

AOU Classification Committee – North and Middle America
Proposal Set 2016-A
10 Nov 2015

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Elevate *Aphelocoma californica woodhouseii* to species rank**Background:**

During the 2009-2010 proposal period a proposal was submitted to revise species limits in the Western Scrub-Jay (*Aphelocoma californica*) based primarily on mitochondrial DNA (mtDNA) phylogenetic relationships. Please see that proposal (<http://checklist.aou.org/nacc/proposals/PDF/2009-A.pdf>) for detailed background information on the history of taxonomic relationships in the group. Here we propose to elevate *Aphelocoma californica woodhouseii* only, which we refer to below as the *woodhouseii* group. The *woodhouseii* group includes the subspecies *woodhouseii*, *nevadae*, *grisea*, *cyanotis*, *sumichrasti*, and *remota*. The latter two subspecies comprise the *sumichrasti* group and are quite divergent from the other subspecies (see below), but we do not aim to address that potential split within the *woodhouseii* group. Instead, we focus only on the deeper split between the *woodhouseii* and *californica* groups.

Previous research shows that the *woodhouseii* and *californica* groups are readily diagnosable by plumage and morphology. Birds of the *woodhouseii* group are more grayish-blue, with less contrasting plumage, and have a thinner, straighter bill that lacks the hook of birds of the *californica* group (Pitelka 1951). These differences in bill shapes appear to be adaptations to food resources (Peterson 1993; Bardwell et al. 2001), as the two groups occupy different habitats (*californica* in oak woodland versus *woodhouseii* in pinyon-juniper). Furthermore, the groups are known to behave and vocalize differently (e.g., Dunn and Garrett 2001, Curry et al. 2002). Dunn and Garrett (2001) qualitatively described vocal differences between these groups – the calls within the *woodhouseii* group are consistently higher pitched and on average consist of two syllables compared with the harsher, lower pitched, and one-syllabled notes from coastal birds. Previous genetic research provides congruent evidence for divergence in both allozymes (Peterson 1992) and mtDNA (Delaney et al. 2008).

The Western Scrub-Jay as currently defined by the AOU (1998) does not reflect modern phylogenetic hypotheses and recent information on reproductive isolation between populations within the species. Also, several studies (Delaney et al. 2008; McCormack et al. 2011, Gowen et al. 2014) have shown that the Western Scrub-Jay is paraphyletic with respect to Island Scrub-Jay (*A. insularis*). The Western Scrub-Jay was not split based on the last proposal primarily because the putative hybrid zone between *californica* and *woodhouseii* populations in Nevada had not received careful study, and thus the level of reproductive isolation was not clear.

New Information:

Since the last NACC proposal, there have been two more genetic studies bearing on the question of species status of the *woodhouseii* group. McCormack et al. (2011) carried out a phylogeny of the entire genus *Aphelocoma*. Although the number of individuals per taxon was small and largely neglected areas of potential contact, this study confirmed the general patterns of Delaney et al. (2008) that *californica* and

woodhouseii are reciprocally monophyletic in mtDNA (Fig. 2; McCormack et al. 2011). The timing of the split was dated to 1-4 million years ago with mtDNA and nuclear DNA in a concatenated analysis (Fig. 4b; McCormack et al. 2011). The species tree supported more recent divergence times, and *woodhouseii* was not always supported as monophyletic, but this could be due to low information content in the three nuclear genes or possibly gene flow (Fig. 4d; McCormack et al. 2011).

Gowen et al. (2014) looked at microsatellite and mtDNA variation across the entire range of Western Scrub-Jays, including nearly 700 specimens. In addition to broad-scale patterns, this study looked specifically at the contact zone between *californica* and *woodhouseii* and attempted to test for reproductive isolation by looking for a signature of Haldane's Rule, which predicts less mtDNA introgression than nuclear introgression across contact zones. They found this signature, and while there are alternate hypotheses for this pattern in addition to Haldane's Rule, it was unlikely to be caused by the most obvious one, differential sex dispersal. Females disperse greater distances than males (Curry et al. 2002), so one would expect greater mtDNA than nuclear introgression. Furthermore, the geographic pattern of introgression showed that contact seemed to be limited to the small area in and around the Pine Nut Mountains, an area of contact previously identified by Pitelka (1951). With its deep sampling of nearly 700 individuals, the study did uncover evidence for rare long-distance dispersal of two *woodhouseii* into the range of *californica*, with one *woodhouseii* even found in a mountain range near Los Angeles. The rarity of these long-distance dispersal events suggests that they have had little, if any, impact on the overall genetic composition of *californica*.

In addition to the Pine Nut Mountains, another contact zone had been proposed by Pitelka (1951) across the Owens Valley. Gowen et al. (2014) confirmed some gene flow across this barrier, but the pattern of nuclear vs. mtDNA variation suggested that the individuals with introgression (all on the west side of the Owens Valley) were advanced backcrosses. Thus the gene flow did not appear to be contemporary. This contrasted with the situation in the Pine Nut Mountains, where contact was current and frequent, although limited in geographic area. Birds in the Pine Nut Mountains represent all variety of crosses from possible F1s to advanced backcrosses (Fig. 3a; Gowen et al. 2014). The area of contact is likely limited by habitat; it is the only smooth transition from oak forests of California into pinyon-dominated ecosystems of the Great Basin. To the south these populations are separated by vast expanses of unsuitable habitat.

With respect to the *sumichrasti* group (*sumichrasti* + *remota* subspecies), Gowen et al. (2014) confirmed reciprocal monophyly of mtDNA with respect to other *woodhouseii* individuals. The divergence between *sumichrasti* and populations of central Mexico is greater than the divergence between *insularis* and *californica* (Fig. 1 below). In microsatellites, individuals of *sumichrasti* and southern populations of *woodhouseii* were largely assigned to different genetic clusters (Fig. 3E; Gowen et al. 2014). However, Gowen et al. (2014) did not assess populations close to the putative area of contact near Mexico City (Pitelka 1951). Despite compelling evidence that the populations in southern Mexico constitute a distinct species, there is insufficient information regarding reproductive isolation to recommend splitting the *sumichrasti* group at this time.

With respect to subspecies, Gowen et al. (2014) found little evidence in mtDNA or microsatellites to support subspecies within *californica*, although subspecific differences are not necessarily observable with these data and analyses. Further fine-scale structure might be observable with a larger set of markers or even with more detailed analyses of the microsatellite data. Within *woodhouseii*, the *texana* subspecies was distinctive in both mtDNA and microsatellites and may warrant species status. In fact, except for one individual, *texana* was monophyletic in mtDNA (see node with 0.87 support in Fig. 1 below with the exception being the individual denoted with an arrow). Intermediate populations between *texana* and *woodhouseii* were not assessed, for example the population in the Davis Mountains, Texas, where these lineages are said to meet and hybridize (Pitelka 1951). We are not recommending splitting them at this time because more work on this potential area of contact is needed to assess gene flow and reproductive isolation. Gowen et al. (2014) also found a genetic break in microsatellites between *woodhouseii* in the US and those in Mexico, which was not observed in mtDNA. It was unclear if this nuclear DNA break was caused by sampling or was a real biological difference. Finally, there was evidence for a break between *remota* and *sumichrasti* subspecies in Mexico, with evidence for some gene flow, as expected for subspecies.

Recommendation:

It is clear that the current taxonomy does not accurately reflect phylogeny (Fig. 1) or the high degree of differentiation between members of the *californica* and *woodhouseii* groups in both mtDNA (Fig. 1) and nuclear DNA (Fig. 2). On the basis of genetic, phenotypic, behavioral, and ecological differences, plus evidence for selection against hybrids, we recommend that the *californica* and *woodhouseii* groups be treated as full species. This treatment recognizes the strong divergence between these groups in multiple traits, support for a measure of reproductive isolation, and also solves the problem of paraphyly. Furthermore, because *californica* and *insularis* are sister lineages, maintaining the status quo is inconsistent with the treatment of *A. insularis* as a full species (AOU 1995).

Recommended English Names:

The names California Scrub-Jay (*californica* group) and Woodhouse's Scrub-Jay (*woodhouseii* group) are widely in use. At least recently, we've seen no alternative English names.

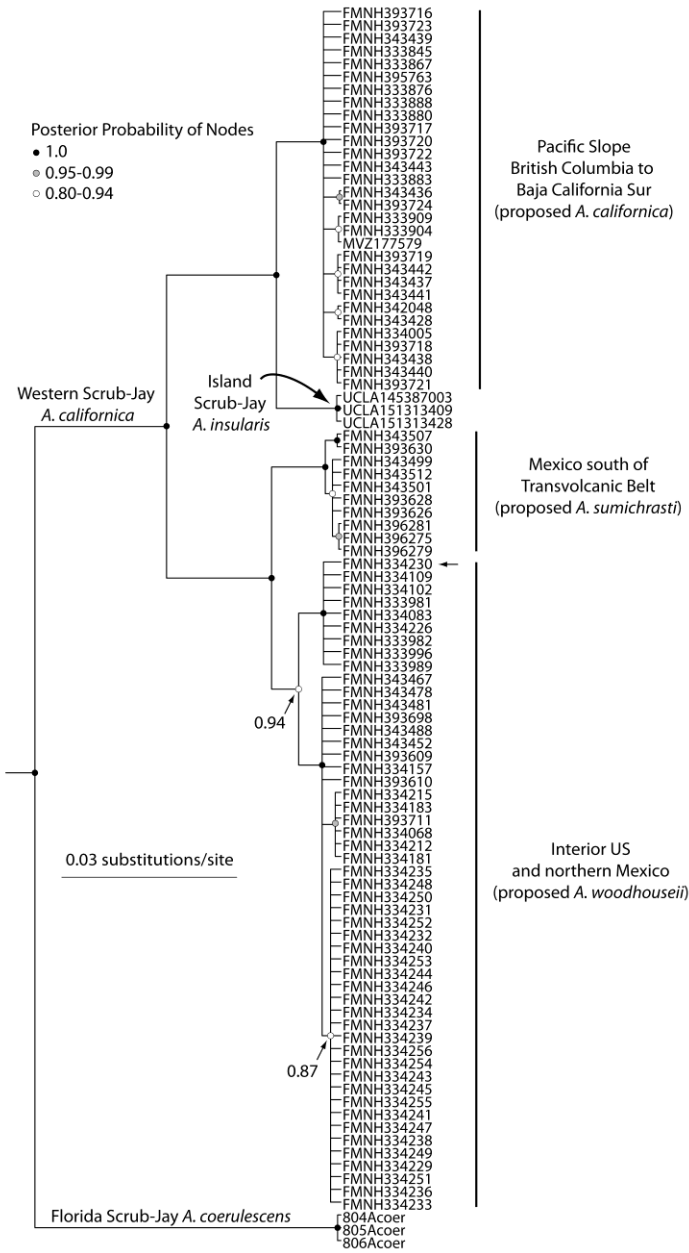


Figure 1. BEAST consensus tree of scrub-jays based on *cyt b* mtDNA sequences. Figure reproduced from Gowen et al. (2014).

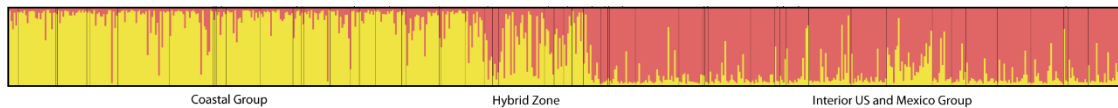


Figure 2. Structure analysis using 13 nuclear microsatellites of scrub-jays. Each line is an individual, yellow represents *californica* genotype and red represents *woodhouseii* genotype. Populations on the left are all identified phenotypically as *californica*, while those on the right are *woodhouseii*. Individuals in the hybrid zone are admixed phenotypically and genotypically. Figure reproduced from Gowen et al. (2014).

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Submitted by:

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Date of Proposal: 27 March 2015

Adopt “Whitestart” as the English surname of species of the genus *Myioborus***Background:**

The English name Redstart is currently used in North America to incorrectly identify three species of the genus *Myioborus*: *Myioborus pictus* (Painted Redstart), *Myioborus miniatus* (Slate-throated Redstart), and *Myioborus torquatus* (Collared Redstart).

While traditional, this misappropriation in my opinion is not only confusing, but also inaccurately ties the coloration of the breast or wings of these species to their name and not the distinguishing feature common to species in the genus *Myioborus*, this feature being a white tail. Adding further confusion is the addition of Common Redstart (*Phoenicurus phoenicurus*) to the AOU checklist, following passage of Proposal 2015-C-3.

