) occurs in western Mexico from Sonora to Chiapas and on the Tres Marías archipelago. Dickinson & Christidis (2014) recognized three subspecies: (1) nominate *rufopalliatus* from Sonora to Puebla, (2) *interior* in the Balsas basin, from Michoacán to Puebla, and (3) *graysoni* on the Tres Marías, and also in coastal Nayarit according to A. R. Phillips (1981, 1991), where sympatry with nominate *rufopalliatus* was used by Phillips (1981) to elevate *graysoni* to species rank. The latter was treated as a separate species (Grayson's Robin) by Ridgway (1907), but Hellmayr (1934) treated it as a subspecies of *rufopalliatus* with the following statement:

> "This is merely a pale, large-billed race of the mainland bird. Certain individuals of the latter in worn breeding plumage closely approach it in coloration, and it is no doubt on such a specimen that Nelson's record of *T. r. graysoni* from Santiago, Nayarit, was based."

Subsequently, all standard references have followed Hellmayr, including those after Phillips (1981), except for Sibley and Monroe (1990) and Howell and Webb (1995), who tentatively treated it as a separate species "*Turdus (rufopalliatus?) graysoni*" but clearly were cautious ("Status needs further study" and "may be resident" on mainland). I wrote a NACC proposal in 1999 to recognize *graysoni* as a separate species based on Phillips's paper, with the following conclusion:

> "<u>Recommendation</u>: I think that the case for a syntopic, resident mainland population of *graysoni* is weak. So far, we do not even have specimen evidence of year-round presence on the mainland, much less breeding. Yes, the number of specimens rules out casual wandering in my opinion, but until *graysoni* is shown to breed there, I think the conservative treatment is to consider it a non-breeding visitor there, with one anomalous late June record. If this is correct, then their seasonal overlap is irrelevant to species limits. Also, the absence of any comparative information on voice or anything else other than plumage prevents any real analysis of differentiation of *graysoni* vs. *rufopalliatus*. As for the plumage difference, the degree of paleness of *graysoni* vs. *rufopalliatus* is roughly comparable to the paleness of the isolated southern Baja population of Am. Robin (*T. m. confinis*) relative to "regular" Am. Robin. As long as we continue to treat *confinis* (San Lucas Robin) as a subspecies of Am. Robin (right or wrong), then treating *graysoni* as a subspecies of *rufopalliatus* represents a consistent philosophy in treatment of isolated, pale thrushes. In other words, I find it difficult to justify treating *confinis* as a subspecies (at least for which tantalizing vocal differences were noted by Howell and Webb) but *graysoni* as a species. All in all, I regard the case for splitting them as weak, especially because I do not think that there are any other Tres Marías endemics ranked as species.

The proposal did not pass. Phillips (1981) himself pointed out that the Tres Marías representative of *Parula*, *P. p. insularis*, migrates to the mainland, so another species shows a pattern of migrating from the islands to the mainland; Phillips treated *insularis* as subspecies of *P. pitiayumi*. The difference in his treatment of *graysoni* as a species is based largely, as far as I can tell, on his conclusion that the June specimen from mainland Nayarit represented a breeding bird. Even Phillips noted the tenuous nature of this conclusion (8 specimens 4 Feb. to 12 May, 1 on 20 June).

Incidentally, *graysoni* shows the typical pattern of an insular representative: duller, less dimorphic, and larger-billed than its mainland counterpart (and was certainly one of the examples that P. R. Grant used in his classic paper on island differentiation patterns).

Evidently nothing is known about the vocalizations of *graysoni*. I could not find any recordings online (Xeno-canto or Macaulay).

New Information:

Montaño-Rendon et al. (2015) used mtDNA sequence data (cyt-b, ND2) from 14 individuals from localities throughout the range of the species, including all three subspecies and including coastal Nayarit. They found a deep divergence between island samples and all mainland samples, including coastal Nayarit. The two groups were reciprocally monophyletic (but in my opinion, with N=14, statements concerning reciprocal monophyly are premature). Montaño-Rendon et al. also quantified and confirmed morphometric differences between *graysoni* and mainland birds.
They made their case for species rank as follows:

> "Insular populations of *T. rufopalliatus* in the Tres Marías Islands are distinguished by a particular combination of traits (Nelson 1899; Ridgway 1907; Hellmayr 1934; Stager 1957; Grant & Cowan 1964; Grant 1965; Phillips 1981; Navarro-Sigüenza & Peterson 2004, this study). Both sexes in the islands are similarly colored, and are duller than their mainland counterpart, where females have duller plumage than males, but still brighter than island birds (Grant 1965). This coloration pattern, in which the mainland birds are brighter than the island ones (see Peterson 1996), is also present in other birds in the Tres Marías Islands (Grant 1965; Cortés-Rodríguez et al. 2008). Coloration and other diagnostic characters including size (Grant 1965, this study) and mtDNA (this study), suggest that the insular populations of *T. rufopalliatus* could be treated as a distinct evolutionary unit under both the Phylogenetic (McKitrick & Zink 1988) and Evolutionary (Wiley & Mayden 2000) species concepts. Moreover, Phillips (1981) reported not having found any hybrids on scientific collections or in birds in coastal Nayarit, where insular and continental forms apparently are occasionally found in sympatry. Evidence also suggests that both island and mainland groups could also conform to the Biological Species Concept definition (Mayr 1963); however, such a decision must wait until data on potential hybridization are available (Mayr 1963; Gill 2014)."

Analysis and Recommendation:

I recommend a NO on this one for several reasons. First, the evidence for sympatry on the mainland is highly tenuous and requires substantiation. Second, vocalizations have not been studied. Song and call note differences led to the split of *Catharus bicknelli* from *C. minimus*, which differ less in terms of phenotype from each other than do the two taxa under consideration (although I have my doubts about this split). In contrast, Hermit Thrush (*C. guttatus*) subspecies differ more in terms of size and plumage than the two taxa under consideration, yet are maintained as one species because, as far as is known, all populations have extremely similar calls and call notes. (By the way, we need to evaluate all the recent evidence for a two-way split in *C. ustulatus*). Third, unless sympatry can be confirmed, I don't think the genetic data can be interpreted either way in terms of taxonomy. The Tres Marías and the mainland are separated by 100 km of ocean and (acc. to references cited by Montaño-Rendon et al.) were submerged until ca. 120,000 years ago. I would surprised, even with occasional migrants or wanderers to the mainland, that some genetic differences did not accrue post-colonization of the Tres Marías, particularly given the tendency for small island populations to differentiate rapidly. Certainly the phenotypic differences, likely products of selection, must have a genetic basis as well. Whether *graysoni* has diverged to the level associated with species rank in thrushes is an open question. The bar for this is very low in phenotype (as in Bicknell's Thrush), so a study of vocalizations is what is needed, in my opinion.

English names: Grayson's Robin is the English name associated with this taxon.

Literature Cited:

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Phillips, A. R. 1991. The Known Birds of North and Middle America. Part II. Allan R. Phillips, Denver, Colorado, 249 pp.

Submitted by: Van Remsen

Date of Proposal: 8 December 2016

Recognize newly described species *Arremon kuehnerii*

Navarro-Sigüenza et al. (2013) described a new species of *Arremon* brushfinch in the *A. brunneinucha* group, *Arremon kuehnerii.* The name is based on the holotype and three paratypes from Guerrero in southwestern Mexico; a sample of 65 specimens from the range of the new taxon was used for morphometric and plumage comparisons to *A. b. suttoni* (central and western Oaxaca) and *A. virenticeps.* The genetic analyses were based on 6 individuals of *kuehnerii*, 2 *A. virenticeps*, 4 *A. b. suttoni*, and 2 nominate *Arremon brunneinucha* from the Sierra Madre Occidental.

The impetus for giving the Guerrero population taxonomic status is that although it is phenotypically identical (as confirmed in Navarro-Sigüenza et al.'s analysis) to *A. b. suttoni* and thus traditionally classified as that taxon, genetic data revealed that they cluster with adjacent *Arremon virenticeps.* Cadena et al. (2007) found that *A. brunneinucha* was paraphyletic with respect to *Arremon virenticeps*, with *virenticeps* the likely sister to nominate *brunneinucha*. Navarro-Sigüenza et al. (2008) found similar results (although they did not cite Cadena et al. despite publishing subsequently in the same journal); with better population sampling in Mexico, Navarro-Sigüenza et al. found that the Guerrero population of *A. b. suttoni* was sister to *A. virenticeps* rather than Oaxacan populations of *A. b. suttoni* (where the type locality is). The purpose of Navarro-Sigüenza et al. (2013) was to follow up those results with an analysis of 4 nuclear gene regions. Those data also show those same results (and that the *virenticeps-kuehnerii* sister relationship itself is embedded in *A. brunneinucha*).

Clearly, plumage-based taxonomy does not reflect the phylogenetic history revealed by neutral loci. Here are some specimen photos overlain on a map of Mexico: from NW to SE along the Pacific coast are *virenticeps*, *kuehnerii*, and *suttoni*, with nominate *brunneinucha* on the Atlantic slope. As you can see, ventrally, *virenticeps* is the outlier in lacking a breast band and being vaguely streaked; nominate *brunneinucha* is darker than the other two; *kuehnerii* and *suttoni* are identical --- the differences you see are artifacts of individual specimen preparation. Dorsally, all four are identical except that *virenticeps* has a striped greenish crown (other differences are artifacts of individual specimen preparation).

Navarro-Sigüenza et al.'s (2013) solution to this interesting result was to treat the Guerrero population as a separate species, for which they provided the new name, *kuehnerii*. Thus, we have the world's first species diagnosed strictly by genetic characteristics and indistinguishable from the taxon in which the population was formerly included.

For those not familiar with geographic variation in these *Arremon* brushfinches, plumage variation from population to population is dramatic, with repeated themes in distant populations; the breast band in particular "comes and goes". These phenotypic patterns were the catalyst for Chapman's classic paper and have led to modern investigations by Navarro and colleagues and Daniel Cadena and colleagues (Cadena et al. 2007), who

subsequently found that many of these subspecies had diverged strongly in vocalizations, to the degree associated with species rank (Cadena and Cuervo 2010).

Analysis and Recommendation:

It seems to me that Navarro-Sigüenza et al. (2013) have established: (1) the Guerrero population cannot be phenotypically distinguished from the taxon in which it was always included, *A. b. suttoni*, (2) it differs strongly in neutral loci from *A. b. suttoni*, and (3) it is more closely related to another species *Arremon virenticeps*. I suppose it was only a matter of time, given the stochastic factors that contribute to differentiation at the population level. That these factors produce situations that do not fit tidily into our artificial taxonomic boundaries is predictable. This is a very cool finding, in my opinion, that did not get enough attention. Regardless, what do we do, taxonomically? Dickinson & Christidis (2014) "solved" this by footnoting that *kuehnerii* was included in *A. brunneinucha* without assigning it to a subspecies and not acknowledging that genetic data indicate a closer relationship to *Arremon virenticeps.*
I do not have a solid recommendation on this. Recognizing at the species level a taxon for which there are no phenotypic characters that distinguish it from other taxa would be a radical move at this time, and so I recommend a NO. Footnotes in the published version of a classification outlining the issue would be the way I would handle it at present; trying to assign the Guerrero population to *suttoni* based on phenotype ignores that it is closer to *virenticeps* genetically, at least in terms of neutral loci (and that's why Dickinson & Christidis (2014) did not do this specifically.

