An examination of species limits in the *Aulacorhynchus* “prasinus” toucanet complex (Aves: Ramphastidae)

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The number of species recognized in *Aulacorhynchus* toucanets has varied tremendously over the past century. Revisors seem to disagree on whether head and bill coloration are useful indicators of species limits, especially in the *A. “prasinus”* complex. Using morphometrics, I tested the hypothesis that the major color-based subspecific groups of *A. “prasinus” sensu lato* are simply “cookie-cutter” (i.e., morphologically nearly identical) toucanets with different head and bill colorations. Univariate and multivariate analyses show that they are not simply morphological replicates of different colors: a complex array of morphometric similarities and dissimilarities occur between the major subspecific groups, and these variations differ between the sexes. Latitude and longitude had a small but significant association with female (but not male) PC1 and PC2. Hybridization and intergradation were also considered using plumage and bill characters as a surrogate to infer gene flow. Hybridization as indicated by phenotype appears to be substantial between *A. “p.” cyanolaemus* and *A. “p.” atrogularis* and nonexistent between other major groups, although from genetic evidence it is likely rare between *A. “p.” albivitta* and *A. “p.” cyanolaemus*. The congruence and complexities of the morphological and color changes occurring among these groups suggest that ecological adaptation (through natural selection) and social selection have co-occurred among these groups and that species limits are involved. Further, hybridization is not evident at key places, despite in many cases (hypothetical) opportunity for gene flow. Consequently, I recommend that this complex be recognized as comprising five biological species: *A. wagleri, prasinus, caeruleogularis, albivitta*, and *atrogularis*. Four of these also have valid subspecies within them, and additional work may eventually support elevation of some of these subspecies to full species. Species limits in South America especially need more study.
AN EXAMINATION OF SPECIES LIMITS IN THE

AULACORHYNCHUS “PRASINUS” TOUCANET COMPLEX (AVES: RAMPHASTIDAE)

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Abstract.—The number of species recognized in *Aulacorhynchus* toucanets has varied
tremendously over the past century. Revisors seem to disagree on whether head and bill
coloration are useful indicators of species limits, especially in the *A. “prasinus”* complex. Using
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INTRODUCTION

In spite of ongoing advances in the description and recognition of biodiversity, few genera can offer such an incongruous history as *Aulacorhynchus* Gould (Aves: Piciformes: Ramphastidae). The *Aulacorhynchus* toucanets inhabit montane forests from Mexico to Guyana and Bolivia, and there are many allopatric taxa. Although generic limits have been generally consistent during the past century, the number of species within the genus has been a matter of considerable disagreement.

**Taxonomic History**

In the second edition of his monograph on the Ramphastidae, Gould (1854) recognized 10 species in the genus *Aulacorhamphus* (now *Aulacorhynchus* by priority), but several taxa remained undescribed at that time. Between them, Salvin & Godman (1896) and Brabourne & Chubb (1912) recognized 15 species in the genus. Ridgway (1914) followed this treatment. Cory (1919) considered one of these species (*A. erythrognathus*) to be only a subspecies, and he treated the genus as having 14 species. Although a new species was described in 1933 (*A. huallagae*, Carriker, 1933), Peters (1948) reduced many of the formerly recognized species to subspecific status and presented the species-level diversity of the genus as just seven taxa. Haffer (1974) followed Peters (1948), except that he reduced one species (*A. calorhynchus*) to subspecies status (after Schwartz, 1972), leaving just six. Sibley & Monroe (1990) followed this treatment, but they presented a further reduction of the apparent diversity by mentioning only two subspecific groups below the species level. Although more comprehensive subspecific inclusion and discussion were given by Short & Horne (2001, 2002), six full species were retained. The treatment of this genus since 1891 is summarized in Table 1.