Redstarts are now known to be part of the Old World flycatcher family Muscicapidae. The family Muscicapidae is restricted to Europe, Africa and Asia. Whitestarts on the other hand are part of the New World warbler family Parulidae. They, as members of the genus *Myioborus*, are identified as having white on the tail. “Start” of course is the modern English reflex of Middle English stert, Old English steort, tail of an animal. North American species to which we attribute the errant English name “Redstart” all have the prominent white outer tail feathers characteristic of the genus *Myioborus*. Other current authorities, such as the Handbook of the Birds of the World (vol 1-16), and IOC World Bird Names, version 3.04, assign the English surname of each of these species as “Whitestart”.

Recommendation:

Based on the above, I believe we could clarify and reduce confusion by changing the English names of *Myioborus pictus* (Painted Redstart), *Myioborus miniatus* (Slate-throated Redstart), and *Myioborus torquatus* (Collared Redstart) to the more appropriate Painted Whitestart, Slate-throated Whitestart, and Collared Whitestart.

This change has three advantages: (1) it eliminates misleading names from North American birds, (2) it prevents widespread confusion on naming conventions, and (3) it increases knowledge of correct species taxonomy and emphasizes its importance in bird identification.

If we keep the names as they are, we would thus continue to misappropriate and perpetuate the ignorance of the general public. Likewise, we already have the English name “Whitestart” for the genus *Myioborus*, already accepted by multiple authorities, of which the structure of the English name would be familiar, pronounceable, and far more accurate.

Submitted by: Jonathan Coffey

Date of Proposal: 28 March 2015

Lump Common Redpoll *Acanthis flammea* and Hoary Redpoll *A. hornemanni* into a single species

Effect on NACC: 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.

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. However, Troy (1985) documented substantial overlap in phenotypic variation among *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 polymorphisms or 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), while 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. Mason and Taylor

(2015) also took bill and plumage measurements in addition to RNA samples of multiple tissues from ten individuals in a single wintering flock, 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 represents 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 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 is 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, while multigenic patterns of differential gene expression did correlate with phenotypic variation.

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) suggest 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) also 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, continuous phenotypic variation, and overlapping suitable habitat among currently recognized species in the genus *Acanthis*. While the possibility persists that *A. hornemanni* and *A. flammea* 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.

Recommendation:

Lump *Acanthis flammea* and *A. hornemanni* into a single species, *A. flammea*.

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Figures:

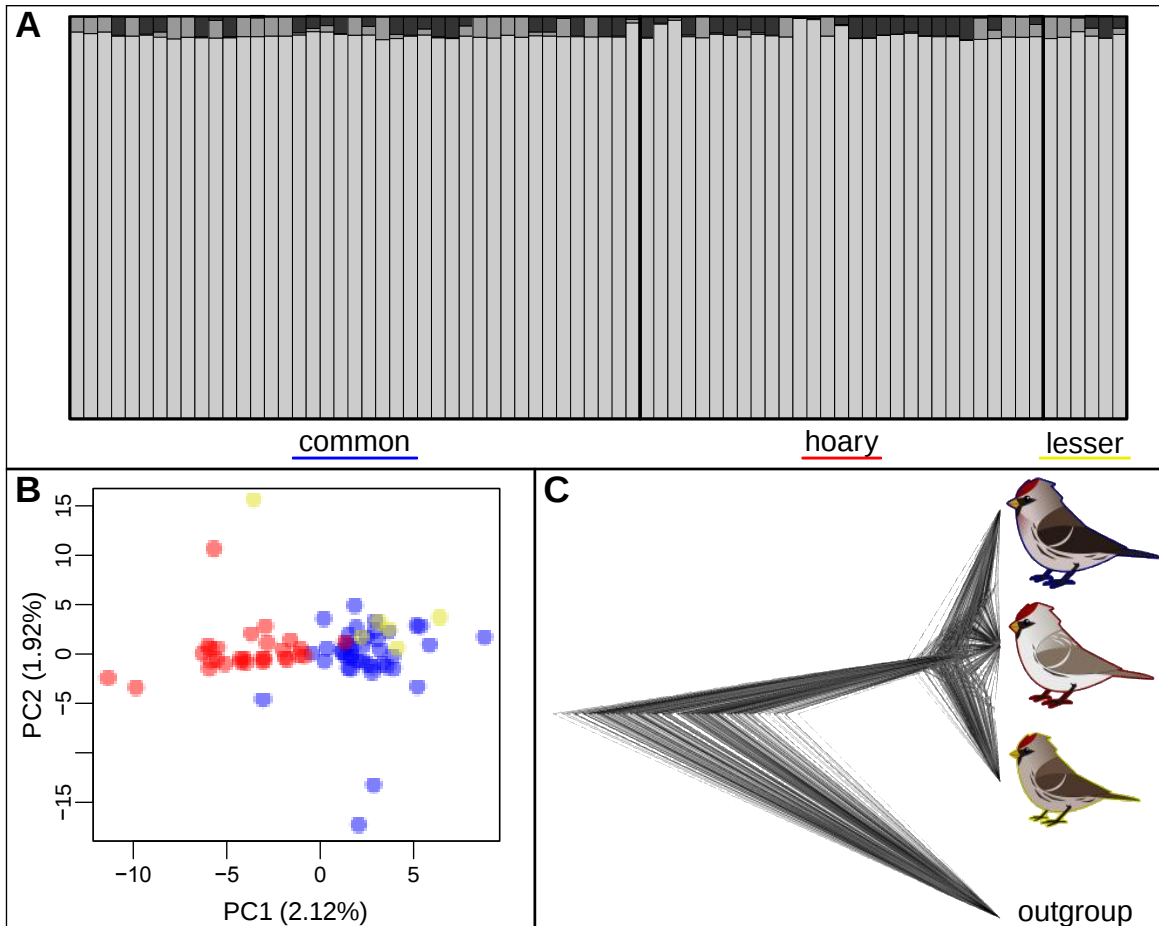


Figure 1: Redpoll population genetic analyses. (A) Bayesian assignment probabilities from STRUCTURE showing lack of population clustering among currently recognized redpoll species using 20 721 SNPs. (B) Genetic PCA plot indicating weak population structure among currently recognized species of redpolls. 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).

Submitted by:

Nicholas A. Mason and Scott A. Taylor, Cornell University

Date of Proposal: 23 April 2015

Revise generic assignments of woodpeckers in the genus *Picoides***Background:**

The current classification of the genus *Picoides* was created by Short (1982) based mostly on body plumage coloration. All small, pied North American woodpeckers are now lumped into this genus:

Picoides scalaris (Ladder-backed Woodpecker)
Picoides nuttallii (Nuttall's Woodpecker)
Picoides pubescens (Downy Woodpecker)
Picoides fumigatus (Smoky-brown Woodpecker)
Picoides villosus (Hairy Woodpecker)
Picoides arizonae (Arizona Woodpecker)
Picoides stricklandi (Strickland's Woodpecker)
Picoides borealis (Red-cockaded Woodpecker)
Picoides albolarvatus (White-headed Woodpecker)
Picoides dorsalis (American Three-toed Woodpecker)
Picoides arcticus (Black-backed Woodpecker)

New Information:

In a series of excellent studies, now more than ten years old, Weibel and Moore (2002a, 2002b) used molecular genetics to show that this genus is actually mix of distantly related species. As stated by Weibel and Moore (2002a; p. 65), their results indicate “that this large, cosmopolitan genus is in need of systematic revision in order to reflect evolutionary history”. Since then other notable studies (e.g., Winkler et al. 2014, Fuchs and Pons 2015) have supported the findings of Weibel and Moore (2002b, p. 255) that “it is clear that the genus *Picoides* as presently defined is an arbitrary collection of species that were lumped together” and “the molecular-based species tree...shows that similarities in non-molecular characteristics arose via convergent evolution” (e.g., Weibel and Moore 2005). In short, “the genus should be split” (Weibel and Moore 2002a p. 73). These conclusions were supported in a comprehensive study by Fuchs and Pons (2015), who made similar recommendations to split the genus *Picoides*. Fuchs and Pons (2015) suggested nine genera of pied woodpeckers. Those who study woodpecker behavior in the field would agree that many species in this genus are only distantly related, as evidenced by distinctly different behaviors, calls, and even drumming cadences.

This is an appropriate time for the recommendations of these research studies to be seriously considered by the AOU, as several prominent but distantly-related members of this genus are declining and at-risk. Most notably, the Black-backed Woodpecker (*Picoides arcticus*) has been proposed for listing under the Endangered Species Act (Federal Register, 9 April, 2013, Vol. 78:21086-21097), while the White-headed

Woodpecker (a distantly related species, but nevertheless called *Picoides albolarvatus*) is a sensitive, endangered, or species of concern in all states and provinces where it occurs. The Red-cockaded Woodpecker (a species related to the White-headed Woodpecker but only distantly to the Black-backed Woodpecker, now called *Picoides borealis*) has been considered an endangered species in the southeastern U.S. for decades (Federal Register, 13 October 1970, Vol. 35 199:16047). I recommend that the AOU revise the genus *Picoides* based on recommendations of Fuchs and Pons (2015) and classify species in an order that better reflects their true relatedness and evolutionary past. This will aid researchers who are tasked with providing recommendations to resource managers for these at-risk woodpecker species.

Phylogenetic trees based on the combined nuclear and mitochondrial data from Fuchs and Pons (2015):

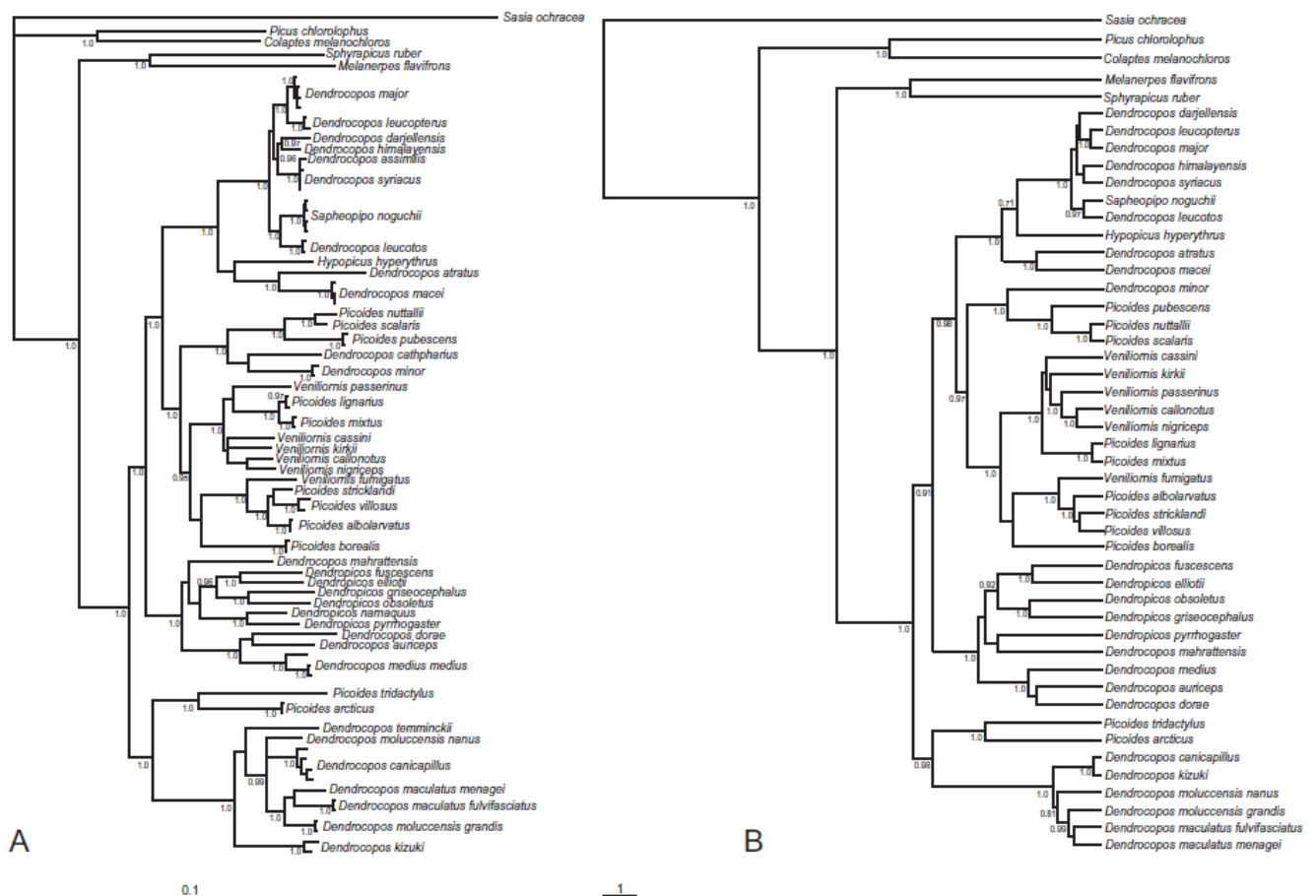


Fig. 4. 50% Majority rule consensus tree obtained from the analyses of the concatenated nuclear introns and mitochondrial locus (partitioned by locus and codon position – six partitions; A), and species tree analyses using the phased nuclear alleles and the mitochondrial locus (*Beast, B). Posterior probabilities are indicated when greater than 0.95 (concatenated) or 0.70 (species tree). The two topologies were very similar and differences only involved poorly supported nodes.