The broader problem is trying to apply Linnaean taxonomy to gene-based population-level data. Although application of the criterion of monophyly to taxa above the species level is universal, it is complicated at the population level, where mosaic patterns of character distribution and past and ongoing gene flow make "monophyly" difficult to define. In fact, Hennig himself did not use the term at the population level because of this problem (see Rieppel 2010). With increasingly sophisticated genetic sampling of bird populations, we as a committee have come to terms on policy. In my opinion, paraphyly at the species level is not only acceptable but also inevitable, as outlined long ago by Funk & Omland (*ARES* 2003).

This reminds me that I also need to work on a separate proposal dealing with the paraphyly of *A. brunneinucha* (with respect to *A. virenticeps).*

Voice has not been studied, as far as I know, in any of these populations, and given the Cadena and Cuervo's (2010) results in a congener with voice, this needs to be investigated.

English names:

No English name was recommended in the proposal. If the proposal passes, then "Guerrero Brushfinch" would be the obvious choice, although "G3PDH Brushfinch" has a strong appeal in reflecting the reality of the situation.

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Submitted by: Van Remsen

Date of Proposal: 15 December 2016

Revise the classification of the Icteridae:
(A) Add seven subfamilies; (B) Split *Leistes* from *Sturnella*; (C) Resurrect
***Ptiloxena* for *Dives* atroviolaceus; (D) Modify the linear sequence of genera**

Background:

Our current classification of the Icteridae has remained essentially unchanged since the Peters check-list and is based largely on historical momentum. We do not recognize any subfamilies, and the sequence of genera is as follows:

Dolichonyx
Agelaius
Nesopsar
Chrysomus
Sturnella
Xanthocephalus
Dives
Euphagus
Quiscalus
Molothrus
Icterus
Amblycercus
Cassiculus
Cacicus
Psarocolius

New Information:

Scott Lanyon's lab has been working on a gene-based phylogeny of the Icteridae for a couple of decades. This culminated in the paper by Powell et al. (2014), which built a comprehensive phylogeny for the family based on a variety of nuclear and mitochondrial loci for all 108 species, including whole mitochondrial genome sequences for 23 species. Remsen et al. (2016) used these data to propose a revised classification of the family:
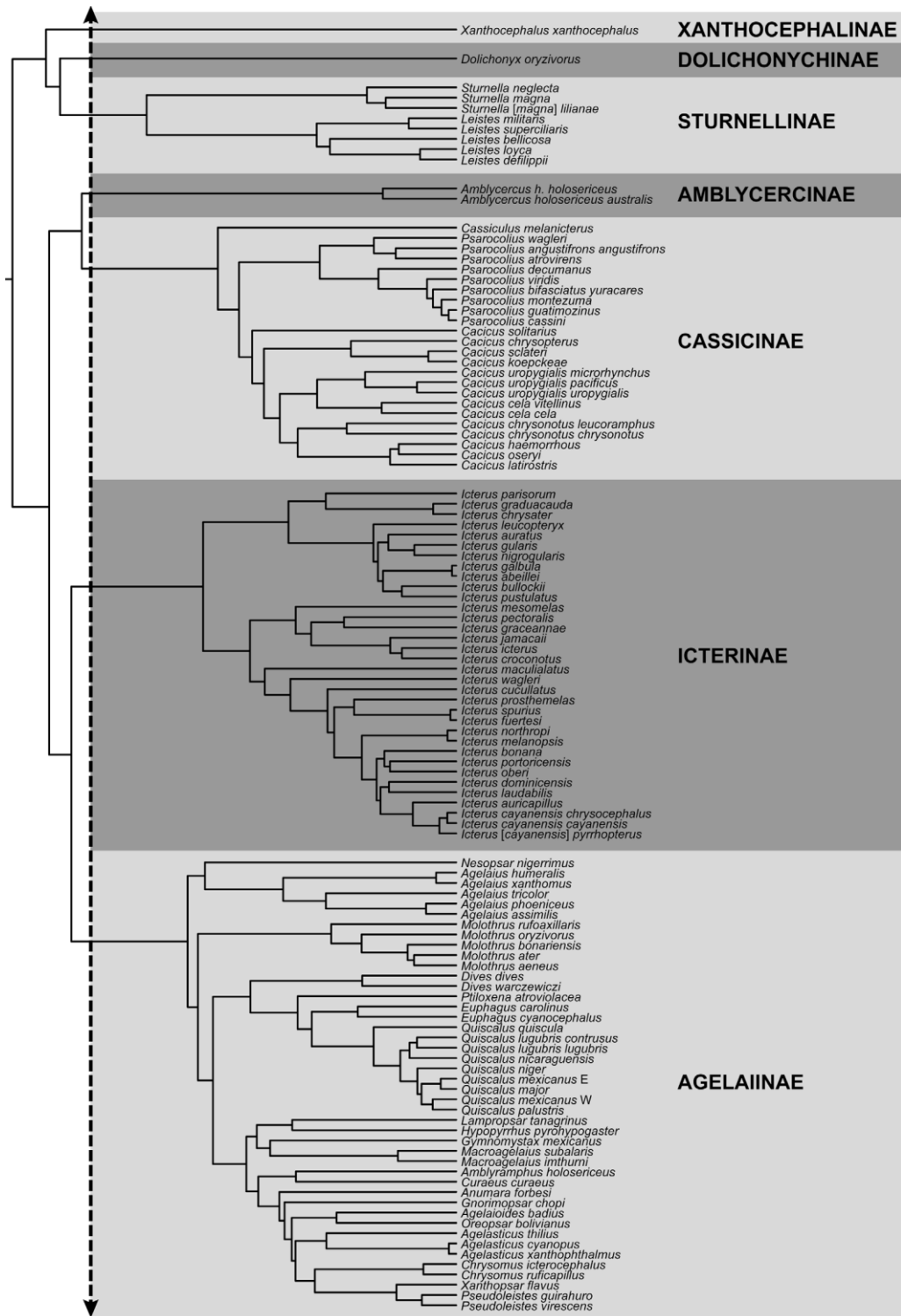
FIGURE 1. Phylogeny of the New World blackbirds (Icteridae) inferred from mitochondrial and nuclear DNA sequences of 118 taxa (outgroups not shown)—topology taken from the best tree found under maximum likelihood by Powell et al. (2014; fig. 4); branch lengths estimated in BEAST 1.7.4 (lognormal uncorrelated relaxed clock model for mtDNA, strict clock for nDNA; Drummond et al. 2012) using the same data and mitochondrial partitioning as Powell et al. (2014), but nuclear sequences partitioned by locus. Dashed line marks the threshold used to assign subfamily ranks. Species are listed in the order given by this tree topology and (starting from the deepest node) following the conventions of listing the taxon in the least-diverse clade first, or for equally diverse clades, the northwestern-most lineage first.

The biggest surprise is that *Xanthocephalus* (Yellow-headed Blackbird) isn't just another yellow-headed blackbird but an old lineage that is sister to all other icterids. The other major surprise is that *Amblycercus* (Yellow-billed Cacique) is sister to all other caciques and oropendolas. As can be seen in the tree, the family separated into seven lineages relatively early in its history, all roughly 8 million years old. Given this deep divergence, we proposed subfamily rank for each of the seven lineages.

Most of the revisions in generic boundaries had been published in previous papers and have already been dealt with by NACC (e.g., expanded *Molothrus*) and SACC. The exception was the proposed split of *Leistes* from *Sturnella*. (The authors disagreed among themselves on whether to split *Icterus* into two genera, but such a split would require a new genus name.) We also devised a linear sequence to reflect these phylogenetic data, following standard conventions.

Analysis and Recommendation:

A. Recognition of seven subfamilies. Note that the name Cassicinae was corrected to Cacicinae by Schodde & Remsen (2016). I recommend a YES on this because these designations mark seven divergent lineages. I think the only area for debate, other than whether to recognize any subfamilies at all, is whether to place *Amblycercus* in its own subfamily vs. including it in same subfamily as the caciques and oropendolas. We decided to do this because this split is as old as the other major splits in the family and to also call attention to how divergent this bird is from other "caciques."

B. Split *Leistes* from *Sturnella*. The South American group was previously treated in either *Leistes* or *Pezites* until Short (1968) provided rational for the merger by pointing out the plumage and morphological similarities among the meadowlarks. What Short did not take into account (and in some cases could not have known in the pre-gene-based phylogenetic era) was how conservative plumage evolution is in the family in general. For example, as shown by the Lanyon lab, the South American blackbirds long included in *Agelaius* are only distantly related to them despite similar plumage features. As you can see from the tree, the split between North American and South American members of broadly defined *Sturnella* is deeper and thus presumably older than that between any two genera in the tree. Therefore, I recommend a return to the pre-Short treatment of the South American species in a separate genus. This falls under NACC purview only by virtue of one species, *S. militaris*, barely occurring in our area; this species and its southern allospecies *S. superciliaris* are unmeadowlark-like in morphology and behavior (when the SACC version of this proposal is submitted, I will likely propose restoration of *Pezites* for the more-meadowlark-like group). I recommend a YES on splitting *Leistes* from *Sturnella* (which has already been done by Dickinson & Christidis 2014).

C. Resurrect *Ptiloxena* Chapman, 1892, for *Dives atroviolaceus*. As can be seen in the tree above, *Dives* as currently constituted is paraphyletic. The Cuban Blackbird is sister to *Euphagus*. As noted by Powell et al. (2014) and Remsen set al. (2016), this requires resurrection of *Ptiloxena* for this species (which has already been done by Dickinson & Christidis 2014). *Ptiloxena* is feminine whereas *Dives* is masculine (Dickinson &

Christidis 2014), requiring a change in the variable ending of the species name to *Ptiloxena atroviolacea.*

D. <u>Revise linear sequence</u>. Remsen et al. (2016) used the standard conventions for converting a phylogeny to a linear sequence (e.g., taxa from least-diverse branch first; allotaxa arranged NW to SE) to produce the following sequence (here pruned to reflect only the genera in NACC area). I recommend a YES for this.