The massive lumping of Peters (1948) proceeded with neither the presentation of data nor...
with discussion. Careful study of one taxon, *A. calorhynchus*, by Schwartz (1972) supported the single species-level change that was made between Peters (1948) and Haffer (1974), and Haffer’s (1974) important work has been cited to support maintaining a broad *A. prasinus* (*sensu lato*; AOU, 1998). Haffer (1974) and Short & Horne (2001, 2002) used evidence of hybridization and intergradation to support their conclusions that the whole *A. “prasinus”* complex represented one biological species with many subspecies (14 and 13 subspecies, respectively); at the species level across the genus Short & Horne’s (2001, 2002) treatment reflected that of Dickinson & Remsen (2013) in Table 1 except that they considered *A. whitelianus* a subspecies of *A. derbianus*, as Peters (1948) did. Presumably similar reasoning was behind Peters (1948). But subspecies, even those distinctive enough to have been considered full species for a century, can get lost in the shuffle. For example, oversimplification of subspecific variation led Sibley & Monroe (1990) and the American Ornithologists’ Union (AOU, 1983, 1998) to completely omit mention of the very distinct form *A. “prasinus” wagleri* from southwestern Mexico. The AOU (1983, 1998) considered Middle American diversity in the genus as being just two subspecific groups of a single species, *A. prasinus*.

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”* 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 *A. prasinus*” (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 et al., 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). Most disagreement has been in the *A. prasinus*” complex, and it is on this group that I focus.

*The A. “prasinus” complex.*—As currently treated (e.g., Table 1, Dickinson & Remsen, 2013; del Hoyo & Collar, 2014), *A. prasinus* either is a widely distributed and highly variable biological species or it comprises multiple species (Fig. 1). So far as is known, *Aulacorhynchus* toucanets are nonmigratory (AOU, 1998), but as O'Neill & Gardner (1974) and Navarro et al. (2001) noted, members of the genus can wander widely during the nonbreeding season. Short & Horne (2001) considered Central American forms from Mexico to Panama to be partially migratory, with downslope movements to lowlands also occurring during the nonbreeding season (but less commonly) throughout the *A. “prasinus”* range. The sexes are alike by plumage (sexually monochromatic), but sexual size dimorphism is apparent in all taxa examined.

In past work there has been too little discussion of the fact that different levels of differentiation occur among the subspecies of *A. prasinus, sensu lato*. All of the named forms do not represent equally differentiated populations; there are major subspecific groups of one or more described subspecies. Objectively determining what these groups are can be done by following taxonomic history, coupled as it is with a color-based clustering. Cory (1919)
recognized eight species that were later lumped by Peters (1948) into _A. prasinus_ (Table 1). It seems that four of these (_A. wagleri, lautus, cyanolaemus, and dimidiatus_) were not available for Cory (1919) to examine, however (he noted which taxa were in the Field Museum of Natural History at that time). Two of these taxa, _A. lautus_ and _A. dimidiatus_, may have been included as full species through intetia. This was not uncommon: Ridgway (1914) considered that the genus had 15 species, but he was uncertain because he had only been able to examine seven of them. The subsequent rediscovery and examination of _A. dimidiatus_ (O'Neill & Gardner, 1974) showed intergradation with _A. “prasinus” atrogularis_, and the Santa Marta isolate _A. “prasinus” lautus_ is, by plumage, clearly a relatively minor derivative of the _A. “p.” albivitta_ group. These considerations reduce the number of major, color-based subspecific groups in the _A. “prasinus”_ complex to six (_A. “p.” wagleri, prasinus, caeruleogularis, albivitta, cyanolaemus, and _A. “p.” atrogularis_).

The rather pronounced differences among these major groups are illustrated in Fig. 1, together with examples of some of the less-pronounced variation (though still between named subspecies) occurring within two of these groups. Del Hoyo & Collar (2014) presented an analysis of colors that reaffirms this approach, coming back to the same six color-based subspecific groups and treating them as full biological species. Diagnostic characters of these six groups are given in Table 2. It is these six groups that form the basis for my comparisons. They are the color-based groupings that have been recognized by students of the birds themselves.

The troubled taxonomic history of _Aulacorhynchus_ (especially _A. prasinus, sensu lato_) reflects disagreement among revisors over the ability of plumage and bill colors and patterns to represent species limits. Members of the _A. “prasinus”_ group in particular are effectively ecologically similar geographic replacements (Mallet, 2007), and where named taxa have been
found to come together hybridization has been described (e.g., Haffer, 1974; Short & Horne, 2001). Given evidence of hybridization, it is unclear how the birds themselves perceive these differences. Is this group (A. “prasinus” sensu lato) really one in which head and bill colors and patterns are very plastic, resulting in species that include a high degree of color variation? Or are full species being overlooked? If bill and head color characteristics are plastic and not indicative of species limits, as many treatments since 1948 suggest, then strikingly color-based taxa, most of Cory’s (1919) species and the six of del Hoyo & Collar (2014), would not likely show a great deal of morphometric distinctiveness. If, on the other hand, substantial, concordant morphological changes are also occurring, then perhaps the concept of ecologically similar geographic replacements, which seems broadly applicable to A. prasinus, sensu lato, is masking important group-specific evolutionary adaptations that go beyond the existing color changes, the latter of which likely reflect social selection. Such morphological differences might suggest adaptive changes among groups that would make immigrants and hybrids less fit (Price, 2008).