Recommendation:

A revised classification for this genus was provided by Fuchs and Pons (2015; p. 36) based on their own research and recommendations by Weibel and Moore (2002a,

2002b) and Winkler et al. (2014). This new classification recognizes nine genera of pied woodpeckers, and divides species currently placed in *Picoides* among four genera, two of which (*Dryobates* and *Leuconotopicus*) are newly resurrected. I recommend acceptance of the Fuchs and Pons (2015) revision of *Picoides*, as below (species in the AOU area are in bold and include two species recognized by the AOU, *dorsalis* and *arizonae*, but not included in Fuchs and Pons):

Picoides (Lacépède 1799): **arcticus**, **dorsalis**, *tridactylus*

Dryobates (Boie 1826): *cathpharius*, *minor*, **pubescens**, **scalaris**, **nuttallii**

Leuconotopicus (Malherbe 1845): **albolarvatus**, **arizonae**, **borealis**, **fumigatus**, **stricklandi**, **villosus**

Veniliornis (Bonaparte 1825): *spilogaster*, *passerinus*, *frontalis*, *maculifrons*, *cassini*, *affinis* (including *chocoensis*), *kirkii*, *callonotus*, *sanguineus*, *dignus*, *nigriceps*, *lignarius*, *mixtus*

[NOTE from Committee Chair: These changes would necessitate a new linear sequence for species currently placed in *Picoides* (note that accidental species *Dendrocopos major* also belongs to the same clade), which according to the combined trees in Fuchs and Pons (2015) would be as follows:

Picoides dorsalis (American Three-toed Woodpecker)

Picoides arcticus (Black-backed Woodpecker)

Dendrocopos major (Great Spotted Woodpecker) A

Dryobates pubescens (Downy Woodpecker)

Dryobates scalaris (Ladder-backed Woodpecker)

Dryobates nuttallii (Nuttall's Woodpecker)

Leuconotopicus borealis (Red-cockaded Woodpecker)

Leuconotopicus fumigatus (Smoky-brown Woodpecker)

Leuconotopicus albolarvatus (White-headed Woodpecker)

Leuconotopicus villosus (Hairy Woodpecker)

Leuconotopicus arizonae (Arizona Woodpecker)

Leuconotopicus stricklandi (Strickland's Woodpecker)]

Literature Cited:

- Fuchs, J., and J. M. Pons. 2015. A new classification of the pied woodpeckers assemblage (Dendropicini: Picidae) based on a comprehensive multi-locus phylogeny. *Molecular Phylogenetics and Evolution* 88: 28–37.
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- Weibel, A. C., and W. S. Moore. 2002a Molecular phylogeny of a cosmopolitan group of woodpeckers (genus *Picoides*) based on COI and cyt b mitochondrial gene sequences *Molecular Phylogenetics and Evolution* 22: 65–75.
- Weibel, A. C., and W. S. Moore. 2002b A test of a mitochondrial gene-based phylogeny of woodpeckers (genus *Picoides*) using an independent nuclear gene, β -fibrinogen intron 7. *Molecular Phylogenetics and Evolution* 22: 247–257.

- Weibel, A. C., and W. S. Moore. 2005. Plumage convergence in *Picoides* woodpeckers based on a molecular phylogeny, with emphasis on plumage convergence in Downy and Hairy woodpeckers. *Condor* 107: 797–809.
- Winkler, H., A. Gamauf, F. Nittinger, and E. Haring. 2014. Relationships of old world woodpeckers (Aves: Picidae): new insights and taxonomic implications. *Annalen des Naturhistorischen Museums in Wien, B* 116: 69–86.

Submitted by:

Teresa Lorenz, Ph.D., PNW Research Station

Date of Proposal: 4 June 2015

Split Cuban Bullfinch *Melopyrrha nigra* into two species

Background: The current (7th Edition) of the Check-list considers the Cuban Bullfinch *Melopyrrha nigra* to be a single species that breeds on Cuba, the Isle of Pines, and the Cayman Islands. The species has generally been considered to be polytypic, with *M. n. nigra* found on Cuba and the Isle of Pines, and *M. n. taylori* on Grand Cayman.

New Information:

Garrido *et al.* (2014) have recently proposed that these be recognized as separate species, based on differences in size, coloration, and vocalizations. The bullfinches from the Cayman Islands are consistently and significantly larger than those from Cuba, and larger-billed (e.g. male culmen length av. 11.3 mm on Cuba and 12.9 mm from Grand Cayman). In addition, the plumage of the Cuban birds is said to be glossy black whereas that of the birds from Grand Cayman is less glossy. The females are duller in coloration, with the color dimorphism somewhat greater in the Cayman Islands birds. The call of the Cayman birds is an insect-like *chi-p* or *zee zee* whereas the call of the Cuban birds is a staccato *chi-dip* and a thin *tsee*. “Songs of Cuban birds reach distinctly higher frequencies than those on Grand Cayman during the first two seconds. Songs of *M. taylori* [Grand Cayman] possess a series of introductory elements with more uniform frequency than Cuban birds, with a duration of c. 1.5 seconds, followed by a drop rather than an increase in frequency.” On Cuba there are different dialects in different regions. Songs are illustrated in the paper.

Recommendation:

The differences in size, coloration, and vocalizations are clear. However, this is usual for island populations. Breeding may commence earlier in the season on Grand Cayman Island than on Cuba, but there is overlap in breeding chronology. I would be happy to accept the authors’ proposal to accept these as separate species, but note that these differences are less than those for some other island isolates that we have not accepted as separate species. I do not see any inherent need to be consistent; nevertheless, on the basis of these data I do not see any immediate need to split these taxa at the specific level.

Literature Cited:

Garrido, O. H., Wiley, J. W., Kirkconnell, A., Bradley, P. E., Günther-Calhoun, A., and Rodriguez, A. 2014. Revision of the endemic West Indian genus *Melopyrrha* from Cuba and the Cayman Islands. *Bull. Brit. Orn. Club* 134: 134-144.

Submitted by: J. D. Rising

Date of proposal: 18 June 2015

**Split Rufous-naped Wood-Rail *Aramides albiventris* from
Gray-necked Wood-Rail *Aramides cajaneus***

Background:

The taxa presently associated with *Aramides cajaneus* had a somewhat convoluted taxonomic history in the 19th and early 20th century. *Aramides cajaneus* itself was described based on a bird from Cayenne, French Guiana, and several names were proposed in the following centuries for Central American birds allied to it. The status (specific or subspecific) and limits of these putative taxa, however, were rather controversial (reviewed in Marcondes and Silveira 2015), until Peters (1934) and Hellmayr and Conover (1942) lumped them all as subspecies of *Aramides cajaneus*. That treatment has been followed, largely uncritically, into the modern era (e.g., Taylor 1996, Taylor 1998), such that *A. cajaneus* is considered a polytypic species containing nine subspecies, eight of which occur in the NACC area.

New Information:

Marcondes and Silveira (2015) reviewed the morphological (very good sampling – 800 skins and good geographical coverage) and vocal (not such good sampling - 92 recordings, with significant geographical gaps, but see below) variation of *Aramides cajaneus* throughout its range. In what concerns this Committee, we established that the mountains of the Chorotega Volcanic Front in lower Central America segregate populations that differ considerably in morphology and voice. In comparison with birds from South America, Panama and southwestern Costa Rica (*Aramides cajaneus sensu stricto*), those from northeastern Costa Rica and further north, to which the name *Aramides albiventris* Lawrence 1868 applies, have a much more strongly-colored nape, have longer bills and tarsi, and a different song.

Plumage differentiation (Marcondes and Silveira 2015, fig. 3), albeit shown in only one plumage patch, is fixed, and the two forms replace each other parapatrically with no intermediates (Marcondes and Silveira 2015, fig. 2). Morphometric differentiation is also sharply geographical, with clear discontinuity in variation in the area where the two forms abut each other (Marcondes and Silveira 2015, fig. 4). Finally, most striking is the difference in song. The vocal sampling for *A. albiventris* is rather sparse (Marcondes and Silveira 2015, fig. 5), but we argue that this is not an issue because there are no vocal intermediates between the two taxa. In fact, the songs are different to the point that it is impossible to come up with hypotheses of homology between their elements (Marcondes and Silveira 2015, figs. 6 and 7), and the degree of differentiation is comparable to that observed between *A. cajaneus* and other species in the genus, such as *A. ypecaha* or *A. saracura*. Below are links to examples of the song of each taxa:

A. cajaneus: <http://macaulaylibrary.org/audio/51765>

A. albiventris: <http://macaulaylibrary.org/audio/23151>

Recommendation:

We suggest that sharp parapatric differentiation from *A. cajaneus* in plumage, morphometrics, and especially song are enough indirect evidence to corroborate species status for *A. albiventris* under any species concept. We propose the English name Rufous-naped Wood-rail. White-bellied Wood-rail, as proposed by the IOC (<http://www.worldbirdnames.org/updates/proposed-splits/>), is not adequate, because this character is not constant within the species (Marcondes and Silveira 2015, fig. 10).

Literature Cited:

- Hellmayr CE, Conover B (1942) Catalogue of birds of the Americas and the adjacent islands in Field Museum of Natural History, part 1, number 1. Field Museum of Natural History Zoological Series vol. 13, 636 pp.
- Marcondes RS, Silveira LF (2015). A taxonomic review of *Aramides cajaneus* (Aves, Gruiformes, Rallidae) with notes on morphological variation in other species of the genus. Zookeys 500:111-140.
- Peters JL (1934) Check-List of Birds of the World, volume 2. Harvard University Press, Cambridge, Massachusetts, 401 pp.
- Taylor PB (1996) Family Rallidae. In: Del Hoyo J, Elliot A, Sargatal J (Eds.) Handbook of the Birds of the World, vol. 3. Lynx Edicions, Barcelona, 821 pp.
- Taylor PB (1998) Rails: A Guide to the Rails, Gallinules and Coots of the World. Pica Press, Sussex, 600 pp.

Submitted by:

Rafael S. Marcondes, Louisiana State University
Luís Fábio Silveira, Universidade de São Paulo

Date of Proposal: 9 July 2015

Move Motacillidae and Prunellidae to the “core passeridans”**Effect on AOU-CLC Area:**

Acceptance of part A of this proposal would mean moving Motacillidae (for which several species are known, many as vagrants, from the AOU-CLC area) from its current position between Prunellidae and Bombycillidae into the core Passerida. However, exactly where in the sequence Motacillidae best fits will be more contentious, especially given the current uncertainty over familial limits and the great recent flux of species from one family to another.