    Xanthocephalus
    Dolichonyx
    Sturnella
    Leistes
    Amblycercus
    Cassiculus
    Psarocolius
    Cacicus
    Icterus
    Nesopsar
    Agelaius
    Molothrus
    Dives
    Ptiloxena
    Euphagus
    Quiscalus
    Chrysomus

Literature Cited:

Dickinson, E. C., and L. Christidis (eds.). 2014. The Howard and Moore complete checklist of the birds of the World. Vol. 1. Passerines. Aves Press, Eastbourne, U.K., 752 pp.

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Schodde, R. and J. V. Remsen, Jr. 2016. Correction of Cassicinae Bonaparte, 1853 (Aves, Icteridae) to Cacicinae Bonaparte, 1853**.** Zootaxa 4162:188**.**

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Submitted by: Van Remsen

Date of Proposal: 21 December 2016

**Revise familial limits and the linear sequence of families
within the nine-primaried oscines**

If approved, this proposal would reassign six warbler species to different families, resurrect some previously used families, and recognize three new families of nine-primaried oscines. Pending acceptance of those familial classifications, this proposal would also change the linear sequence of nine-primaried oscine families to reflect our growing knowledge of their evolutionary relationships.

Background:

The nine-primaried oscines comprise a widespread, diverse assemblage of songbirds that accounts for nearly 10% of all birds. In our current taxonomic classification, numerous taxa are included in the linear sequence as *incertae sedis*, which reflects our uncertainty of the phylogenetic placement of these taxa within the avian tree of life. In addition, six species assigned to Parulidae (*Zeledonia coronata*, *Icteria virens*, *Xenoligea montana*, *Microligea palustris*, *Teretistris fernandinae*, and *Teretistris fornsi*) do not show a close relationship to wood warblers and can now be assigned elsewhere. A recent series of publications has improved our understanding of evolutionary relationships within and among lineages of nine-primaried oscines, providing an opportunity to improve our current classification.

New Information:

Barker et al. (2013) conducted a multilocus systematic study of nine-primaried oscines in which they sampled exemplars from every genus of Cardinalidae, Emberizidae, Icteridae, Parulidae, and Thraupidae. The study also sampled multiple exemplars of genera known to lack monophyly and genera not recognized by the current taxonomy for a total of 204 ingroup taxa. Barker et al. (2013) also included representatives of Fringillidae and Motacillidae as outgroup samples for a total of 213 taxa in the complete data set. The study included two mitochondrial gene regions (ND2 and cyt *b*) in addition to one exon (RAG1) and three introns (MB-I2; FGB-I5; sex-linked ACO1-I9). The authors conducted multiple phylogenetic analyses on different partitions of the data set, including analyses on each gene region separately, a concatenated analysis, and a species tree analysis (Fig 1). The authors also conducted time-calibrated phylogenetic analyses and considered associations between the stem age of families and their species richness (Fig 2). A later study (Barker et al. 2015) combined these data with mitochondrial data from additional species resulting in a total data set of 791 of an estimated 832 species involved in this large clade (95% sampling). Barker et al. (2015) used the concatenated and species tree phylogenies of Barker et. al (2013) to create a "pseudoposterior" distribution of species-level supertrees. In this proposal, we focus our discussion on the relationships presented by Barker et al. (2013) to propose a new familial classification for the nine-primaried oscines. In proposing a new familial classification, we try to minimize changes to the current classification unless strongly

supported nodes imply that the current classification is inaccurate. We consider support for recognizing each family in our proposed classification and present them below in a revised linear sequence (see also Table 1). Type designations and diagnoses for all new families are given in the Appendix of Barker et al. (2013), and these families are already in use by Winkler et al. (2015) and Lovette and Fitzpatrick (2016).
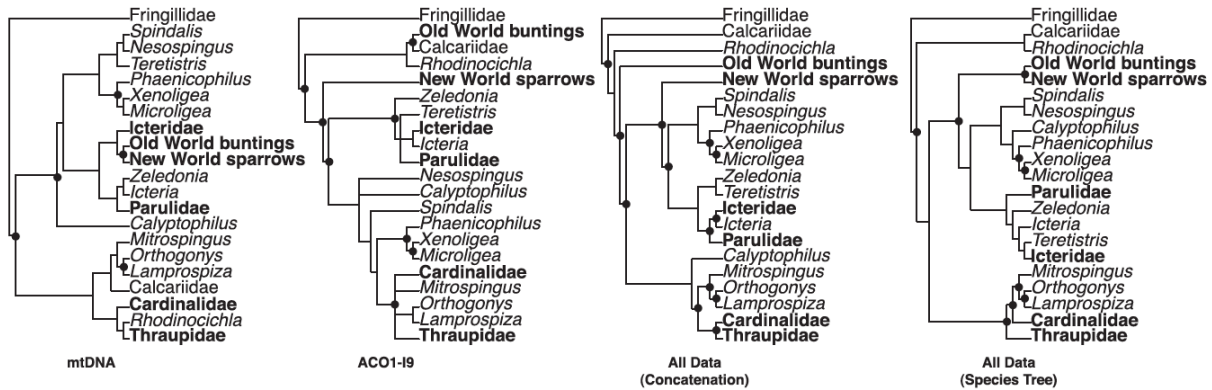
Figure 1: Phylogenetic analyses of Barker et al. (2013) regarding relationships among nine-primaried oscines. Phylogenies presented here are based on mtDNA, sex-linked ACO1-19, concatenated data sets, and species tree analyses. Dark circles indicate strongly supported nodes.
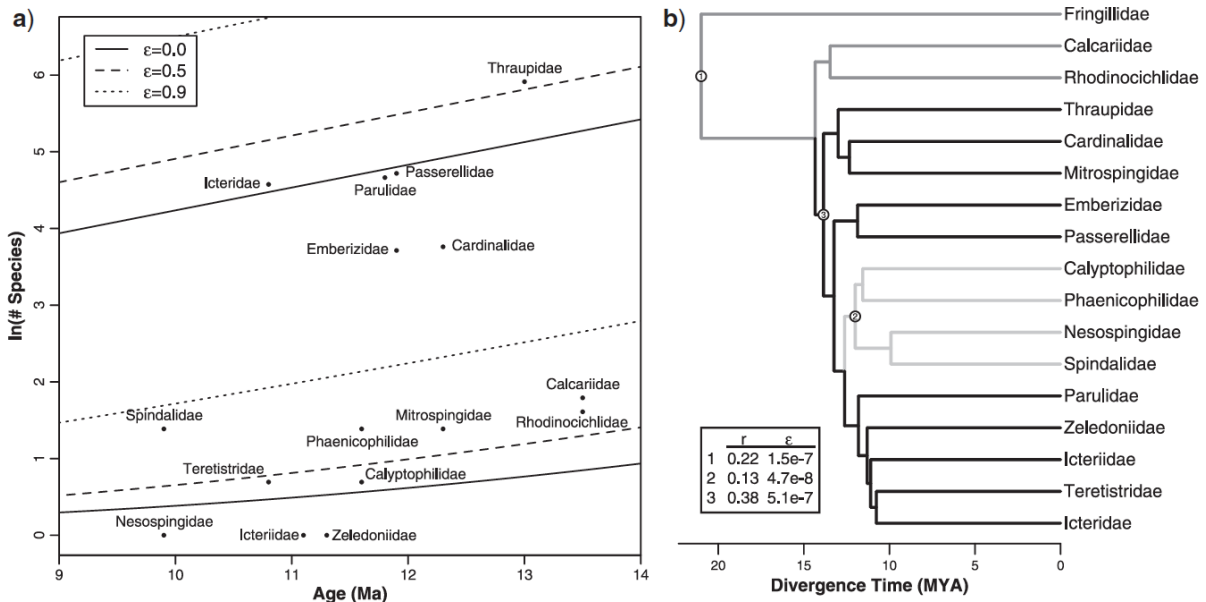
Figure 2: Panel (a) shows associations between species richness and stem age for proposed families. Panel (b) shows a time-calibrated phylogeny of lineages within the nine-primaried oscines.

Fringillidae — This long-recognized family of finches forms a monophyletic group that is sister to the remaining nine-primaried oscines. This phylogenetic placement was well supported in all analyses presented by Barker et al. (2013). No changes are needed to this family.

Calcariidae — Longspurs and snow buntings, including six genera in three species. No changes to the composition of this family are required by new studies. In addition, we

propose retaining this family in the linear sequence following Fringillidae. The placement of this family varied among different analyses presented in Barker et al. (2013). In the concatenated data set, it was sister to the remaining nine-primaried oscines; in the species tree analysis, however, it was inferred to be sister to *Rhodinocichla* with low support, and these two taxa were sister to the remaining nine-primaried oscines. The placement of Calcariidae varied substantially among gene trees, albeit typically with low support. An exception was the gene tree for ACO1-I9, in which Calcariidae was sister to the Old-World buntings (Emberizidae) with high support. Nonetheless, the topologies inferred with the concatenated and species tree analyses were largely congruent in placing Calcariidae near the beginning of the sequence, and retaining Calcariidae as a family near the beginning of the sequence will cause the least disruption to the current classification.

Rhodinocichlidae — Barker et al. (2013) proposed placing *Rhodinocichla rosea*, the Rosy Thrush-Tanager, in its own family, Rhodinocichlidae. Historically, this aberrant species has been difficult to place, with some authors noting similarities to Mimidae. Eisenmann (1962) showed that it lacked similarities to Mimidae, but shared features with nine-primaried oscines. He considered it best placed with the tanagers, acknowledging that this placement was in part due to the varied nature of tanagers themselves. Most classifications have considered this species to be a tanager (e.g., AOU 1998). With limited genetic data, Seutin and Bermingham (1997) were able to confirm a closer relation of *Rhodinocichla* to nine-primaried oscines than to Mimidae. However, they were unable to definitively show that it was a tanager. In the current AOU classification, *Rhodinocichla* is listed as *incertae sedis*. Barker et al. (2013) reaffirmed the genetic distinctiveness of this species, with no clear relationship to existing families. *Rhodinocichla* was sister to the remaining nine-primaried oscines in the concatenated analyses, while the species tree analyses inferred a sister relationship between *Rhodinocichla* and Calcariidae (Fig. 1). Neither relationship was strongly supported, however. Nonetheless, it seems likely that *Rhodinocichla* falls outside of the clade that includes the most recent common ancestor of Old World buntings and tanagers. *Rhodinocichla* is also phenotypically and behaviorally distinct: it has vinaceous plumage on the throat and belly and forages among leaf litter in the undergrowth. We therefore suggest that *Rhodinocichla* be placed in the previously recognized monotypic family Rhodinocichlidae. Note also the relative older stem age of *Rhodinocichla*, compared to other recognized nine-primaried oscine families (Fig. 2a).