My question then is simple: Are these color-based subspecific groups just “cookie-cutter” (i.e., morphologically nearly identical) toucanets bearing different throat and bill colorations, or are there also significant morphological changes occurring among them? If substantial morphometric changes occur concurrently with dramatic color changes, then species limits should probably be reconsidered, as several have suggested (Navarro et al., 2001; Puebla-Olivares et al., 2008; Bonaccorso et al., 2011; del Hoyo and Collar, 2014).

Morphometrics alone are unlikely to be important components of species limits in forms like these where colors are obviously important, and this is not meant as a study of how morphology varies within the group independently of color-based clustering. Navarro et al. (2001) did a morphological analysis based on 17 allopatric groupings, and this is not meant to
repeat those analyses. Geography alone can affect morphology (e.g., Bergmann’s rule; Mayr, 1963), and my analyses account for this. In this study I will 1) test for univariate differences between pairwise groups that are geographically closest to each other; 2) compare these groups in multivariate, principal component space (because univariate measures can be correlated with each other); and 3) visually examine specimens for evidence of hybridization because such evidence has been historically important in the taxonomy of the group.

**METHODS AND RESULTS**

I used morphometrics to examine how body characteristics vary among the major, color-based subspecific groups in the *Aulacorhynchus “prasinus”* complex (Fig. 1, Table 2). Museum specimens (institutions listed in Acknowledgments) were visually examined and measurements of wing chord, tail, tarsometatarsus, bill, bill height, and bill width (all three bill measures from anterior edge of nares) were made to the nearest 0.1 mm using vernier calipers following Baldwin, Oberholser & Worley (1931). Wing tip (length of longest primary to first secondary) was also measured to the nearest 0.1 mm using vernier calipers. Although Navarro et al. (2001) raised the possibility that bill growth in this group might be indeterminate, with my larger sample size of 98 male *A. prasinus* sensu stricto (see Appendix) I found that bill length had a normal distribution, so it is retained in my analyses. Morphometric geographic variation within these six major subspecific groups was not examined, because that is not related to the hypothesis being tested, i.e., are morphological changes occurring concurrently with color-based changes (see also Navarro, 2001). However, the effects of geography upon the data are examined after the main questions posed are addressed. Some of these major subspecific “groups” have named subspecies within them. *Aulacorhynchus prasinus* has four (*prasinus, warneri, virescens, volcanius*), *A. “p.” caeruleogularis* two (*caeruleogularis, cognatus*), *A. “p.” albivitta* four (*lautus,
griseigularis, phaeolaemus, albivitta), and A. “p.” atrogularis two (atrogularis, dimidiatus); the
other two major subspecific groups (wagleri, and cyanolaemus) have no named subspecies
within them (Appendix). Color differences formed the basis for the majority of characters used
to describe all of these named subspecies, with size being mentioned (in addition to color) in just
three of 14 cases. Within-group variation is accounted for in the standard statistical manner (e.g.,
Table 3). Immature individuals were not measured.

I examined and measured 578 specimens of the six major subspecific groups of A.
“prasinus.” The distributions of these groups (Fig. 2) were found to be allopatric or parapatric, as
others have depicted (e.g., Haffer, 1974; Short & Horne, 2001; Ridgely & Greenfield, 2001;
Restall, Rodner & Lentino, 2006). Morphometric data exhibited male-biased sexual size
dimorphism (Table 3), so all analyses were performed separately for each sex.

Univariate mensural characteristics (Table 3) were visually examined to determine
whether it was warranted to apply statistical testing for differences. This was done to reduce the
overall number of tests made, which enhances the power of individual tests when applying
multiple-test corrections. No statistical tests were done on mass (due to small sample sizes), and
tests were applied in a pairwise manner between groups most proximate to each other (except for
A. “prasinus” albivitta-atrogularis). The Bonferroni-style of multiple-test correction is highly
conservative, so I did not use it; in controlling for table-wide Type I error (rejecting the null
hypothesis when it is true), it raises the likelihood of Type II error (incorrectly accepting the null
hypothesis) at the level of the single test (Sokal & Rohlf, 1995; Whitlock & Schluter, 2009).