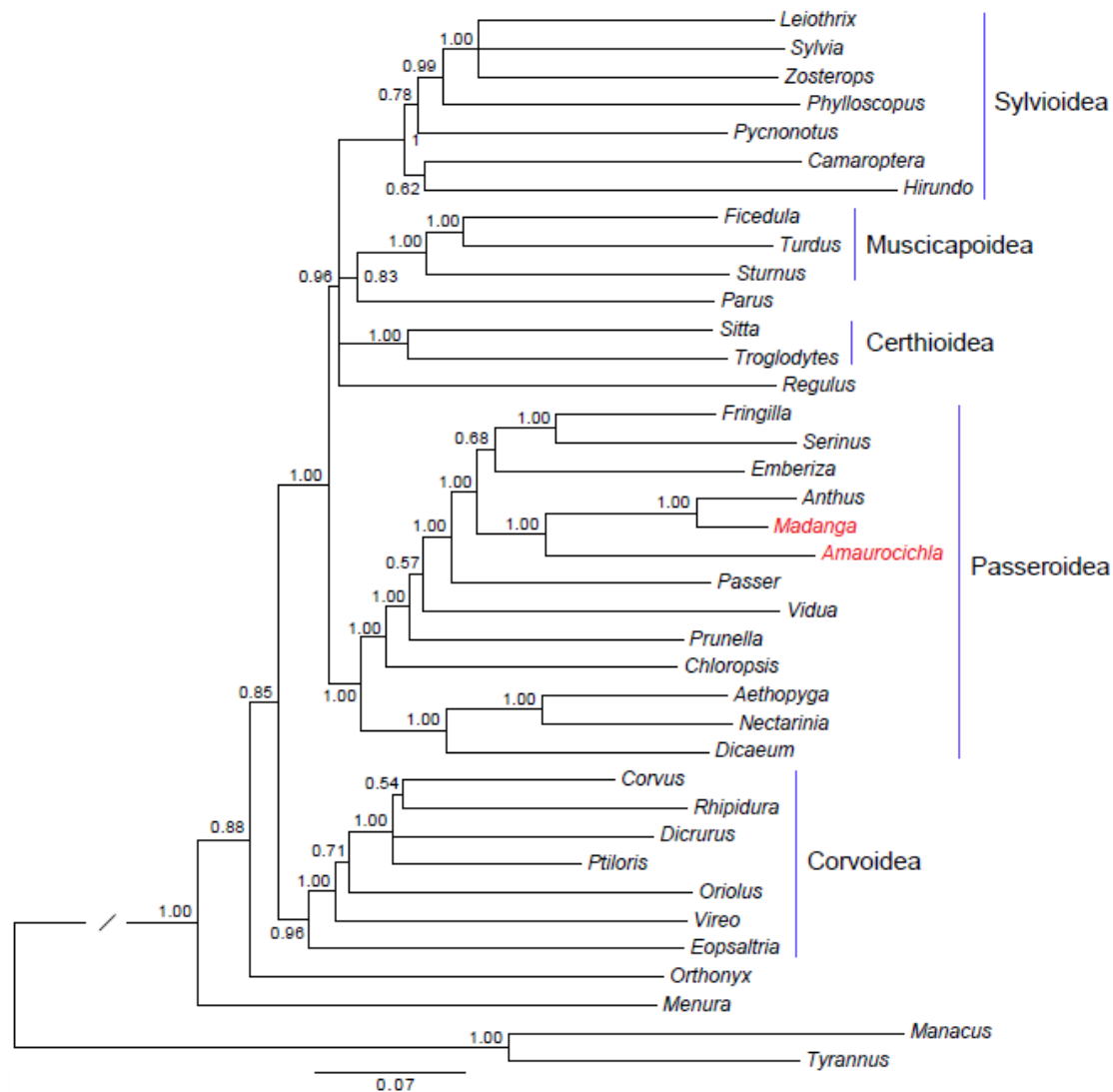
Acceptance of part B of this proposal would mean moving Prunellidae (for which a single species, Siberian Accentor *Prunella montanella*, is known from the AOU-CLC area as an accidental) from its current position in the linear sequence between Sturnidae and Motacillidae into the core Passerida.

Background:

The pipits and wagtails Motacillidae and the accentors Prunellidae are currently placed in our linear sequence between Sturnidae and Bombycillidae (<http://checklist.aou.org/taxa>). However, since Sibley and Ahlquist (1990), several molecular phylogenetic studies (e.g., Groth 1998; Barker et al. 2002, 2004; Johansson et al. 2008; Treplin et al. 2008) indicate that the Motacillidae and Prunellidae are actually core passeridan oscines (sensu Cracraft 2014).

New Information:

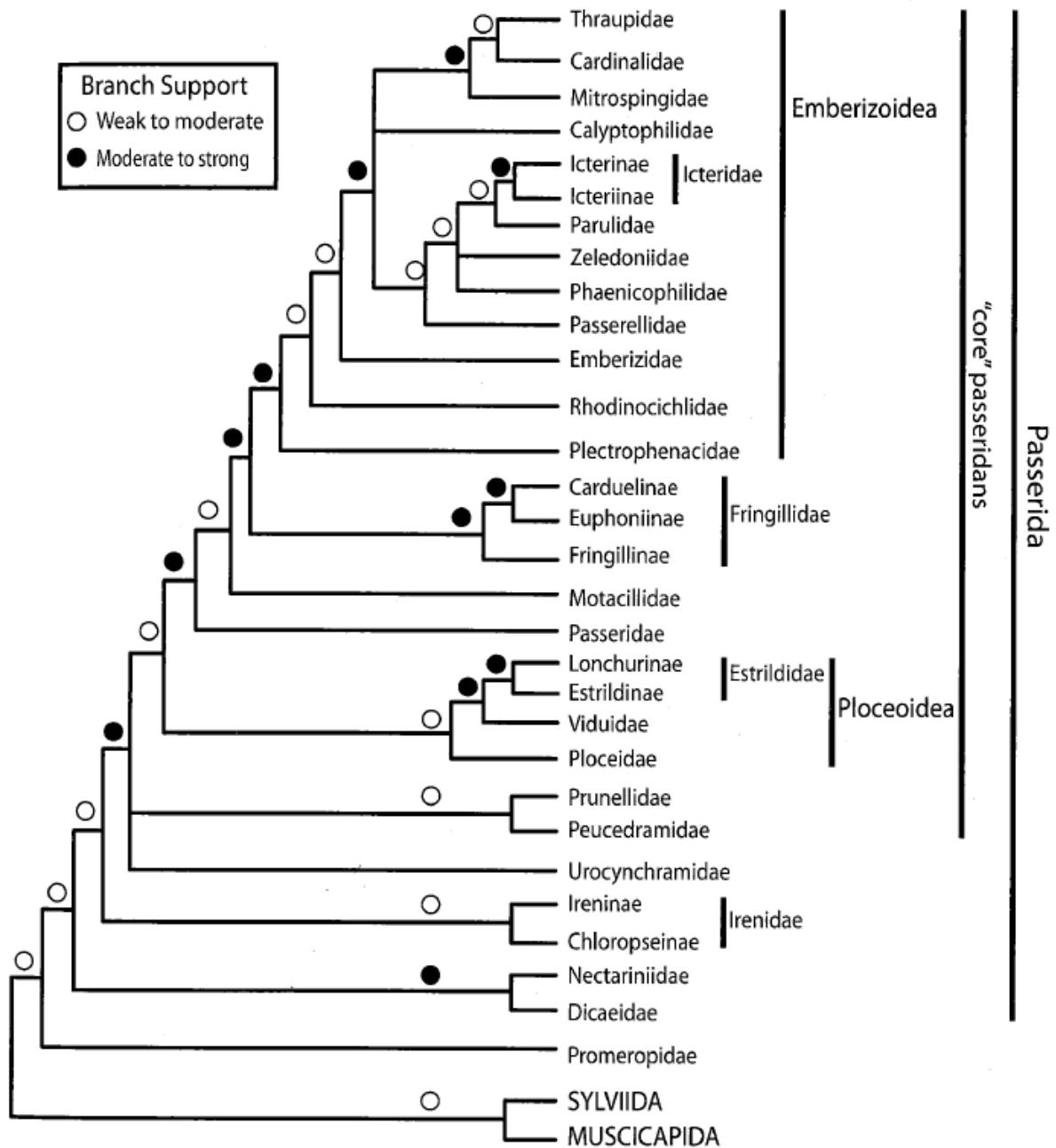
A new DNA phylogeny (Alström et al. 2015 – see tree below) focused on the finding that two odd Old World insular taxa (*Madanga* and *Amaurocichla*) are nested within Motacillidae recovers a sister-group relationship between Motacillidae and Emberizidae-Fringillidae within the Passeroidea.



In Alström et al. (2015), *Prunella* is sister to a clade including *Vidua*, *Passer*, the motacillids, the emberizids, and the fringillids, but *Ploceus*, which is sister to *Prunella* in Barker et al. (2002, 2004) was not included, whereas in the latter two studies *Vidua* was not included.

Cracraft's summary tree in Dickinson and Christidis (2014 – see tree below) treated Motacillidae as sister to a Fringillidae-Emberizoidea clade, but with weak to moderate branch support. He placed Prunellidae as sister to Peucedramidae, again with weak to moderate branch support.

Figure 4. Parvorder Passerida



In Cracraft's (2014) linear sequence, Prunellidae precedes Peucedramidae, and Motacillidae precedes Fringillidae:

Parvorder Passerida

- Family Promeropidae
- Family Dicaeidae
- Family Nectariniidae
- Family Irenidae
 - Subfamily Ireninae
 - Subfamily Chloropseinae
- Family Urocynchramidae *incertae sedis*
- Family Prunellidae
- Family Peucedramidae
- Superfamily Ploceoidea
 - Family Ploceidae
 - Family Estrildidae
 - Subfamily Estrildinae
 - Subfamily Lonchurinae
 - Family Viduidae
- Family Passeridae
- Family Motacillidae
- Family Fringillidae
 - Subfamily Fringillinae
 - Subfamily Euphoniinae
 - Subfamily Carduelinae
 - Tribe Coccothraustini
 - Tribe Drepanidini
 - Tribe Carpodacini
 - Tribe Pyrrhulini
 - Tribe Carduelini
- Superfamily Emberizoidea⁵
 - Family Plectrophenacidae
 - Family Rhodinocichlidae
 - Family Emberizidae⁶
 - Family Passerellidae
 - Family Phaenicophilidae
 - Family Zeledoniidae
 - Family Parulidae
 - Family Icteridae
 - Subfamily Icteriinae
 - Subfamily Icterinae
 - Family Calyptophilidae
 - Family Mitrospingidae
 - Family Cardinalidae

As for the taxa nearest Motacillidae and Prunellidae in the legacy AOU-CLC linear sequence, the position of the Bombycillidae has been unresolved (Spellman et al. 2008), but Cracraft (2014) included the Superfamily Bombycilloidea within the Parvorder Muscicapida. Sturnidae, however, clearly belongs in the Superfamily Muscicapoidae (Cracraft 2014, Alström et al. 2015).

Subsequent Treatments:

The 4th edition of the Howard and Moore checklist (Dickinson and Christidis 2014) followed Cracraft's (2014) linear sequence, as outlined above. In the SACC list (2015), Motacillidae precedes Thraupidae and the rest of the Emberizoidea; Fringillidae follows the Emberizoidea. Prunellidae does not occur in South America.

Recommendation:

The move of Motacillidae (part A) into the core passeridans seems non-controversial and overdue, and I recommend acceptance. We could simply follow Cracraft's (2014) treatment of Motacillidae as sister to the Fringillidae-Emberizoidea. However, I think exactly where in the sequence it is best inserted should be discussed among the committee, particularly as committee members have active research programs on some of the groups involved and can better advise. Please vote yes or no for (part A.1) movement of Motacillidae into the core Passerida, and then (part A.2) yes or no to following Cracraft's placement as sister to Fringillidae. If voting no to part A.2, please provide alternative(s) and rationale.

The move of Prunellidae (part B) into the core passeridans similarly seems strongly warranted, so my recommendation for this subproposal is also for acceptance. Perhaps Cracraft's (2014) placement of Prunellidae as sister to Peucedramidae is the best course, but again, the exact placement of Prunellidae within the Passeroidea should be determined by committee discussion. Please vote yes or no for (part B.1) movement of Prunellidae into the core Passerida, and then (part B.2) yes or no to following Cracraft's placement as sister to Peucedramidae. If voting no to the latter, please provide alternative(s) and rationale.

Literature Cited:

- Alström, P., K. A. Jønsson, J. Fjeldså, A. Ödeen, P. G. P. Ericson, and M. Irestedt. 2015. Dramatic niche shifts and morphological change in two insular bird species. *Royal Society Open Science* 2:140364.
- Barker, F. K., G. F. Barrowclough, and J. G. Groth. 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence. *Proceedings of the Royal Society of London* 269:295–308.
- Barker, F. K., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences* 101:11040–11045.
- Cracraft, J. 2014. Avian higher-level relationships and classification: Passeriformes. Pp. xvii-xlv in: Dickinson, E.C. and L. Christidis (eds.) 2014. *The Howard and Moore Complete Checklist of the Birds of the World*. 4th ed., vol. 2. Aves Press, Eastbourne, U.K.
- Dickinson, E.C. and L. Christidis (eds.) 2014. *The Howard and Moore Complete Checklist of the Birds of the World*. 4th ed., vol. 2. Aves Press, Eastbourne, U.K.

- Groth, J. G. 1998. Molecular phylogenetics of finches and sparrows: consequences of character state removal of cytochrome b sequences. *Molecular Phylogenetics & Evolution* 10:377–390.
- Johansson, U. S., J. Fjeldså, and R. C. K. Bowie. 2008. Phylogenetic relationships within Passerida (Aves: Passeriformes): a review and a new molecular phylogeny based on three nuclear intron markers. *Molecular Phylogenetics and Evolution* 48:858–876.
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- Sibley, C. G., and J. E. Ahlquist. 1990. *Phylogeny and Classification of Birds*. Yale University Press, New Haven, Connecticut.
- Spellman, G. M., A. Cibois, R. G. Moyle, K. Winker, and F. K. Barker. 2008. Clarifying the systematics of an enigmatic avian lineage: what is a bombycillid? *Molecular Phylogenetics and Evolution* 49:1036–1040.
- Treplin, S., R. Siegert, C. Bleidorn, H. S. Thompson, R. Fotso, and R. Tiedemann. 2008. Molecular phylogeny of songbirds (Aves: Passeriformes) and the relative utility of common nuclear marker loci. *Cladistics* 24:328–349.