Emberizidae — In the current AOU classification, Emberizidae includes both Old World buntings and New World sparrows. In the phylogenies presented by Barker et al. (2013), Old World buntings were sister to New World sparrows in the species tree analysis, but sister to the remaining nine-primaried oscines in the concatenated data set (Fig. 1). These alternate topologies were strongly supported in their respective analyses. Thus, there was significant conflict in the placement of these two groups relative to each other. However, Old World buntings and New World sparrows consistently formed two monophyletic groups that were mutually exclusive. Barker et al. (2013) argued for splitting these two groups into separate families for the sake of future taxonomic stability and to recognize biological and biogeographic differences between

the two clades. In addition, Calcariidae is sometimes seen as being more closely aligned to Old World Buntings. Using three separate names: Calcariidae, Emberizidae (for Old World buntings only), and Passerellidae (for New World sparrows, see below) could prevent future taxonomic problems in case new data support different relationships among these three clades. *Emberiza*, *Latoucheornis*, *Melophus*, and *Miliaria* were assigned by Barker et al. (2013) to Emberizidae, but only *Emberiza* occurs in the AOU area.

Passerellidae — As discussed above, the New World sparrows are currently considered part of Emberizidae by the current AOU classification. Species tree analyses suggested that they are sister to the Old World buntings, while the concatenated data indicated that they are sister to the lineage containing the most recent common ancestor of *Spindalis* and Parulidae (Barker et al. 2013; Fig. 1). Despite uncertainty in its topological placement, Passerellidae consistently formed a strongly supported, monophyletic group that excludes other taxa. For the reasons outlined above, we recommend reassigning all genera in our current Emberizidae (except *Emberiza*) to Passerellidae (the oldest family name available for this group; Barker et al 2013).

Calyptophilidae — *Calyptophilus* consists of two species of chat-tanagers endemic to Hispaniola and historically considered part of Thraupidae. *Calyptophilus* is placed as *incertae sedis* in the current AOU classification. In the concatenated analysis, *Calyptophilus* was sister to a clade containing Mitrospingidae and Thraupidae (Barker et al. 2013; Fig. 1). In the species tree analysis, *Calyptophilus* was sister to Phaenicophilidae (Barker et al. 2013; Fig. 1). Given that there are no genetic or morphological characters uniting *Calyptophilus* to other species, we recommend following Barker et al. (2013) and resurrecting Calyptophilidae for these species.

Phaenicophilidae — This family would include species from three genera that share a biogeographic affinity in the Caribbean: *Phaenicophilus*, *Microligea*, and *Xenoligea*. *Phaenicophilus* was traditionally included in Thraupidae, but is *incertae sedis* in the current AOU classification, whereas *Microligea* and *Xenoligea* are included in Parulidae. Genetic studies (e.g., Lovette and Bermingham 2002, Klein et al. 2004) have shown that *Microligea* and *Xenoligea* are not closely related to Parulidae, and Klein et al. (2004) identified a close relationship among the three genera considered here, to the exclusion of warblers and tanagers. Barker et al (2013) confirmed this result. In both the concatenated analysis and the species tree analysis, these three genera formed a strongly supported clade (Barker et al. 2013). Due to their common ancestry, plumage similarities, and biogeography, we propose that these genera be classified together in a single family. Phaenicophilidae was previously used for *Phaenicophilus* alone and can now be expanded to include *Microligea* and *Xenoligea* (Barker et al. 2013).

Nesospingidae — Barker et al. (2013) proposed a new monotypic family for *Nesospingus speculiferus*, the Puerto Rican Tanager. *Nesospingus* has historically been included in Thraupidae, but it is currently considered *incertae sedis* in the AOU classification because several studies (including Barker et al. 2013) have shown this species to fall outside the 'core' Thraupidae. Instead, Barker et al. (2013) inferred a

sister relationship between *Nesospingus* and *Spindalis* in both the concatenated and species tree analysis, although this node was not strongly supported. In addition, the position of the *Spindalis/Nesospingus* clade was not strongly supported in any analyses, although it typically appeared in clades with other Caribbean genera. Thus, the general placement of *Nesospingus* within the broader clade that contains the most recent common ancestor of *Nesospingus* and Parulidae remains uncertain. Following Barker et al. (2013), we propose using the family Nesospingidae for this genus. Alternatively, an argument could be made to merge *Spindalis* and *Nesospingus* into a single family based on their consistent placement as sister taxa. This has the advantage of making the age of the clade more in line with other families of nine-primaried oscines (Fig. 2a). However, support is not strong for this relationship.

Spindalidae — Barker et al. (2013) proposed a new family for *Spindalis*, a genus consisting of four non-migratory species endemic to the Greater Antilles. The current AOU classification treats *Spindalis* as *incertae sedis*. As discussed in the previous section, Barker et al. (2013) inferred a sister relationship between *Spindalis* and *Nesospingus* with weak node support. Because the relationships of Spindalidae and Nesospingidae remain uncertain, recognizing both taxa as families presents a stable solution that improves on the current classification.

Zeledoniidae — Barker et al. (2013) proposed resurrecting the monotypic family Zeledoniidae for *Zeledonia coronata*, the Wrenthrush. This species, endemic to Costa Rica and western Panama, has long been recognized as morphologically and ecologically distinct (Hunt 1971). It has previously been classified in Turdidae (e.g., Mayr and Amadon 1951, Beecher 1953) or in its own family, Zeledoniidae (e.g., Wetmore 1960). Raikow (1978) analyzed myological characters and suggested that the species belonged to Parulidae, and the species was placed in Parulidae in the 1998 AOU checklist. However, comprehensive genetic analyses (starting with Lovette and Bermingham 2002) showed this species to fall well outside Parulidae, and it is currently treated in the AOU classification as *incertae sedis*. In the Barker et al. (2013) trees, the placement of *Zeledonia* within the nine-primaried oscines was uncertain, as it differed between the concatenated and species tree analysis with low node support in both phylogenies (Fig. 1). Given that morphological, ecological, and genetic data have failed to find a strong connection of *Zeledonia* to any other nine-primaried oscine, we argue that it is time to return this species to the monotypic family Zeledoniidae.

Teretistridae — *Teretistris* has historically been included with Parulidae, but comprehensive genetic studies (starting with Lovette and Bermingham 2002) showed that it falls outside Parulidae. The two species in the genus are still placed in Parulidae in the current AOU classification. Barker et al. (2013) proposed using the previously recognized family, Teretistridae, which would include *Teretistris fernandinae* and *Teretistris fornsi*. The placement of *Teretistris* was uncertain among the nine-primaried oscines; it was inferred as sister to *Zeledonia* in the concatenated analysis and sister to Icteridae in the species tree analysis, although neither placement received strong support (Fig. 1). Thus, we recommend following Barker et al. (2013) and recognizing family Teretistridae.

Icteriidae — Barker et al. (2013) proposed resurrecting Icteriidae for *Icteria virens*, the Yellow-breasted Chat. This species has traditionally been classified with Parulidae, but that placement has long been questioned (taxonomic history summarized in Lovette and Bermingham 2002). Genetic data in Lovette and Bermingham (2002) showed that the species is not part of the 'core' Parulidae and that the species was perhaps sister to Icteridae. Some of the trees of Barker et al. (2013) contained a similar result, but others did not. In the concatenated analysis, *Icteria* was inferred as sister to Icteridae with strong support. In the species tree analysis, however, *Icteria* was placed as sister to a clade containing *Teretistris* and Icteridae, although this did not receive strong support. Given the lack of consistent support for this species' placement, and given the general distinctiveness of this species relative to warblers and to blackbirds, we agree with Barker et al. (2013) and recommend removing *Icteria* from Parulidae and using Icteriidae for this species.

Icteridae — Barker et al. (2013) showed that blackbirds and allies form a monophyletic group that has been long recognized as a family. The placement of Icteridae remains uncertain—it was sister to *Icteria* in the concatenated analysis with strong support, but has uncertain placement in the species tree analysis. No changes in species composition of Icteridae are needed.

Parulidae — Six species that the AOU currently classifies in Parulidae need to be assigned to other families in order for the classification to be consistent with the data. The remaining wood warblers formed a monophyletic group in the trees of Barker et al. (2013). In the concatenated data set, Barker et al. (2013) inferred with strong support that Parulidae is sister to a clade containing *Icteria* and Icteridae. In the species tree analysis, it was sister to a lineage that includes *Zeledonia*, *Icteria*, *Teretistris,* and Icteridae, although this relationship was not strongly supported (Fig. 1).

Mitrospingidae — Barker et al. (2013) proposed a new family that includes *Mitrospingus*, *Orthogonys*, and *Lamprospiza*. These three genera formed a strongly supported clade in both the concatenated and species tree analyses (Barker et al. 2013; Fig. 1). All of these genera have been historically classified in Thraupidae, but none were sister to or nested within Thraupidae in any of the phylogenies presented by Barker et al. (2013). Thus, we recommend following Barker et al. (2013) to recognize Mitrospingidae for these species.

Cardinalidae — Cardinals and allies have long been recognized as a family, Cardinalidae. In Barker et al. (2013), they formed a monophyletic group that is sister to Thraupidae in the concatenated data set and sister to Mitrospingidae in the species tree analysis. No changes in species composition are needed for this group.

Thraupidae — The tanagers and allies are currently classified in the family Thraupidae. Barker et al. (2013) inferred a sister relationship between Thraupidae and Cardinalidae in the concatenated data set. In the species tree analysis, Thraupidae was sister to a clade containing Cardinalidae and Mitrospingidae. No changes in species composition are needed for this group; the committee dealt with these in a recent supplement.

Table 1: Current linear classification is shown in the first column, while the linear classification presented in this proposal is shown in the second column.

Current Linear Classification	Proposed Linear Classification
Fringillidae	Fringillidae
Calcariidae	Calcariidae
Parulidae*	Rhodinocichlidae
Thraupidae	Emberizidae
Nesospingus *(incertae sedis)*	Passerellidae
Phaenicophilus *(incertae sedis)*	Calyptophilidae
Calyptophilus *(incertae sedis)*	Phaenicophilidae
Rhodinocichla *(incertae sedis)*	Nesospingidae
Mitrospingus *(incertae sedis)*	Spindalidae
Spindalis *(incertae sedis)*	Zeledoniidae
Emberizidae**	Teretistridae
Cardinalidae	Icteriidae
Icteridae	Icteridae
	Parulidae
	Mitrospingidae
	Cardinalidae
	Thraupidae

* Includes *Zeledonia*, *Teretistris*, *Icteria*, *Microligea*, and *Xenoligea*
** Includes Passerellidae

Recommendation:

We recommend that the committee rearrange familial limits within the nine-primaried oscines to reflect the findings of recent molecular systematics studies, and modify the linear sequence of taxa within the nine-primaried oscines to correspond to this new classification. Although some may argue that this results in too many families, keep in mind that this clade contains nearly 10% of all birds. Previous assignments were largely based on the presumed importance of feeding morphology, but we now have the opportunity to organize the diversity of this major group of birds using phylogenetic evidence for the first time.

A YES vote would accept the above classification.

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Submitted by: Nicholas A. Mason, Cornell University; Kevin J. Burns, San Diego State University

Date of Proposal: 7 January 2017

Lump *Acanthis flammea* and *Acanthis hornemanni* into a single species

If approved, this proposal would merge the species *Acanthis flammea* and *Acanthis hornemanni* into a single species, *Acanthis flammea* Linnaeus 1758, which has taxonomic priority over *A. hornemanni* Holboell 1843. **NOTE: this proposal has been modified from the proposal submitted in 2015 to include additional information at the request of the NACC.**

Background:

Species in the genus *Acanthis* are small-bodied, granivorous finches that are collectively distributed throughout the Holarctic. Species limits within the genus have been contentious; taxonomists have recognized from one to six species, among other alternative treatments (Coues 1862; Harris et al. 1965; Troy 1985; Herremans 1989; Seutin *et al.* 1992; Marthinsen *et al.* 2008). Currently, Clements et al. (2014) recognize three species within the genus, including two in North America: *A. flammea*, which typically has a longer bill and more streaking on the rump and crissum, and *A. hornemanni*, which typically has a shorter, more conical bill with less streaking on the rump and crissum. The third species, *A. cabaret* of western Europe, is the smallest-bodied taxon within the redpoll complex and is characterized by a brown back with buffy flanks.

Troy (1985) documented substantial overlap in phenotypic variation between *A. flammea* and *A. hornemanni*, suggesting that phenotypic variation may be continuous rather than discrete. Previous molecular studies within the genus inferred ample genetic variation, but no evidence of sorting or monophyly among individuals classified as separate species by phenotype (restriction fragment length polymorphism (RFLPs), Marten and Johnson 1986; RFLPs, Seutin *et al.* 1995; mitochondrial control region, Ottvall et al. 2002; mitochondrial control region and ten microsatellites Marthinsen *et al.* 2008). The apparent lack of genetic differentiation suggests either substantial gene flow and weak reproductive isolation among currently recognized species or extremely recent divergence accompanied by incomplete lineage sorting that is amplified by large effective population sizes (Marthinsen *et al.* 2008). It is difficult to distinguish among these possibilities given the limited number of loci that have been studied to date. Additionally, patterns of assortative mating are largely anecdotal and mixed among the literature. Some studies allude to assortative mating by phenotype in Norway (Lifjeld & Bjerke 1996), whereas others document the presence of mixed pairs (Harris et al. 1965), and the presence of hybrid pairs has been debated (Molau 1985). Thus, species limits within *Acanthis* remain largely unresolved; however, recent molecular findings have provided new insight into the evolutionary dynamics within *Acanthis*.

New information:

Mason and Taylor (2015) sampled 77 individuals within the genus, including representatives of *A. flammea* (n = 42)*, A. hornemanni* (29), and *A. cabaret* (6), and used a double-digest restriction-associated digest (ddRAD-Seq) in combination with the Stacks pipeline (Catchen et al. 2013) to assemble 20,712 genome-spanning anonymous loci and assess genetic variation and differentiation. This ddRAD-Seq analysis sampled the three currently recognized species and included samples from different regions of both the Old World and New World ranges of the species' distribution, although not all subspecies were sampled (see below). In addition to examining variation among anonymous loci from the nuclear genome, Mason and Taylor (2015) also took bill and plumage measurements and RNA samples of multiple tissues from ten individuals in a single wintering flock in central New York, including three *A. hornemanni* and seven *A. flammea* that spanned a phenotypic continuum. Individual libraries were aligned to a *de novo* transcriptome to quantify patterns of gene expression and identify 215,825 single nuclear polymorphisms (SNPs) among putative genes for the ten RNA-Seq libraries.

Using these data, Mason and Taylor (2015) performed an array of population genetic analyses to examine population structure, patterns of coalescence, and associations between phenotype and genotype among currently recognized species (Figure 1). The first PC axis of a genetic PCA analysis using the 20,712 ddRAD-Seq SNPs revealed weak differentiation among individuals of *A. flammea* and *A. hornemanni*, although this variation represented only 2.2% of the total variation. This pattern may be driven partially by isolation by distance and the sampling scheme of Mason and Taylor (2015), who included more *A. hornemanni* from the Old World and more *A. flammea* from the New World. STRUCTURE (Pritchard et al. 2000), a Bayesian population assignment program, placed all individual redpolls in a single population, regardless of phenotype and current classification. A similar pattern was observed by analyzing the 215,825 SNPs among the ten individuals with RNA-Seq libraries. Analyses within a multispecies coalescent framework based on 35 SNPs with no missing data favored a species delimitation model with a single species over the current taxonomy (Bayes factor = 36.80), which was also supported by a data set of 200 randomly selected SNPs (BF = 15.22). Mason and Taylor (2015) also documented a pattern of isolation by distance, such that individuals were more closely related to geographically proximate individuals regardless of their phenotype and current species status. An Analysis of Molecular Variance (AMOVA) indicated that 98.11% of genetic variation was partitioned within species compared to 1.89% among species. Mason and Taylor (2015) also looked at correlations between continuous phenotypic variation and different components of genetic variation among the ten individuals that they collected from a single wintering flock. These analyses found no relationship between variation at anonymous SNPs and phenotypic variation; however, they revealed a strong correlation between phenotypic variation and multidimensional scaling scores of gene expression. In other words, anonymous, neutral SNPs did not correlate with phenotypic variation, whereas multigenic patterns of differential gene expression did correlate with phenotypic variation.
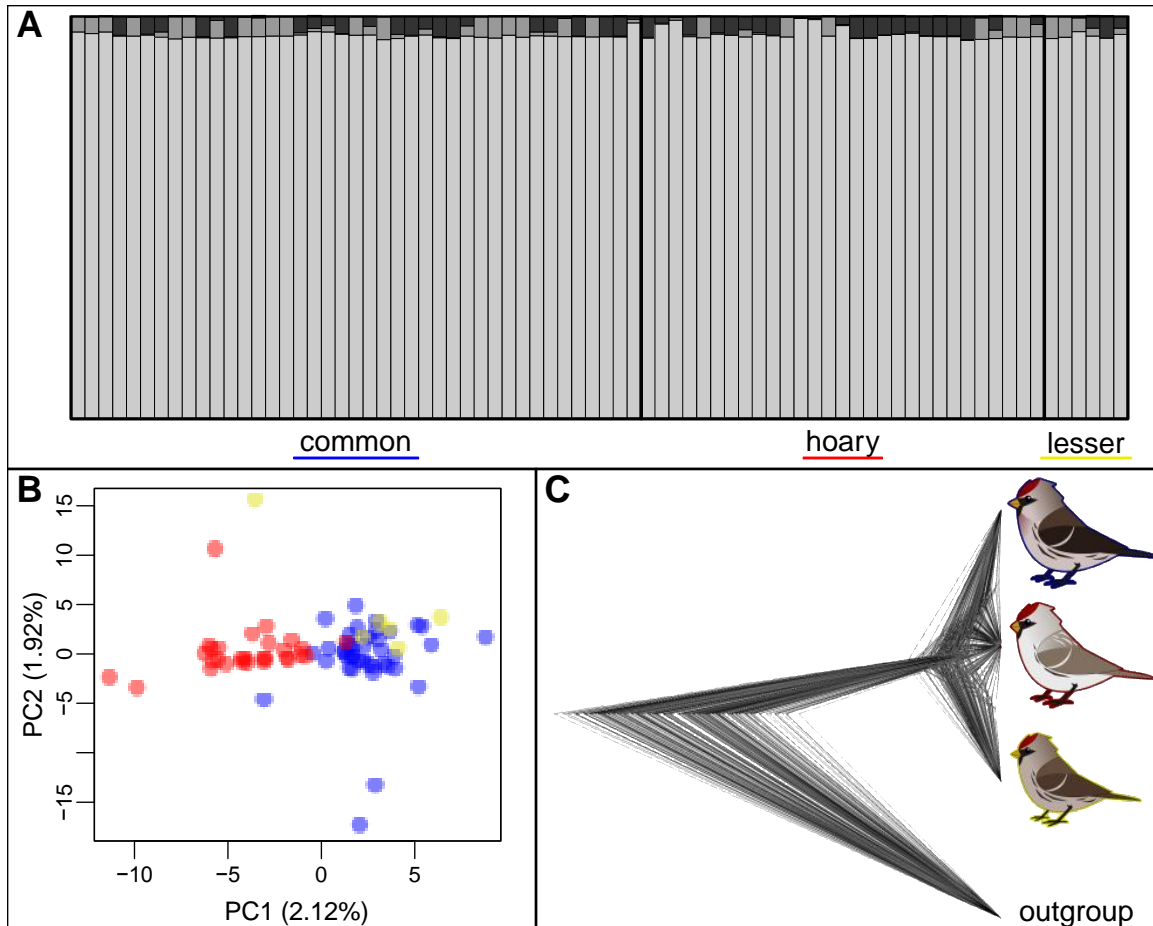
Figure 3: Redpoll population genetic analyses. (A) Bayesian assignment probabilities from STRUCTURE showing lack of population clustering among currently recognized redpoll species using 20 721 SNPs. (B) Genetic PCA plot indicating weak population structure among currently recognized species of redpolls. Common redpoll is represented with blue, hoary redpoll is represented with red, and lesser redpoll is represented with yellow dots. (C) SNAPP tree using 1587 SNPs for common, hoary and lesser redpoll, and white-winged crossbill (grey). Bayes factor delimitation strongly favoured lumping redpolls into a single species (Bayes factor = 36.80).

Analysis:

The analyses presented by Mason and Taylor (2015) suggest that differentially expressed genes are correlated with continuous phenotypic variation among redpolls, despite largely undifferentiated genomes. These patterns may be caused by high levels of ongoing gene flow between polymorphic populations, incomplete lineage sorting accompanying extremely recent or ongoing divergence, variation in cis-regulatory elements, or phenotypic plasticity, but do not support a scenario of prolonged isolation and subsequent secondary contact. It is still difficult to discriminate between gene flow and incomplete lineage-sorting without more comprehensive data regarding current patterns of assortative mating among phenotypic variants of redpolls. However, studies in other systems have found increased resolution of species limits with similar data sets in African cichlids (Wagner et al. 2013) and Neotropical passerines (e.g., Harvey and Brumfield 2015).