Submitted by:

Pam Rasmussen, Michigan State University

Date of Proposal: 19 October 2015

Change the linear sequence of genera in the family Odontophoridae**Background:**

Our current linear sequence of the family Odontophoridae has remained unchanged from the seventh edition of the checklist (AOU 1998). The sequence of genera is as follows:

Dendrortyx
Oreortyx
Callipepla
Philortyx
Colinus
Odontophorus
Dactylortyx
Cyrtonyx
Rhynchortyx

No source was provided for this linear sequence. Johnsgard (1988) is sometimes cited for relationships among New World quail but his phyletic hypothesis is not entirely congruent with our sequence.

New Information:

Hosner et al. (2015 – see tree below) recently published a molecular phylogeny, based on sequences of three mitochondrial genes and eight nuclear introns, of the Odontophoridae. Their study included all genera and most species (23/33) in this family; most of the missing species were from the genus *Odontophorus*. Their concatenated tree confirmed that the Old World genus *Ptilopachus* was sister to a clade containing all New World species. Within the New World clade, *Rhynchortyx cinctus* was sister to all other species, which were divided into two clades, one consisting of *Oreortyx*, *Dendrortyx*, *Philortyx*, *Colinus*, and *Callipepla*, and the other of *Cyrtonyx*, *Dactylortyx*, and the large genus *Odontophorus*. Support for most nodes in the tree was excellent (100% bootstrap, 1.0 posterior probability), although a few nodes, half of them within *Odontophorus*, were less well supported.

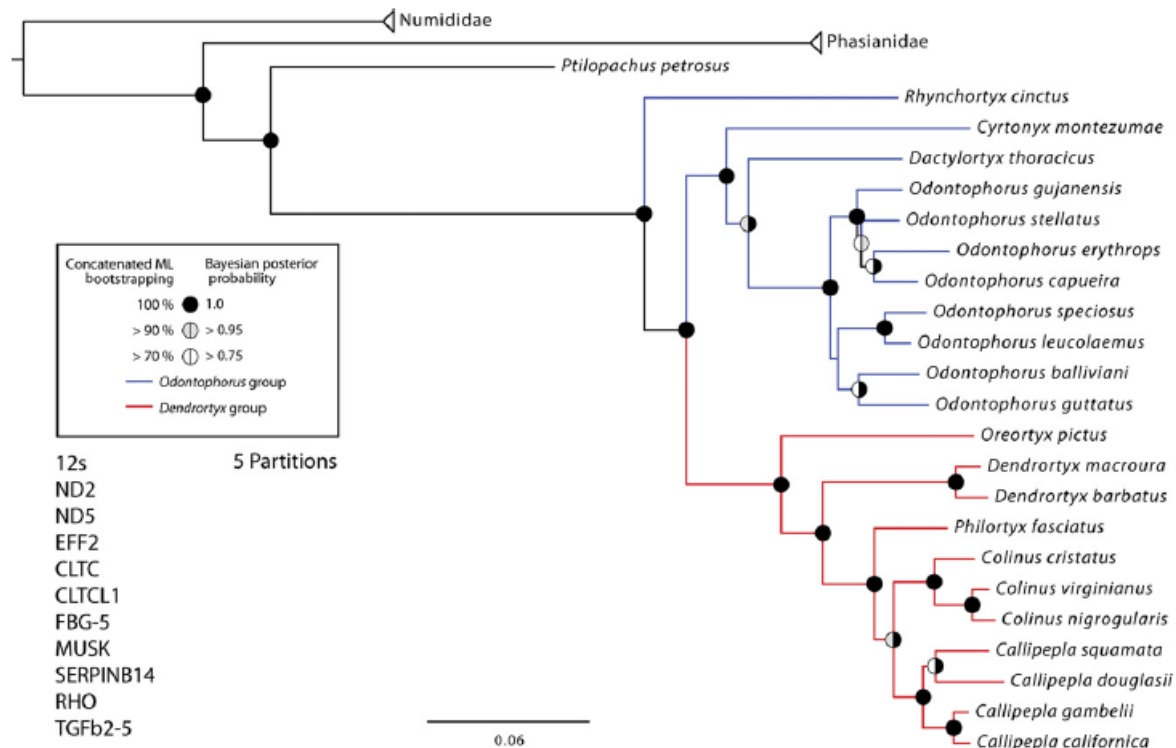


Figure 2 Concatenated maximum likelihood (ML) phylogeny of New World quail, inferred from 11 gene alignments. Support for each node is the ML bootstrap percentage (GARLI) and the Bayesian posterior probability (BEAST).

Recommendation:

Hosner et al. (2015) presented by far the best phylogenetic information on relationships within the Odontophoridae. Although their sampling (and discrepancies within *Odontophorus* depending on the type of data analysis) precludes making conclusions about species relationships within genera, their data on relationships of genera are well supported. I recommend that we modify the linear sequence of genera for this family to conform to our sequencing protocols (species listed from the deepest node in the tree, beginning with the branch with the least number of species). This would result in the following linear sequence:

Rhynchortyx
Oreortyx
Dendrortyx
Philortyx
Colinus
Callipepla
Cyrtonyx
Dactylortyx
Odontophorus

Literature Cited:

- Hosner, P. A., E. L. Braun, and R. T. Kimball. 2015. Land connectivity changes and global cooling shaped the colonization history and diversification of New World quail (Aves: Galliformes: Odontophoridae). *J. Biogeogr.* 42: 1883-1895.
- Johnsgard, P. A. 1988. The quails, partridges, and francolins of the world. Oxford University Press, New York.

Submitted by: Terry Chesser

Date of Proposal: 25 October 2015

Merge Caribbean Coot *Fulica caribaea* into American Coot *F. americana***Background:**

Fulica caribaea, the Caribbean Coot, was first included in the AOU Checklist in the 6th edition (1983), when our geographical coverage expanded to include the West Indies. At this time, the AOU also recognized the first records of this species from the US, based on a specimen and six other birds observed near Ft. Lauderdale, Florida (Bolte 1974), and a record from Tennessee. The distinguishing feature of *F. caribaea* is its broader, higher, and bulbous frontal shield, whereas *F. americana* has a lower, narrower, and less bulbous frontal shield, typically with a red callus at the top of the shield; however, in some individuals of *F. americana* the callus is not present and the white shield can appear somewhat enlarged and yellowish. Photographs of the first and third birds found near Ft Lauderdale were sent to the NMNH and the AMNH for verification, and Alexander Wetmore and Bud Lanyon were among those who concurred in the identifications. The second bird found near Ft Lauderdale was eventually collected and deposited in the National Museum (USNM 567252). Bolte (1974) noted at the time that the intermediate frontal shields of some *F. americana* suggest that the two species may have been hybridizing.

The notes for this species in the 6th edition stated the following: “The relationships of *F. americana* and *F. caribaea* are not fully understood; the latter may eventually prove to be a morph of *F. americana*. Individuals with intermediate characteristics have been reported from southern Florida, Cuba, Hispaniola, and St. Croix.” This statement was repeated in the 7th edition (1998) with the additional statement that “Mixed pairs of *F. americana* and *F. caribaea* with young have been observed on St. John, Virgin Islands (1984, Amer. Birds 38: 252).

Most of the data bearing on the relationship of *F. americana* and *F. caribaea* concerns observations of Caribbean Coot-like individuals in North America and their interactions with American Coots. For example, Roberson and Baptista (1988) reviewed characters purported to separate the two species, reviewed records of *F. caribaea* from throughout the US, and conducted new surveys of coots in California. They found additional records scattered across North America, including Michigan, Texas, British Columbia, and Indiana, in addition to Florida and Tennessee. They concluded, based on the geographical spread of these records, reports of hybrids, and their survey findings that a small but noteworthy percentage (1.4%) of California birds had characters typical of *F. caribaea*, that records of this form in North America are indicative of variation within *F. americana* rather than the presence of *F. caribaea* and “that there is no evidence to show that coots of Caribbean origin have occurred anywhere in North America.”

New Information:

McNair and Cramer-Burke (2006) studied nesting of *F. americana* and *F. caribaea* at Southgate Pond on the Caribbean island of St Croix. Using the criteria of Roberson and

Baptista (1988) to distinguish the two forms, they determined that most pairings there were non-assortative. They identified both members of 17 nesting pairs (of 22 total nests): 6 of these were both *F. caribaea*, whereas the other 11 pairs were mixed pairs. Based on this pattern, McNair and Cramer-Burke suggested that *F. americana* and *F. caribaea* are morphs of a single species.

Although unpublished, information on voice (comment from Alvaro Jaramillo on the website of David Sibley, at <http://www.sibleyguides.com/2011/03/the-caribbean-coot-in-north-america/>) also suggests that *F. americana* and *F. caribaea* represent a single species. Jaramillo noted that vocally the two species are “extremely similar if not the same” and that both species respond to calls of *F. americana* on Guadeloupe. This contrasts with the differences in voice typically observed between other species of New World coots.

Recommendation:

The single feature purportedly separating Caribbean Coot *F. caribaea* and American Coot *F. americana* is the morphology of the frontal shield, but this character is inconsistent: both forms occur in both the Caribbean and mainland North America and the forms appear to mate non-assortatively where they have been studied. Thus, morphology and behavior do not serve to separate these two forms. I don’t see any evidence to suggest that they are two species; rather, there may be something of a cline in frontal shield morphology. It would be ideal to have a bit of genetic data as the final nail in the coffin, but a finding of substantial genetic differences would be an extremely surprising result given the rest of the evidence. If we were building a checklist from scratch, I doubt that a two-species arrangement would be seriously considered. I recommend that we merge *Fulica caribaea* into *F. americana*. As for the English name, nothing occurs to me that would be better than simply calling the lumped species American Coot, although I’m open to alternatives.

Literature Cited:

- Bolte, W. J. 1974. Caribbean Coot, *Fulica caribaea*, in Florida. American Birds 28: 734-735.
- Roberson, D., and L. F. Baptista. 1988. White-shielded coots in North America: a critical evaluation. American Birds 42: 1241-1246.
- McNair, D. B., and C. Cramer-Burke. 2006. Breeding ecology of American and Caribbean coots at Southgate Pond, St. Croix: use of woody vegetation. Wilson J. of Ornith. 118: 208-217.

Submitted by: Terry Chesser

Date of Proposal: 29 October 2015

Revise the classification of the Caprimulgiformes

Synopsis: To maintain the monophyly of our current Caprimulgiformes and Apodiformes, this would elevate two families to the rank of order: Steatornithiformes and Nyctibiiformes.

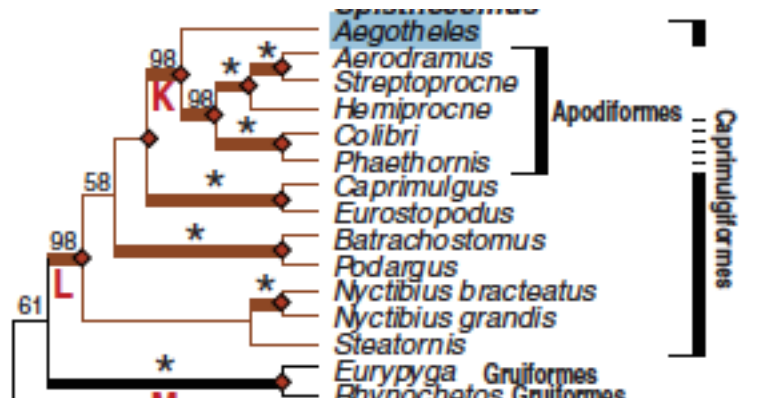
Background:

Our current classification treats the Caprimulgiformes as containing three families: Caprimulgidae (nightjars), Nyctibiidae (potoos), and Steatornithidae (oilbird). Our Apodiformes contains two families: Apodidae (swifts) and Trochilidae (hummingbirds). These two orders have long been regarded as closely related. Traditional classifications also place the Old World Podargidae (frogmouths) and Aegothelidae (owlet-nightjars) in the Caprimulgiformes.