The lack of genetic differentiation within *Acanthis* inferred by Mason and Taylor (2015) is consistent with previous studies (e.g. Marthinsen 2008); however, the recent findings are based on a much larger data set that includes orders of magnitude more loci. Thus, Mason and Taylor (2015) suggested that genetic homogeneity is pervasive across *Acanthis* genomes and that *Acanthis* most likely comprises a single evolutionary lineage, which is substantiated by their population genetic analyses and species delimitation modeling. Recently, Amouret et al. (2015) sampled mtDNA and nuclear markers of Icelandic redpolls (*A. f. islandica*) in addition to *A. hornemanni* and *A. cabaret* and similarly concluded that all redpolls likely comprise a single species. Mason and Taylor (2015) documented continuous phenotypic variation in their winter flock sample where plumage and bill characteristics spanned from those typical of *A. flammea* to those typical of *A. hornemanni*. This pattern that was also documented and discussed by Troy (1985). Intriguingly, Mason and Taylor (2015) found that phenotypic variation within *Acanthis* was correlated with broad-scale patterns of gene expression.

Associations between phenotype and gene expression may be due to undocumented variation among *cis*-regulatory elements, phenotypic plasticity associated with environmental differences, or both. Importantly, differential gene expression among currently recognized redpoll species does not imply that they have experienced prolonged reproductive isolation. If differential gene expression is triggered by environmental conditions, then phenotypic variation may be due to phenotypic plasticity rather than genetic differences accumulated during isolated evolutionary histories. Mason and Taylor (2015) found pervasive genomic homogeneity among currently recognized species in the genus *Acanthis*, and continuous phenotypic variation and overlapping suitable habitat in *A. hornemanni* and *A. flammea*. Although the possibility persists that these species may have diverged extremely recently (i.e., more recently than the last glacial maximum), there is no evidence that supports a scenario of prolonged reproductive isolation and assortative mating within the genus. Given these recent findings, we feel that the burden of proof now lies on those who would recognize multiple species within *Acanthis*; a more parsimonious explanation may be that *Acanthis* consists of a single, polymorphic evolutionary lineage that may be experiencing ongoing bouts of local adaptation, which has induced continuous, yet geographically heterogeneous, phenotypic variation among redpoll types.

Nevertheless, we note that neither *A. h. hornemanni* nor *A. f. rostrata*, which breed in Greenland and northern Canada, was sampled for our genetic analyses, leaving the status of these subspecies and/or populations unclear. These two subspecies differ phenotypically from the remaining subspecies and from each other: *A. h. hornemanni* is the largest and whitest of the *A. hornemanni* subspecies, whereas *A. f. rostrata* is the largest and darkest subspecies of *A. flammea*. Salomonsen (1950) treated *A. f. rostrata* and *A. h. hornemanni* as subspecies, but noted that the two breeding ranges replace each other as one moves from south to north across Greenland. Salomonsen (1950) also observed multiple hybrid individuals, mixed breeding pairs and colonies that included both forms and intermediates, and collected a mixed pair during copulation. Based on their apparent interbreeding and phenotypic intermediates between *A. f. rostrata* and *A. h. hornemanni* observed among series in Iceland and elsewhere,

Salomonsen (1950) treated the two forms as a single species. Future research on patterns of breeding in potential areas of sympatry, including Greenland, northeastern Canada, and northern Europe, may reveal assortative mating that is not reflected in genetic data. Alternatively, such a study may confirm that *A. flammea* and *A. hornemanni* hybridize freely in accordance with the genetic data at hand.

Although the Lesser Redpoll (*A. cabaret*) is extralimital to the AOU area, its status is still pertinent to the AOU's treatment of the redpoll complex (i.e., whether all redpolls are lumped into a single species). Mason and Taylor (2015) included six samples of *A. cabaret* in the ddRAD-Seq portion of their study and found no evidence of genetic differentiation. However, previous studies have presented evidence in favor of assortative mating. Specifically, Lifjeld and Bjerke (1996) documented eleven nests with no mixed pairs between *A. flammea* and *A. cabaret* during an irruptive breeding season in southern Norway, leading many authorities to elevate and maintain *A. cabaret* as a separate species (e.g., Knox 2001, current BOU list, Dickinson and Christidis 2014). Although Mason and Taylor (2015) found no evidence of genetic differentiation, we suggest that the NACC treat *A. cabaret* a distinct species due to the evidence of assortative mating and apparent reproductive isolation in certain populations, and the phenotypic distinctiveness of *A. cabaret*. We also note that the committee is generally reluctant to lump purely extralimital species when these are currently recognized by the local authorities.

Recommendation:

Based on the genetic and genomic data, the phenotypic data, and Salomonsen's (1950) conclusions regarding *flammea rostrata* and nominate *hornemanni*, we believe that the burden of proof has shifted to those who would treat *flammea* and *hornemanni* as separate species, and therefore recommend lumping *A. flammea* and *A. hornemanni* into a single species, *A. flammea*. Despite the genetic and genomic data, however, we recommend treating *A. cabaret* as a separate species, pending future studies of assortative mating and any reconsideration of this species by local authorities.

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Submitted by: Nicholas A. Mason and Scott A. Taylor, Cornell University
Date of proposal: 23 April 2015, revised 12 Jan. 2017

Split *Lanius excubitor* into two or more species

Background:

Through the fourth edition of the Check-list (AOU 1931), *Lanius borealis* was treated as specifically distinct. Subsequently, the Great Grey Shrike (*Lanius excubitor*) was delimited as including taxa distributed in many races across the Holarctic south to northern Africa and India (Vaurie 1959), but not including the Chinese Grey Shrike (*L. sphenocercus*) or Loggerhead Shrike (*L. ludovicianus*). Marked polytypy within *excubitor* led some (e.g., Lefranc and Worfolk 1997) to conclude that it was better treated as two species, Northern Grey Shrike (*L. excubitor*) and Southern Grey Shrike (*L. meridionalis*), and it has been treated thus by most authorities in the past two decades.

New Information:

Several fairly recent papers that have used mtDNA to evaluate *Lanius* phylogeny have included representatives of the *L. excubitor* complex (Gonzalez et al. 2008, Klassert et al. 2008, Olsson et al. 2010, Peer et al. 2011). Nuclear DNA has rarely been sequenced in this group, and in those papers that have used nuDNA, little resolution of this group has been achieved. Without exception, those mtDNA analyses that have included members of *L. excubitor, L. meridionalis*, and *L. ludovicianus* have found that there is no support for a polytypic southern species *L. meridionalis* vs. a polytypic northern Holarctic *L. excubitor*; rather they have shown: (1) that the Iberian form *meridionalis* is not closely related to other taxa formerly allied with it in the polytypic *meridionalis*; (2) that *meridionalis s.s.* is more closely related to the North American *borealis* than it is to the clade including northern European nominate *excubitor* and several other western Palearctic forms; (3) that Holarctic *L. excubitor s.l.* is non-monophyletic because *L. ludovicianus* and *L. sphenocercus* are more closely related to the *borealis* group than to the nominate *excubitor* group. In an analysis that included only *L. e. excubitor, L. e. borealis*, and *L. ludovicianus, ludovicianus* was again found to be nested within *excubitor s.l.* (Johnsen et al. 2010).
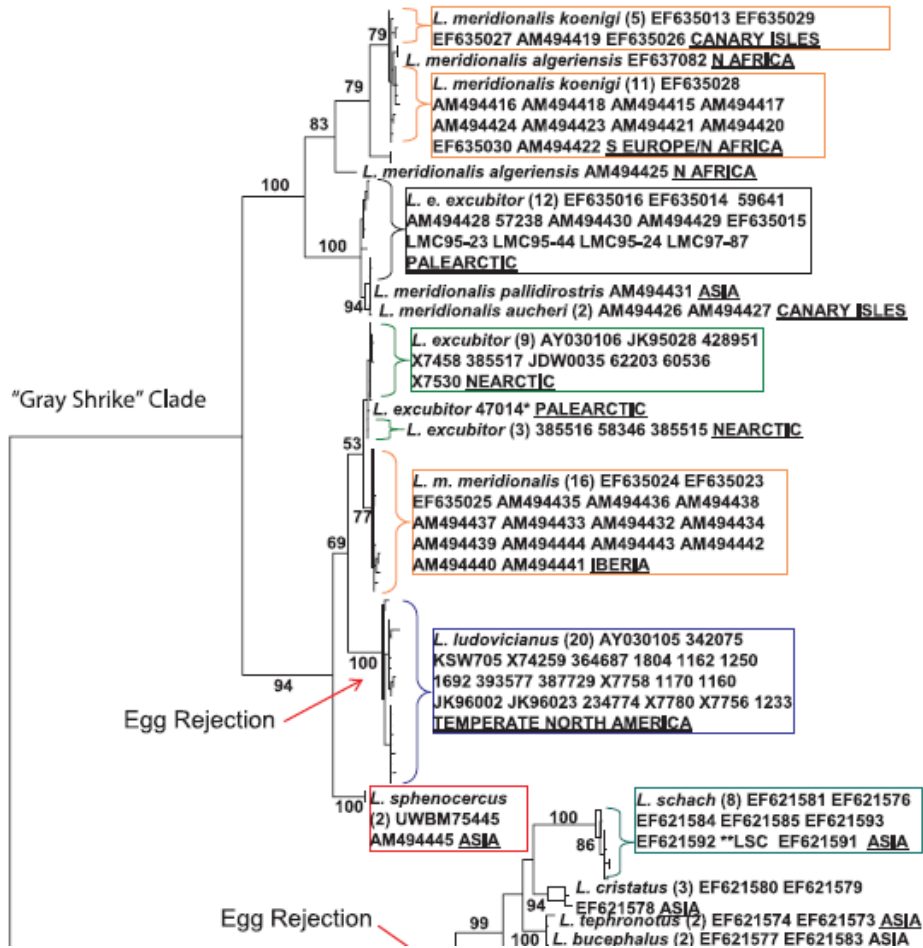
Below are pasted the three most recent trees:

From Olsson et al. 2010:
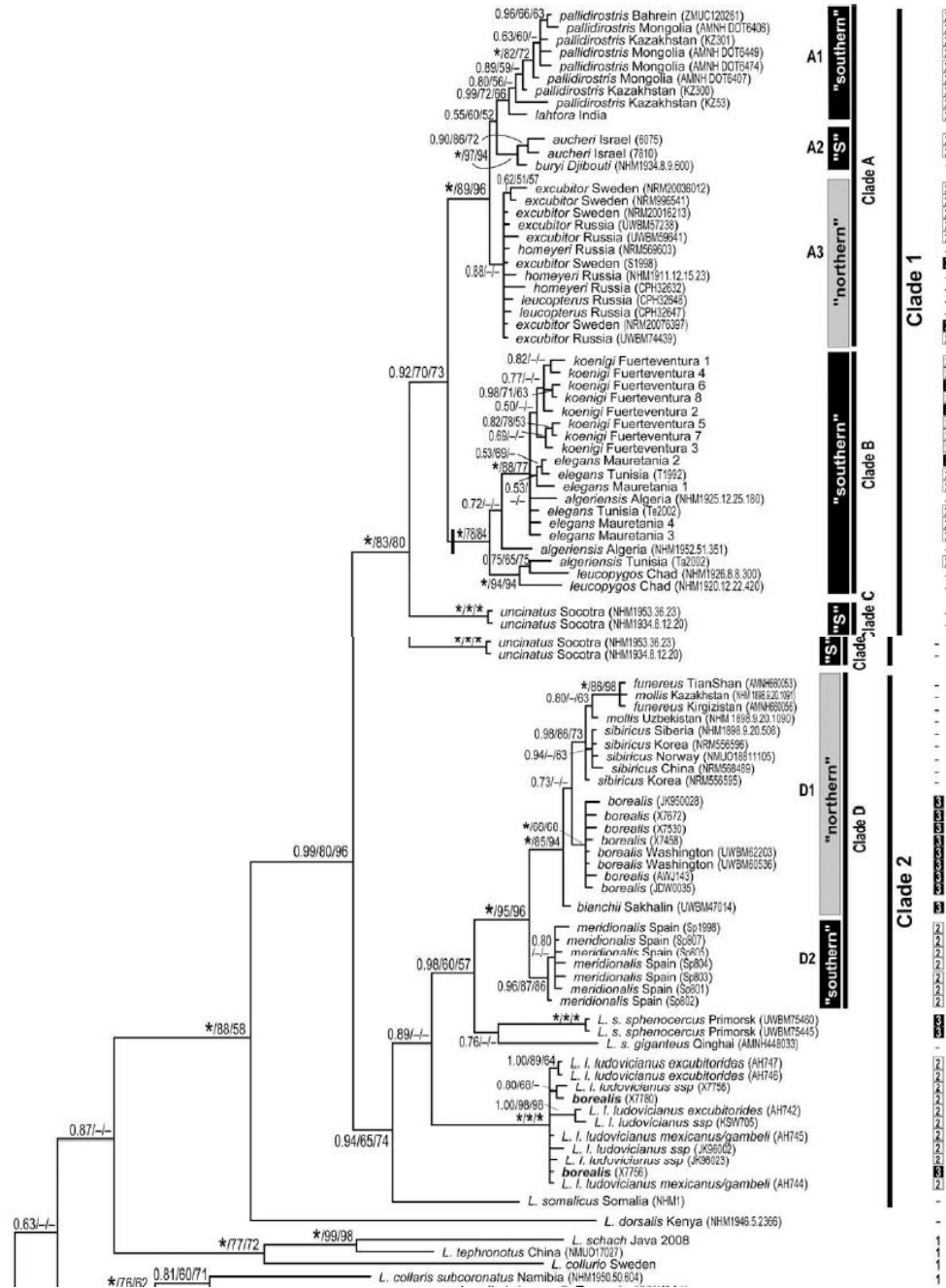
From Peer et al. 2011:

From Johnsen et al. 2010:

Fig. 3 Neighbor-joining tree (based on the Kimura 2 parameter) for three *Lanius* species, with *Corvus cornix* as outgroup. The tree illustrates the paraphyletic relationship between *Lanius excubitor* from North America (*upper/blue box*) and Scandinavia (*lower/red box*). For each individual, the scientific name is followed by the BOLD process ID number and the sampling locality
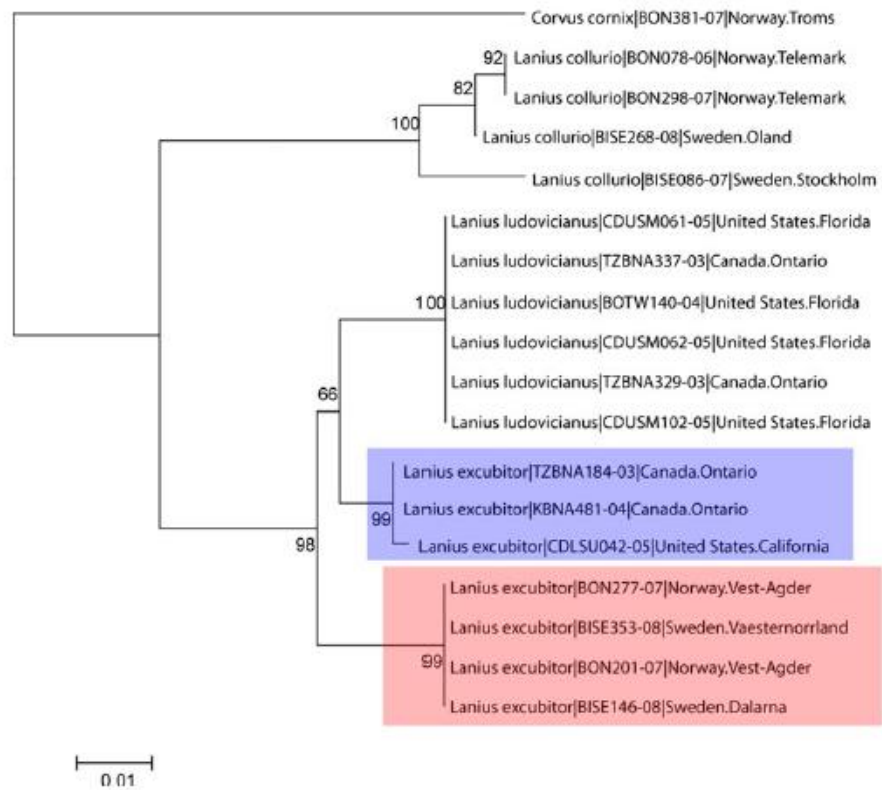
Although further work is needed on the details of relationships among various Old World taxa, it seems clear that *L. ludovicianus* and the New World *borealis* group are more closely related to each other than to the Old World nominate *excubitor* group. However, Olsson et al. (2010) showed that the *borealis* Vieillot, 1808 group also includes Eastern Palearctic (mainly Siberian) taxa *sibiricus* Bogdanov, 1881, *funereus* Menzbier, 1894, *mollis* Pallas, 1811 (according to Mayr and Greenway 1960, or Eversmann, 1853 and subsuming *funereus*, according to Dickinson and Christidis 2014), and *bianchii* Hartert, 1907 (see clade/sampling map from Olsson et al. 2010, pasted below). (Because *borealis* is the oldest name for this clade, if we split it now, stability would be served because in the unlikely event that a realignment of any of the Eastern Palearctic races becomes desirable, no further name change would be necessary for the AOU region.) *Lanius meridionalis meridionalis* Temminck, 1820, of Iberia, although genetically close to the *borealis* clade at least on mtDNA, seems biogeographically and on plumage unlikely to be best treated as conspecific with *borealis*.

This split has already been adopted elsewhere, e.g. Dickinson and Christidis (2014). Tajkova and Red'kin (2014) conducted a morphological analysis of the diagnosability of the Eurasian races of *L. excubitor s.s.* and *L. borealis sibiricus*, the latter being a vagrant to Ukraine from farther east. Although it seems probable that little is known of the zone of contact implied by the map in Olsson et al. (2010; below), Tajkova and

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Red'kin (2014) consider that some hybridization occurs (as it does in several shrikes universally considered full species, e.g. Grey-backed (*L. tephronotus*) with Long-tailed (*L. schach*). The results of the Olsson et al. (2010) paper have also been taken as supporting much deeper splitting (Poelstra 2014), although the authors of the former paper clearly advised caution in over-interpreting their results.
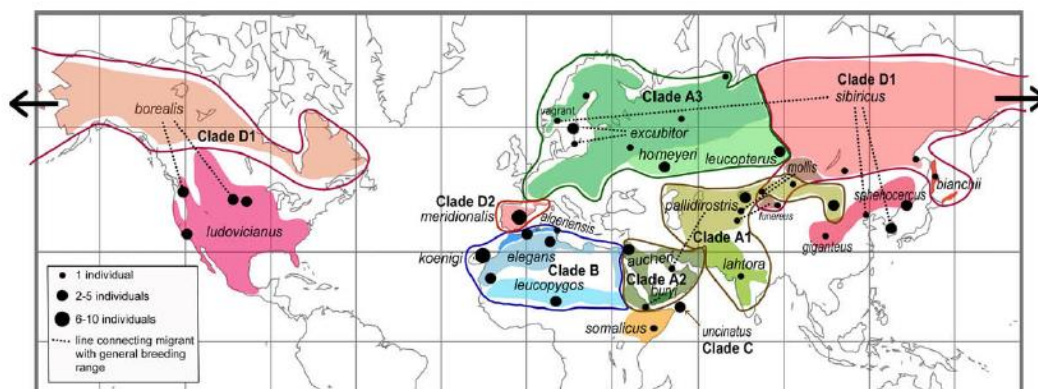
From Olsson et al. (2010):

Fig. 1. Breeding distribution of the taxa in the *Lanius excubitor* complex (based on e.g. Cheng, 1987; Cramp and Perrins 1993; Harris, 2000; Lefranc and Worfolk, 1997). The sites of the DNA samples used in the present study are marked by filled circles (sizes representing samples sizes, as explained in figure). Lines encircling ranges conform with the clades in Fig. 2. Filled circles denoting individuals of migratory species collected away from the breeding grounds are connected to the appropriate taxon by a dashed line.

Recommendation:

I recommend splitting *Lanius borealis* (along with the Siberian races *sibiricus, bianchii, mollis*, and *funereus*) from *L. excubitor*. I further recommend retaining the entrenched common name Northern Shrike for *L. borealis*, which adequately distinguishes it from the name used in the Old World, Great Grey Shrike for *L. excubitor*.

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Submitted by: Pamela C. Rasmussen, Michigan State University

Date of Proposal: 16 January 2017

Add Mangrove Rail *Rallus longirostris* to the Main List

Background:

In 2014, Clapper Rail was split (Proposal 2014-A-5, Maley and Brumfield 2013, Chesser et al. 2014), and *Rallus longirostris* was removed from the Main List. This revised taxon was only known to occur along the coasts of South America. The common name Mangrove Rail was accepted for *Rallus longirostris* by both the North American Classification Committee and the South American Classification Committee (Proposal 639).

New Information:

In 2010 Robert Gallardo and Mayron Mejía discovered a large rail on the Pacific Coast of Honduras (Jones and Komar 2011). A breeding population was confirmed in 2012, when John van Dort (2013) found a pair with two chicks. As no specimens were known to exist, the identification of this population was unclear, especially after Clapper Rails were split.

In 2013, James Maley and colleagues collected a small series from Honduras for study. They sequenced mtDNA, and compared the skins to available material from the US, Mexico, the Caribbean, and South America. The birds were most closely related genetically to the birds in South America (Maley et al. 2016). They differed sufficiently from the nearest populations to warrant description of a new taxon, the Fonseca Mangrove Rail (*Rallus longirostris berryorum*). Mangrove Rails were also discovered in El Salvador and Nicaragua (van Dort 2013). Based on vocal identification, Mangrove Rails also occur along the Pacific Coast of Costa Rica (Maley et al. 2016), where they have been found breeding (Garrigues and Garrigues 2016).