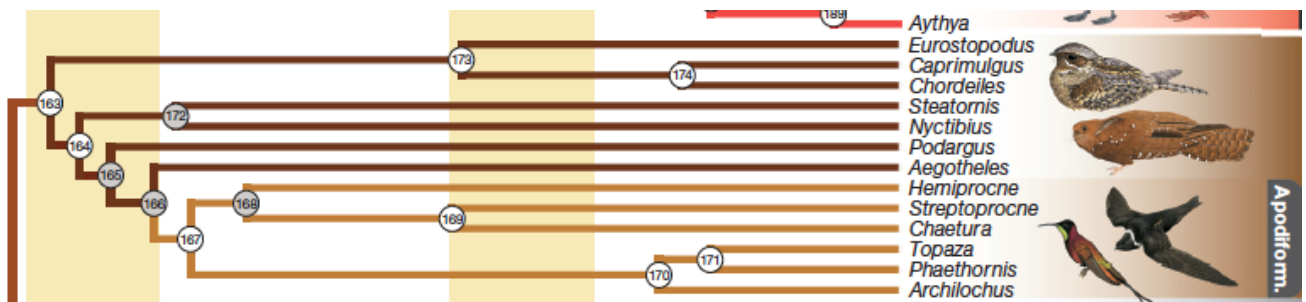
New Information:

Recent genetic data (e.g., Ericson et al. 2006, Hackett et al. 2008, Prum et al. 2015) are concordant in finding that the Aegothelidae are actually sister to Apodidae + Trochilidae, and also that these three families are embedded in the Caprimulgiformes, thus making traditional Caprimulgiformes paraphyletic with respect to Apodiformes.

Here is the relevant portion of the tree from Hackett et al. (2008):



And here is the relevant portion of the tree from Prum et al. (2015):



Cracraft (2013) in Dickinson & Remsen (2013) [despite my objections] maintained the monophyly of Caprimulgiformes by elimination of Apodiformes as an order and inclusion of Trochilidae and Apodidae as families of the Caprimulgiformes. If this proposal is voted down, then Cracraft's solution is the simplest alternative option.

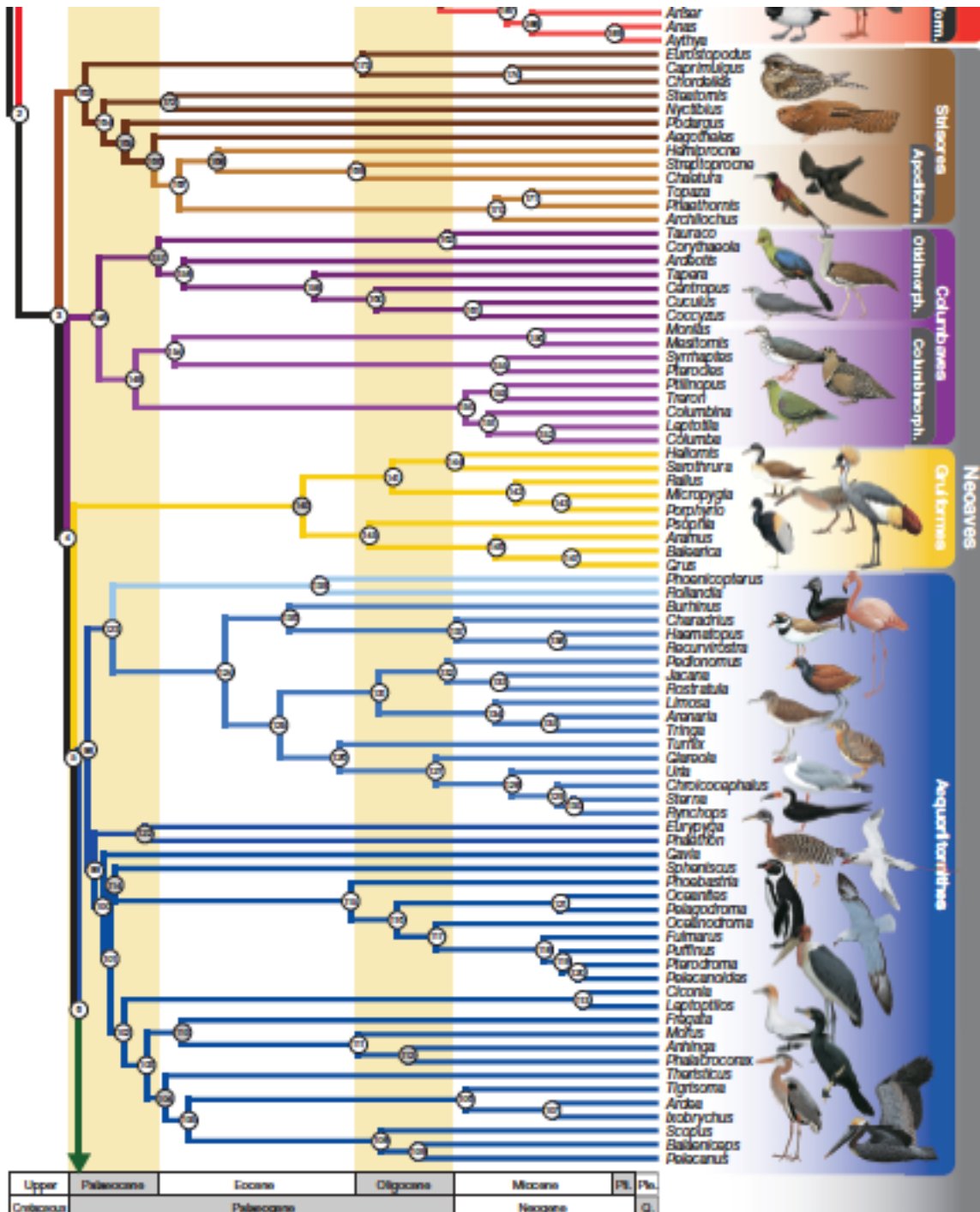
However, an expanded Caprimulgiformes would include several lineages that are as old or older than many other taxa ranked traditionally as orders; it would also be spectacularly heterogeneous in terms of morphology – think of the profound differences, for example, between a potoo and a hummingbird.

On the following page is a broader view of the Prum et al. (2015) time-calibrated tree, with geological time periods along the bottom; calibration points are enumerated in the Supplementary material. The resolution here is lousy; so if anyone needs a pdf, just let me know.

With all appropriate caveats concerning the uncertainty of the underlying data, let's use this figure as a gauge of relative lineage ages. If you draw an imaginary vertical line through the tree in the very early Eocene at roughly 54 mya, the following lineages are predicted to have been evolving separately at that point (with taxa currently ranked as families by NACC marked in red):

1. **Caprimulgidae**
2. **Steatornithidae**
3. **Nyctibiidae**
4. **Aegotheidae**
5. traditional Apodiformes (Trochilidae + Apodidae + Hemiprocniidae/inae)
6. Musophagiformes
7. Cuculiformes + Otidiformes
8. Mesitornithiformes
9. Pterocliiformes
10. Columbiformes
11. Gruiformes
12. Phoenicopteriformes + Podicipediformes
13. Charadriiformes
14. Eurypygiformes
15. Phaethontiformes
16. Gaviiformes
17. Sphenisciformes
18. Procellariiformes

22. our current Pelecaniformes minus Threskiornithidae



Thus, the lineages currently called families in Caprimulgiformes are as old or older than most lineages we label as orders.

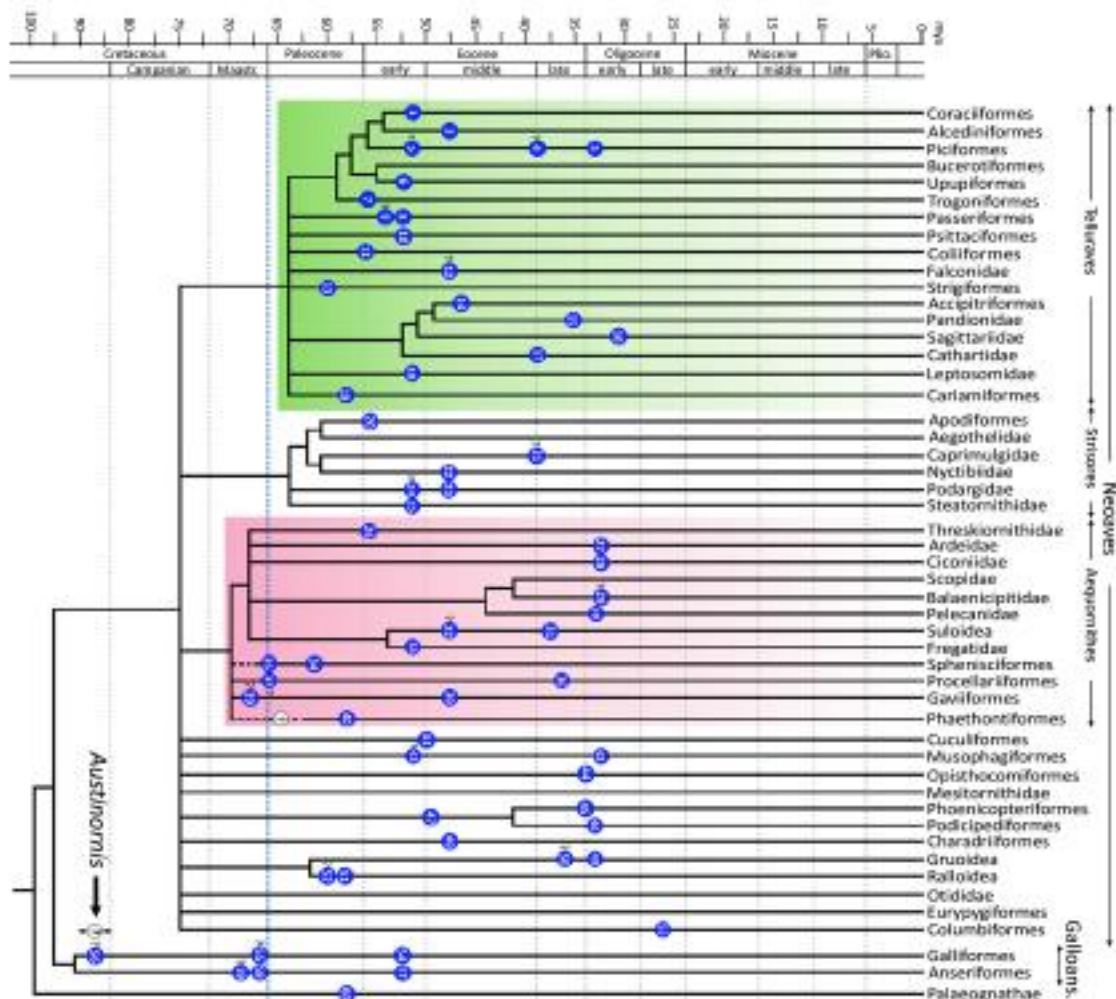
If you zoom out to the full view of the tree in this figure, the following lineages also intersect the line through the early Eocene:

23. all ratites plus tinamous
24. Galliformes
25. Anseriformes
26. Opisthocomiformes
27. **Cathartidae** (treated as an order Cathartiformes by SACC and others)
28. Accipitriformes minus Cathartidae
29. Strigiformes
30. Coliiformes
31. Trogoniformes
32. Upupiformes + Bucerotiformes
33. Coraciiformes
34. Piciformes
35. Cariamiformes
36. Falconiformes
37. Psittaciformes
38. Passeriformes

Thus, the signal is even stronger when one looks at the entire figure – lineages as old as ca. 54 mya are consistently ranked in our classification as orders or even ancestors to two or more orders. Of the 6 exceptions, 4 are in traditional Caprimulgiformes. That leaves Cathartidae, already treated as an order by some (e.g., SACC), and Threskiornithidae, which I previously argued for similar reasons should be treated as an order (a couple of years ago when I voted against a proposal for a broad Pelecaniformes).

I emphasize that I recognize that the Prum et al. tree represents preliminary analyses of new data, and that modifications are inevitable. Nonetheless, note that the topology and chronology are generally consistent with other data, both fossil (see Mayr tree below) and genetic – in other words, this is not a radical overhaul of what we know about relationships or how we portray them in hierarchical classification. Using Prum et al. (2015), however, at least represents an objective approach to higher classification that differs from the current data-free approach maintained by historical momentum.

On the following page is the figure from Mayr's (2014) paper that maps the oldest fossils for crown group birds. (I know the resolution isn't good – let me know if you need a pdf):



The topology differs somewhat from that of Prum et al., but the lineage ages, reconstructed on the basis of fossil data, are similar: namely, all of the caprimulgiform lineages are ancient, all projected to be evolving separately since the Paleocene or early Eocene, i.e. as old or older as most taxa we rank as orders.

So, I propose the following higher-level classification of the group labeled as Strisores by Mayr and Prum et al. (and based on the topology in Prum et al. 2015); brackets indicate extralimital taxa for which we do not have to endorse the ranks explicitly:

- Order Caprimulgiformes
 - Family Caprimulgidae
- Order Steatornithiformes
 - Family Steatornithidae
- Order Nyctibiiformes
 - Family Nyctibiidae
- [Order Podargiformes (extralimital)
 - Family Podargidae]
- [Order Aegotheliformes (extralimital)]

Family Aegothelidae]
Order Apodiformes
[Family Hemiprocnidae (extralimital)]
Family Apodidae
Family Trochilidae

For those of you accustomed to thinking of the old Caprimulgiformes as consisting of several similar family-level taxa of night birds, consider that the phenotypic differences among these groups is masked somewhat by a degree of convergent evolution on cryptic coloration (also accounting for historical placement of Strigiformes next to Caprimulgiformes). Remove that, and these birds differ dramatically from one another. The echolocating Oilbird is the only nocturnal frugivore in Aves and really bears no morphological resemblance to any other bird. Likewise, the potoos bear little resemblance to any other birds, and they have bill and eyelid morphology found in no other group. The owl-nightjars are just bizarre birds that don't seem to resemble anything else. Swifts and hummingbirds likewise are unique groups in birds, and once you take away parallel extreme adaptations for flight in terms of reduced feet and elongated primaries, they share little in terms of plumage and morphology – one could even make an argument based on lineage age that they should also be treated as separate orders. The morphological distinctiveness of each of these groups is certainly related to the enormous amount of time since they shared common ancestors.

Recommendation: I recommend a YES vote on the proposal. A NO would necessarily generate a proposal (by someone else) to treat them all in the same order Caprimulgiformes (or perhaps some hybrid classification such as including Aegothelidae and Trochilidae in Apodiformes, and potoos and oilbirds in same order, each separate from Caprimulgiformes).

Literature Cited:

- Cracraft, J. 2013. Avian higher-level relationships and classification: nonpasseriforms. Pp. xxi-xliii in *The Howard and Moore Complete Checklist of the Birds of the World*, 4th Edition, Vol. 1. Non-passerines (E. C. Dickinson & J. V. Remsen, Jr., eds.). Aves Press, Eastbourne, U.K.
- Dickinson, E. C., and J. V. Remsen, Jr. (eds.). 2013. *The Howard and Moore complete checklist of the birds of the World*. Vol. 1. Non-passerines. Aves Press, Eastbourne, U.K., 461 pp.
- Mayr, G. 2014. The origins of crown group birds: molecules and fossils. *Palaeontology* 57: 231–242.
- Prum, R. O., J. S. Berv, A. Dornburg, D. J. Field, J. P. Townsend, E. M. Lemmon, and A. R. Lemmon. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526: 569-573.

Submitted by: Van Remsen

Date of Proposal: 1 November 2015

Split *Momotus momota* into two or three species

Background:

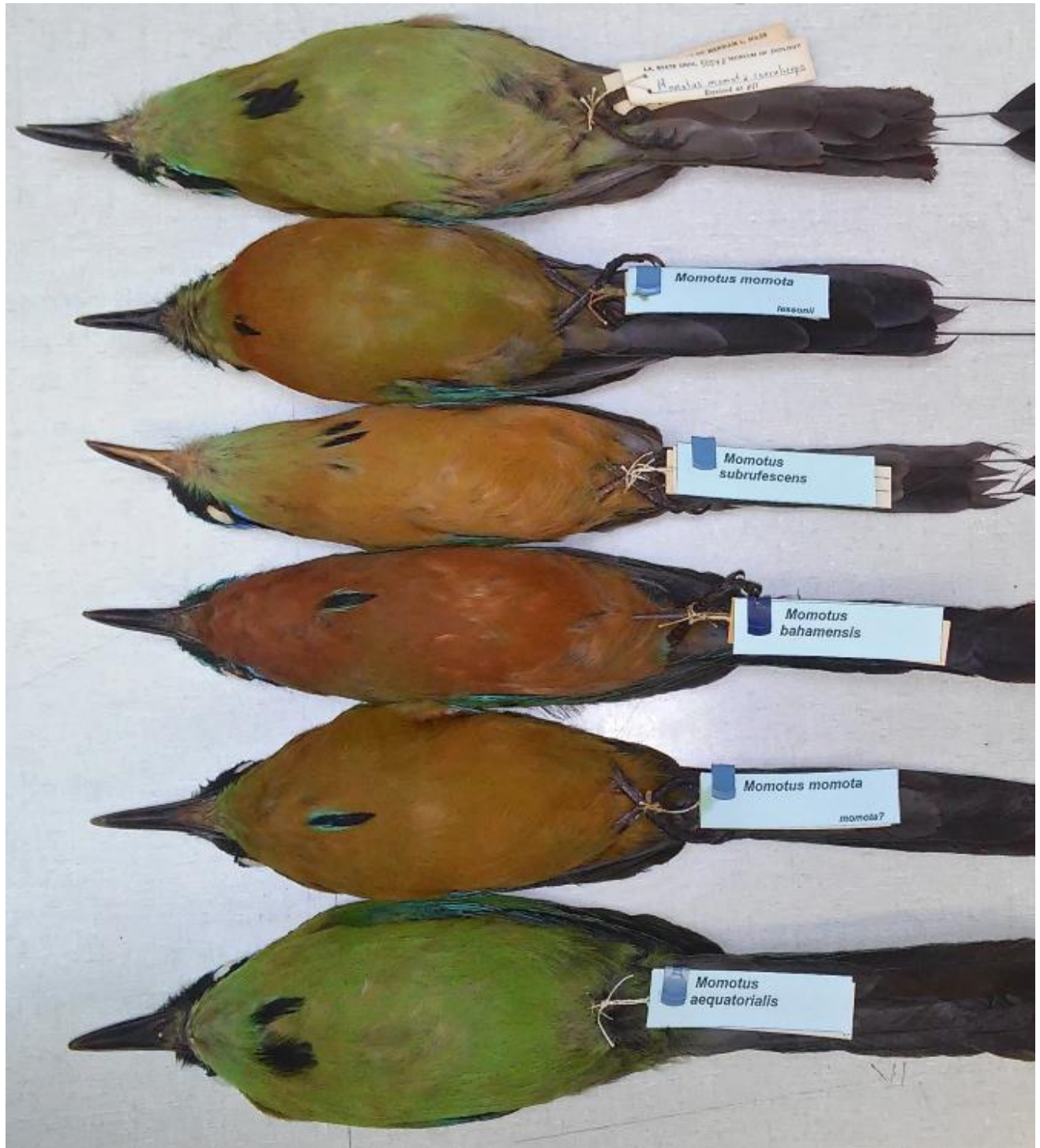
NACC current classification recognizes a single broadly defined species *Momotus momotus* (Blue-crowned Motmot), found from Mexico to Argentina. In the NACC area, there are three main groups of subspecies, as outlined in AOU (1998): (1) *coeruliceps* (NE Mexico; “Blue-crowned Motmot”); (2) *lessonii* (s. Mexico to nw. Panama: including subspecies *goldmani* and *exiguus*; “Lesson’s Motmot”); and (3) *subrufescens* (separated from *lessonii* by a 300 km gap: in e. Panama, where represented by the subspecies *conexus*, which Stiles relegated to the synonymy of nominate *momotus* because he found it undiagnosable from adjacent *subrufescens*; “Tawny-bellied Motmot”).

Ridgway (1914), Cory (1918), and Chapman (1923) all treated *lessonii* (and several South American taxa) as separate species. These were all lumped by Peters (1945) into broad *M. momotus*, and all major authorities subsequently followed that treatment. Peters (1945) of course provided no rationale, but widespread individual variation in several populations that mimicked to some degree the differences in plumage among populations undoubtedly fueled this pulse of Lumperama.

New Information:

Several years ago, SACC proposal 412 (appended to the end of this proposal) split *Momotus momota* into 5 species (4 of the 5 “groups” of AOU 1998) based on Stiles (2009), which analyzed voice, plumage, and morphology of all critical taxa in South America. SACC unanimously endorsed Stiles’s recognition of 5 species, including extralimital (to SACC) *Momotus lessonii*. The reason that this proposal was not subsequently sent to NACC was because Stiles did not study in detail the taxa in Middle America and was ambivalent on whether *lessonii* and *coeruliceps* each should be treated as separate species.

Embedded here are photos of specimens just for reference, from top to bottom: *coeruliceps*, *M. lessonii*, *M. subrufescens*, *M. bahamensis*, *M. momotus*, and *M. aequatorialis* – you should be able to read the blue synoptic series labels for all but *coeruliceps*. (For those not used to *Momotus* variation, ventral color in most taxa is typically highly variable, even among specimens from the same locality.)



Here are the same specimens, dorsal and lateral views:



Subproposals and Recommendations:

This proposal is complicated because any of five treatments is possible:

- (1) keep our classification as is (= NO vote on all subproposals);
- (2) treat *lessonii* (with *coeruliceps*) as separate from *M. momotus* (retaining *subrufescens* group as subspecies of *M. momotus*);
- (3) like 2 above but also treat *subrufescens* group as separate species from *M. momotus*;
- (4) like 3 but also treat Mexican *coeruliceps* as a separate species from *lessonii*;
- (5) like 4 but treat *subrufescens* and *momotus* as conspecific.

Confused? To simplify this, I structure the proposal in a hierarchical way for the three options that I see as most likely: subproposals A, B and C below. If you vote NO on A, then you're done. If you vote YES on A, then go to B and C.

Subproposal A. Recognize *lessonii* (including *coeruliceps*) as a separate species from *M. momotus* or *M. subrufescens*.

See Stiles (2009) for full details, but herein are a few critical items and quotes relative to Central American *lessonii* and the nearest populations in w. Panama and nw. Colombia:

(1) Vocalizations: The differences are great (from the motmot perspective), with the following quote illustrating this qualitatively:

“Upon arriving in Colombia, I was amazed at hearing the vocalizations of motmots in the northern Chocó, which sounded totally different from the birds I had heard for years in Costa Rica (I was later bemused to learn that recordings of the Chocó birds that I sent to J. W. Hardy for archiving were labeled ‘probably misidentified’).”

In my view, plumage and morphological differences among allopatric populations are minimally relevant to species limits without careful placement in a comparative context, e.g. in this case a comparison to other motmot taxa ranked at the species level. Nonetheless:

(2) Plumage: In plumage, *lessonii* is distinctive from all South American taxa:

“Figure 9. Plot of discriminant analysis of 183 individuals of ten taxa of the “*Momotus momota* complex” based on 14 plumage characters. a. Discriminant functions 1 and 2. Note the complete separation of *aequatorialis* and *lessonii* from all other taxa;”

To clarify the figure caption, Andean *aequatorialis* does not overlap in plumage characters with *lessonii*.

(3) Morphometrics: In external measurements, *lessonii* occupies discrete PCA space: see Fig. 10 etc.

As noted above, Stiles (2009) studied only nominate *lessonii* from southern Central America and did not include distinctive *coeruleiceps*:

“Within the area of this revision, *lessonii* and *aequatorialis* are monotypic. Other taxa related to *lessonii* occur in Mexico and will not be treated here, but from the descriptions by Ridgway (1911) seem unlikely to deserve species status with the probable exception of *coeruliceps* with its distinctive all blue crown. This difference appears to be on the order of that between *bahamensis* and the rest of the *subrufescens* group, although it is worth noting that in this northernmost taxon of the complex, the crown feathers have rather extensive blackish bases, such that the blue in this area is often less solid than around the periphery (somewhat like some juveniles of several other forms in the complex). However, ongoing studies by Mexican ornithologists appear to support species status for *coeruliceps* (A. Navarro in litt.).”

Based on the vocal differences documented by Stiles (2009), I recommend voting YES on Subproposal A, namely recognizing minimally two species in our area, *M. lessonii* and, depending on outcome of Subproposal B, either *M. momotus* or *M. subrufescens*.

Subproposal B. Recognize *subrufescens* as a separate species from *M. momotus*.

The split here is an extralimital one, already endorsed by SACC. See Stiles's paper and SACC proposal 412 below for details.

Basically, the species *M. subrufescens*, as defined by SACC (and also Collar & del Hoyo in the recent HBW volume), occurs in northwestern South America and eastern Panama, whereas *M. momota* is strictly east of the Andes and found primarily in the Amazon Basin. The rationale for treating them as separate species is that all members of *subrufescens* group differ from those of both the *momota* group and *lessonii* group by having just a single "hoot" note in their primary vocalization. A quantitative analysis of their primary songs shows no overlap in PCA space (Stiles's Fig. 14). Stiles presented sonograms of many taxa and individuals in his paper. The two groups are allopatric, separated by the Andes, and so there are no known contact zones, although they come close in northwestern Venezuela. They do not overlap in quantitative analyses of plumage and morphology (but that only means, in my view, that they are discrete taxa, not necessarily species).

I recommend a YES vote on B. The differences between the voices are subtle but from the motmot perspective, major, and to emphasize the difference, Stiles's recommended name for the species was Whooping Motmot, subsequently adopted by SACC and others. Here is an example of *subrufescens* from w. Ecuador: <http://www.xeno-canto.org/7219> and of double-noted *momotus* from e. Ecuador: <http://www.xeno-canto.org/257927>.