Recommendation: Mangrove Rail (*Rallus longirostris*) should be added to the Main List. Based on the phylogeny in Maley and Brumfield (2013), they should be inserted between Aztec Rail (*Rallus tenuirostris*) and King Rail (*Rallus elegans*).

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Revise the generic classification and linear sequence of *Anas*

Background:

The current NACC checklist contains 18 species of dabbling ducks in the genus *Anas*:

Gadwall	*Anas strepera*
Falcated Duck	*Anas falcata*
Eurasian Wigeon	*Anas penelope*
American Wigeon	*Anas americana*
American Black Duck	*Anas rubripes*
Mallard	*Anas platyrhynchos*
Mottled Duck	*Anas fulvigula*
Hawaiian Duck	*Anas wyvilliana*
Laysan Duck	*Anas laysanensis*
Eastern Spot-billed Duck	*Anas zonorhyncha*
Blue-winged Teal	*Anas discors*
Cinnamon Teal	*Anas cyanoptera*
Northern Shoveler	*Anas clypeata*
White-cheeked Pintail	*Anas bahamensis*
Northern Pintail	*Anas acuta*
Garganey	*Anas querquedula*
Baikal Teal	*Anas formosa*
Green-winged Teal	*Anas crecca*

This generic classification has been stable in AOU checklists for several decades (AOU 1983, AOU 1998), although earlier checklists had more dabbling duck genera. For example, the 1957 checklist recognized *Mareca* (for *penelope* and *americana*) and *Spatula* (for *clypeata*).

New Information:

Gonzalez et al. (2009) generated a phylogeny of Anseriformes using a concatenated alignment of two mitochondrial genes (ND2 and cyt-b). Taxon sampling included most extant species of Anatini, including most species on the AOU checklist. The genus *Anas* was shown to be non-monophyletic with strong statistical support.

An annotated version of the Gonzalez et al. phylogeny (their Fig. 1) is presented below. Colored boxes indicate clades proposed for generic splits. Yellow stars indicate species on the AOU NACC checklist. Two NACC species, *A. zonorhyncha* and *A. wyvilliana*, were not sampled by Gonzalez et al., but both appear to be closely related to *Anas sensu stricto* (Omland 1997, Johnson and Sorenson 1999, Lavretsky et al 2015). *Anas diazi* and *Anas cyanoptera septentrionalium* are in the phylogeny and occur in the AOU area but are not starred because they are not species-level taxa on the NACC checklist.

The node ages reported in Gonzalez et al. are 9.4 ± 3.0, 11.2 ± 3.2, and 13.5 ± 3.6 (mya ± sd) for nodes A, B, and C, respectively.
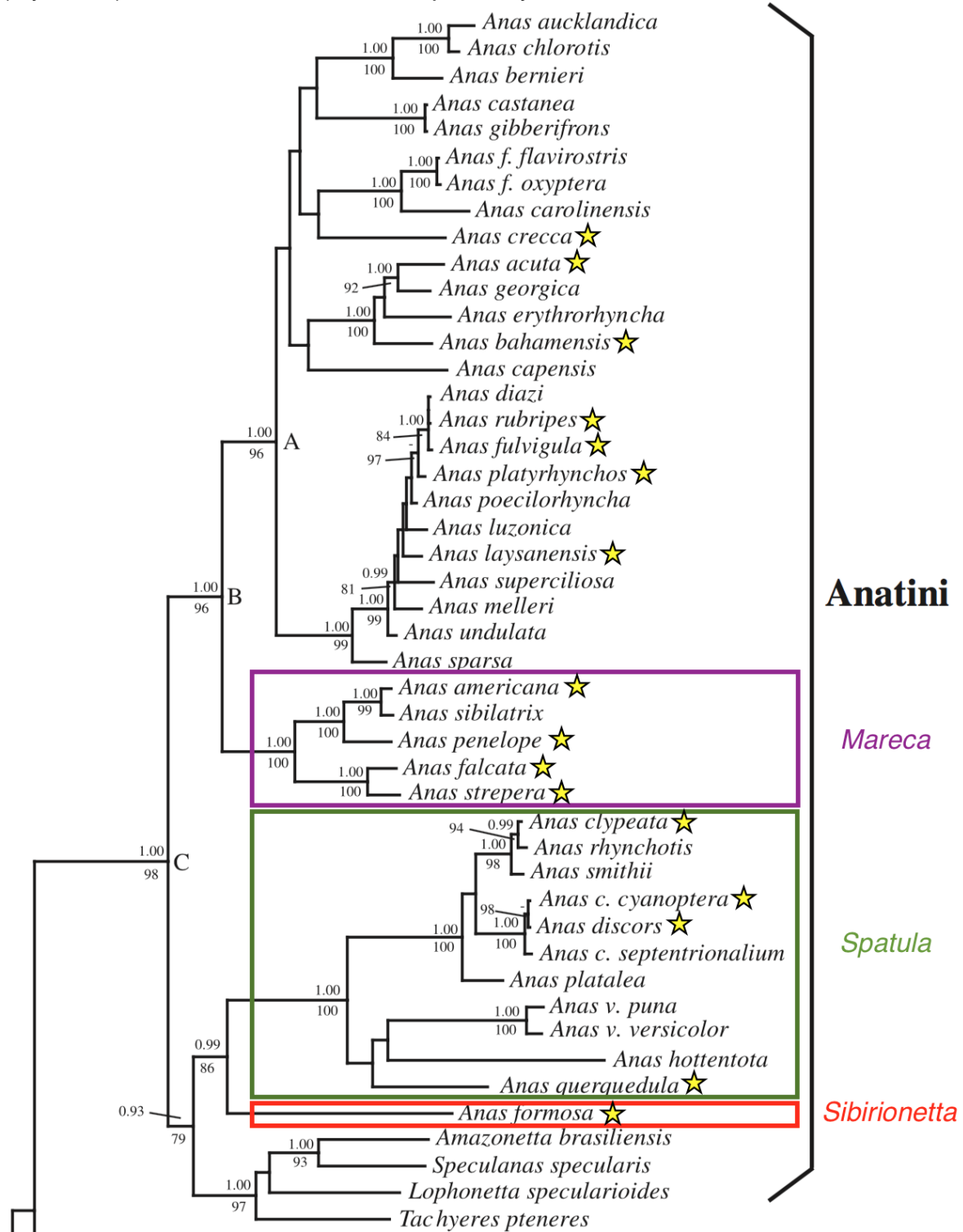
Recommendation:

One approach to resolving the *Anas* non-monophyly problem would be to merge the extralimital *Amazonetta, Speculanas, Lophonetta,* and *Tachyeres* into *Anas*. However, this is not recommended because it would require merging ancient and morphologically distinctive lineages like steamer-ducks (*Tachyeres* spp.) into the same genus as Mallard.

The other way to resolve the non-monophyly is by splitting *Anas*. Dickinson and Remsen (2013) took this approach when resurrecting *Sibirionetta*, *Spatula*, and *Mareca* as annotated in the figure above. To achieve monophyly, it is necessary to remove from *Anas* the species Dickinson and Remsen transferred to *Sibirionetta* and *Spatula*, although two new genera are not necessarily required. Therefore, if we choose to split *Anas*, the questions to be resolved are (1) whether to recognize *Sibirionetta* in addition to *Spatula* (*Spatula* has priority), and (2) whether to recognize *Mareca*. *Sibirionetta* has not generally been recognized and *A. formosa* has been thought, based on morphology, to be typical of *Anas* (Livezey 1991), whereas *Mareca* was previously recognized (e.g., AOU 1957) and its species are distinctive morphologically (see, e.g., Livezey 1991). Nevertheless, genetic data indicate that *formosa* has no close relatives and that it occupies the longest branch in the *Anas* phylogeny (Johnson and Sorenson 1999; Gonzalez et al. 2009). Dickinson and Remsen (2013) cited the depth of phylogenetic tree splits as their rough guide for deciding to split *Sibirionetta* and *Mareca*. We believe that the bulk of the evidence warrants making these splits, as follows:

(A) transfer *A. formosa* to *Sibirionetta*

(B) transfer *A. clypeata, A. cyanoptera, A. discors,* and *A. querquedula* to *Spatula*. If A fails to pass, then B will also transfer *A. formosa* to *Spatula*.

(C) transfer *A. americana, A. penelope, A. falcata*, and *A. strepera* to *Mareca*

Sub-proposal B by itself would solve the non-monophyly problem while minimizing taxonomic changes. Sub-proposals A, B, and C together would replicate the taxonomy of Dickinson and Remsen (2013) and make the phylogenetic depths of generic splits more consistent within Anatini.

The *Anas* non-monophyly problem can be resolved by voting for B only, A+B, B+C, or A+B+C. The status quo taxonomy contains a non-monophyletic *Anas*, so voting YES on B, at least, is recommended. Our recommendation would be to go with A+B+C for the reasons outlined above.

(D) revise the linear sequence of species

To conform to AOU guidelines, the linear sequence of species currently placed in *Anas* would require changes in response to the phylogeny of Gonzalez et al. (2009). The new

linear sequence would be as follows (genus names assume passage of sub-proposals A, B, and C above):

Baikal Teal	*Sibirionetta formosa*
Garganey	*Spatula querquedula*
Blue-winged Teal	*Spatula discors*
Cinnamon Teal	*Spatula cyanoptera*
Northern Shoveler	*Spatula clypeata*
Gadwall	*Mareca strepera*
Falcated Duck	*Mareca falcata*
Eurasian Wigeon	*Mareca penelope*
American Wigeon	*Mareca americana*
Laysan Duck	*Anas laysanensis*
**Hawaiian Duck	*Anas wyvilliana*
**Eastern Spot-billed Duck	*Anas zonorhyncha*
Mallard	*Anas platyrhynchos*
American Black Duck	*Anas rubripes*
Mottled Duck	*Anas fulvigula*
White-cheeked Pintail	*Anas bahamensis*
Northern Pintail	*Anas acuta*
Green-winged Teal	*Anas crecca*

Eastern Spot-billed Duck (*A. zonorhyncha*) and Hawaiian Duck (*A. wyvilliana*) were not sampled by Gonzalez et al. (2009). *Anas zonorhyncha* was formerly (and sometimes still is) considered conspecific with *A. poecilorhyncha*, which was sampled, and the position of *poecilorhyncha* in the phylogeny is consistent with the placement of *zonorhyncha* between *laysanensis* and *platyrhynchos* in the linear sequence above. However, Lavretsky et al. (2015) recently concluded that *A. wyvilliana* formed as the result of an ancient hybridization event between *A. laysanensis* and *A. platyrhynchos*, which means it should probably also occupy the position in the linear sequence occupied by *zonorhyncha*. To resolve this dilemma, *wyvilliana* has been tentatively placed between *laysanensis* and *zonorhyncha*.

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