Subproposal C. Recognize *coeruliceps* as a separate species from *M. lessonii*.

This is the issue that Stiles did not deal with because he had insufficient data. Collar and del Hoyo (recent HBW volume) treated *coeruliceps* as a separate species based strictly on color pattern differences (but see my critique of their approach in recent review in *J. Field Ornithology*). This taxon does have an entirely blue crown and thus differs rather abruptly from any taxon in the entire complex, from central Mexico to Argentina. Other plumage differences seem minor to me.

The taxon *coeruliceps* is endemic to eastern Mexico in Nuevo León, SLP, Tamaulipas, and n. Veracruz (AOU 1998) from tropical lowlands up to ca. 1300 m. The adjacent subspecies in the *lessonii* group, *goldmani*, occurs as far north as s. Veracruz. Because both are lowland taxa, I see no reason why they are not parapatric in Veracruz, but have not had the energy to research the literature on their fine-scale distribution. No break in the distribution is shown in their composite distribution in the range map in Howell & Webb's Mexico guide, nor are any gaps suggested in the usual

range descriptions. As far as I know, only one possible intergrade has been reported (by Chapman 1923):

“We have a skin of *goldmani* from Monte de Cuichapa, Córdoba, with the crown strongly washed with blue of exactly the same shade as in *coeruliceps*, while the general color of the body is decidedly greener than in a specimen of *coeruliceps* from Valles, San Luis Potosi. In the latter the greenish frontal area is less pronounced than in true *coeruliceps*, but if it were accepted as typical of *coeruliceps*, the Córdoba specimen would certainly be referred to that species rather than to *lessoni goldmani*.”

This region has been heavily collected, and so I suspect that if there were any sign of extensive intergradation, it would be in the literature. Perhaps Adolfo can check on this. If they are indeed parapatric without any sign of free gene flow, then by any species definition they should be treated as separate species. Chapman (1923) found strong evidence for intergradation at contact zones among the three subspecies of his *M. lessonii*.

I looked at our series of 19 *coeruliceps* from Tamaulipas and SLP, and they all basically look alike – solid blue crowns with greenish tinge on forehead – and differ from any taxon in the complex. I also looked at our extensive series of the *lessonii* group from Veracruz south, and they all have the characteristic blackish crown patch of the complex.

I am embedding some photos: The two specimens on the right are *coeruliceps*, with our northernmost *lessonii* specimens in the middle (from Veracruz; subspecies *goldmani*), and two specimens of nominate *lessonii* on the left. What you can see is that the two specimens of *coeruliceps* have no black crown patch and also have the greenish forehead; the two specimens of *goldmani* have a pronounced crown patch and no greenish forehead; and the two specimens of nominate *lessonii* are like *goldmani* but the hindcrown border is violet.





The primary vocalization of *coeruliceps* is poorly documented. Xeno-canto and Macaulay have a grand total of 4 cuts. They are either poor or not for-certain homologous to the primary vocalization, or both. In other words, no conclusions are possible. (This is the closest population to the USA, so if some recordist out there wants to make a trip to get some important recordings, these would be valuable.)

So, we are left with plumage pattern and its distribution. In the absence of any evidence to the contrary, I conclude that *coeruliceps* and *M. lessonii goldmani* replace each other abruptly somewhere in the lowlands of central Tamaulipas without any sign of free gene flow (as indexed by plumage characters). If that is the case, then parapatry without extensive gene flow is as good as it gets for solid evidence for species rank. I think burden-of-proof falls on those who would treat them as subspecies of the same species. Further, the head pattern of *coeruliceps* is the most distinctive in the entire complex and may be itself be a driver of reproduction isolation. Finally, keep in mind that Peters (1945) did not provide even a phrase of justification for the lump, nor has anyone else that I know of, and that the detailed analyses of Chapman (1923) and Stiles (2009) reached identical conclusions on species limits with the exception that Stiles did not study *coeruliceps*.

Therefore, I recommend a YES to ranking *coeruliceps* as a separate species.

English names: If any of these proposals passes, then I might do a separate proposal on English names, so be thinking about this as well. HBW used Blue-crowned Motmot for *M. coeruliceps*; if any taxon merits this name, *coeruliceps* does, as reflected in the scientific name. Ridgway used Blue-crowned for *coeruliceps*, so Blue-crowned is the historical name for that species. However, broadly defined *M. momotus* is also widely known as Blue-crowned Motmot, e.g. as in current NACC classification, so there will be those who demand a new name for *coeruliceps* to prevent confusion. So, in case Part C passes, please also indicate your preference here, i.e. Blue-crowned or “[Something else] Motmot” that will not be confused with the former name for the broadly defined species. If the consensus is strong for using Blue-crowned, then I won’t do a proposal.

As for *lessonii*, Stiles (2009) followed a Skutch suggestion (*Ibis* 1964) of Blue-diademed Motmot, in reference to the blue ring around the crown, i.e. a crown in the “royal” sense.

This was also followed by HBW. Ridgway used Lesson's Motmot for nominate *lessonii* (but other names for subspecies *exiguus* and *goldmani*); this is the origin for the AOU 98 group name. However, I see no reason not to follow Stiles and HBW and stay with Blue-diademed.

As for *subrufescens*, AOU 98 called this Tawny-bellied Motmot. Stiles (2009), however, recommended Whooping Motmot (to emphasize its distinctive voice), and this was followed by SACC. Stiles did not discuss Tawny-bellied. Although the match to the scientific name is nice, (1) the name Tawny-bellied could apply aptly to several populations outside the *subrufescens* group, and (2) the subspecies *argenticinctus* in the *subrufescens* group is not tawny-bellied but rather mostly greenish. So again, please indicate if you're willing to stick with Whooping so that I can assess whether a separate proposal is needed.

Literature Cited:

- Chapman, F. M. 1923. The distribution of the motmots of the genus *Momotus*. Bulletin American Museum of Natural History 48: 27–59.
- Cory, C. B. 1918. Catalogue of birds of the Americas. Field Museum Nat. History Publ., Zool. Ser., vol. 13, pt. 2, no. 1.
- Ridgway, R. 1914. The birds of North and Middle America. Bulletin U.S. National Museum, no. 50, pt. 6.
- Stiles, F. G. 2009. A review of the genus *Momotus* (Coraciiformes): Momotidae) in northern South America and adjacent areas. Ornitología Colombiana 8: 29-75.

Submitted by: Van Remsen

Date of Proposal: 1 November 2015

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Proposal (412) to South American Classification Committee:
Split *Momotus momota* into five species

This proposal would reverse the decision of Proposal no. [117](#) which favored lumping the highland form *aequatorialis* (considered a separate species in the baseline list) into a broad *M. momota* due to the lack of published evidence supporting the split, and in view of the fact that other taxa currently included in *M. momota* would probably deserve species rank were a comprehensive analysis to be performed. I have attempted such an analysis (Stiles 2009), now published in Ornitología Colombiana, the online journal of the Asociación Colombiana de Ornitología. Hopefully by now the members of SACC have received from Van a pdf of this study; if not, it can be downloaded from the web page of the journal Ornitología Colombiana: www.ornitologiacolombiana.org/revista/htm.

Basically, I drew my data from three sources: plumage patterns, biometrics and vocalizations, supplemented by information on geographic distributions and ecology. I examined a total of 512 specimens of ten “focal” taxa occurring in the area between southern Central America, northern and western South America from Colombia east to the Guianas and south to northern Peru, and Trinidad-Tobago. I also examined ca. 30 specimens from areas slightly to the south and east to further check for intraspecific variation. I defined 14 characters of plumage pattern and took six 6 measurements of bill, wing and tail. For vocalizations, I restricted the main analysis to the ‘hooting’ “primary song”; motmots have a much broader vocal repertoire but other vocalizations had not been recorded consistently for all taxa. From sonograms, I measured five parameters of frequency and duration for those taxa in which this song consisted of a single note, and six additional parameters for taxa in which the song consisted of two notes. Data were analyzed with t-tests, ANOVA, discriminant analysis and principal components analysis. I defined species limits in this complex on the basis of two general criteria: diagnosability and the probability that the differences observed would assure maintenance of reproductive isolation should currently allopatric groups enter into contact. My results support recognition of five species-level taxa in this complex: *lessonii* Lesson 1842 (including 2-3 additional subspecies in Mexico beyond the scope of this study), *momota* Linnaeus 1766 (including the nominate, *microstephanus* Sclater 1855 and several other subspecies of eastern and southern South America beyond the scope of this study); *M. aequatorialis* Gould 1857 (including the subspecies *chlorolaemus* Berlepsch and Stolzmann 1902); *bahamensis* Swainson 1837 and *subrufescens* Sclater 1853. In the latter species I recognize as subspecies *osgoodi* Cory 1913, *argenticinctus* Sharpe 1892 and *spatha* Wetmore 1946, but find the following taxa not adequately diagnosable and recommend lumping them into nominate *subrufescens*: *conexus* Thayer & Bangs 1906, *reconditus* Nelson 1912 and *olivaresi* Hernandez & Romero 1978.

For the purposes of SACC, my analysis would recognize four species in our area (*lessonii* being restricted to Central America): cis-Andean *momota*, Andean *aequatorialis*, northwestern, trans-Andean *subrufescens* and Trinidad-Tobago *bahamensis*. My conclusions are congruent with a phylogeographic analysis of the Momotidae (as yet unpublished) by Chris Witt, save that *bahamensis* is nested within the *subrufescens* clade; I present arguments, mainly from plumage and biometrics, in support of species status for *bahamensis*. Regarding English names, I propose Amazonian Motmot for *momota* since the Amazon basin includes the vast majority of its distribution (and because of the great variation among the named subspecies, I could devise no adequately descriptive name suitable for all of them); Whooping Motmot for *subrufescens* because its rather long-drawn-out single-note song does indeed sound like a whoop; Andean Motmot for *aequatorialis* because it is indeed restricted to the Andes and because other species of motmot are also “highland” birds; and Trinidad Motmot for *bahamensis*.

The important references for this study are given in Proposal [117](#) and the pdf of this study. I recommend a YES on this proposal (obviously!).

F. Gary Stiles, August 2009

Comments from Robbins: “YES. Gary has thoroughly documented species level differences among these taxa.”

Comments from Zimmer: “YES. Gary has done a nice job of providing the analysis that we all wanted when we voted on Proposal 117. Biometrics, plumage patterns, and vocal data all point toward the proposed splits, and I would further add my support for Gary’s proposed English names for the various resulting species.”

Comments from Cadena: “YES. Gary has done an admirable job describing geographic variation in this group. Because many of the populations are allopatric, several difficulties remain regarding where does one draw species limits, but I think it is likely that these difficulties will persist regardless of how much additional data we throw at problems like this (a similar situation occurs in *Arremon torquatus*, on which I will submit a proposal shortly). Gary’s proposed classification, which considers likelihood of reproductive isolation and also the distinctiveness of evolutionary lineages, is a substantial improvement in comparison to what we had before.”

Comments from Remsen: “YES. Gary has taken all available phenotypic data and partitioned the geographic variation into the units that are most defensible from the standpoint of known or likely reproductive isolation ... a big step forward.”

Comments from Pacheco: “YES. im para a proposição em considerar *momota*, *aequatorialis*, *subrufescens* e *bahamensis* como espécies distintas. Gary fez um excelente trabalho elucidando as interrelações dos vários táxons de *Momota* presentes na região selecionada.”

Comments from Jaramillo: “YES. It is fantastic when a new classification is also a clarification. Traveling around it is clear that members of this group are certainly similar to each other, but at the same time the differences are notable. My first trip to Trinidad and Tobago had me staring at this strange thing, thinking...surely this is not the same creature as in Mexico, or Ecuador...or.... I particularly like that this is a new classification based on traditional methods, and it is tight and well done. It does scream out that while molecular methodology is an indispensable tool, you can attack these problems carefully with traditional datasets and come up with something very strong. I look forward to the eventual publication of molecular datasets on this, which will surely strengthen much of what is put forward here.”

Comments from Nores: “YES, pero con reservas. Aunque considero que el análisis hecho por Gary es excelente y tiene un detalle asombroso, hubiera sido perfecto 10 o 15 años atrás cuando no existían o estaban poco desarrollados los estudios moleculares. En este momento, yo hubiera deseado ver algún análisis molecular antes de realizar la separación en cinco especies. Además, yo soy muy partidario del “biogeographic species concept” developed by Hellmayr: allopatric representatives of a common stock should be considered subspecies. A pesar de esto, considero que hasta tanto haya estudios moleculares está bien en aceptar la propuesta de separar las especies.”