While false discoveries will accrue with multiple testing, determining whether there are
differences at the individual test level is very important for a study of this type. I used an
approach more commensurate with this need, one that controls for the expected proportion of
falsely rejected null hypotheses, the “false discovery rate” (Benjamini & Hochberg, 1995). I report both aspects (uncorrected and corrected), because future investigators of subsets of these taxa should focus on characteristics that differ between them and not be distracted by the additional statistical gyrations that I needed to perform to reduce table-wide error when making so many tests (60 tests for Table 4 and 24 for Table 5).

Significant univariate mensural differences were found among the six groups in both sexes (Tables 3 and 4). The number of significant differences was highest when A. “prasinus” caeruleogularis was compared with A. “p.” prasinus to the north and west (8 differences) and A. “p.” albivitta to the south and east (11 differences; Table 4). After multiple-test correction (which only affected A. “p.” cyanolaemus comparisons in Table 4), the fewest differences occurred when A. “p.” cyanoleamus was compared with A. “p.” albivitta to the north (3 differences) and A. “p.” atrogularis to the south (2 differences), although small sample sizes were likely to be at least partially responsible for this. I included a pairwise comparison between A. “p.” albivitta and A. “p.” atrogularis because of the uncertain taxonomic status of (major/minor group or species/subspecies; Table 1), and small sample sizes available for, A. “p.” cyanolaemus. Intermediate levels of univariate differences occurred between A. “p.” prasinus and A. “p.” wagleri (7 differences) and A. “p.” albivitta and A. “p.” atrogularis (6 differences).

Wingtip, bill width, and tarsometatarsus showed the fewest significant differences between groups, whereas wing chord and tail lengths showed the most (Table 4). A pronounced large-small-large pattern was revealed among A. “p.” prasinus-caeruleogularis-albivitta (Tables 3 and 4). The characteristics exhibiting significant differences between taxon pairs varied among pairs and, in most cases, between sexes (Table 4). In other words, significant mensural differences were decidedly inconsistent between groups.
Morphometric relationships between groups (within sexes) were further explored using principal components analyses (PCA). Two analyses were performed. For each sex, all individuals of all groups were run through a single analysis, and the first two principal components (PC1 and PC2) were extracted from the variance-covariance matrix of the log-transformed data. PC1 and PC2 explained 45.0% and 32.4% of the variance among males and 48.0% and 31.1% among females, respectively. For each of the two sex-specific analyses, principal components scores were generated for each individual on PC1 and PC2, and these individual scores were then compared between the major subspecific groups using $t$-tests. These tests were done to determine whether, on a multivariate basis, morphometric differences between taxon pairs were as heterogeneous as suggested by univariate analyses (Tables 3 and 4). Results suggest that they were; again, differences between groups varied in an unpredicatable manner between the sexes and between the two independent multivariate dimensions (PC1 and PC2; Table 5). Of the multivariate pairwise comparisons, only A. “prasinus” albivitta-cyanolaemus showed no significant differences (Table 5), although several univariate differences were found (Table 4). These results may reflect the small sample size in A. “p.” cyanolaemus. After multiple-test correction, contrasts within the South American forms (the last three rows in Table 5) yielded no significant differences at the table-wide level. Again, while smaller sample sizes likely affected these last results, a “cookie-cutter” effect is not apparent among the major subspecific groups of the A. “prasinus” complex, either in univariate or in multivariate morphometric space (Tables 4 and 5).

The major, color-based subspecific groups of A. “prasinus” do show considerable morphometric differences between them, but are these differences just an expected result from changes of size with latitude under Bergmann’s rule (Mayr, 1963) or otherwise geographically
driven? Variation in the two sex-specific principal components was examined in two multiple
regressions for each sex (PC1 & PC2) against the variables latitude and longitude. Neither
regression was significant in males, but both were in females ($F > 4.0$, $P < 0.02$). However, only
a small proportion of female variation was explained by latitude and longitude, 4% for PC1 ($R^2 =
0.04$) and 6% for PC2 ($R^2 = 0.06$). Thus, geography has a small but significant influence in 5 of
the 11 differences denoted in Table 5, perhaps contributing to the higher significance levels
found in females there. Finally, in considering the individual effects of these two geographic
variables, stepwise multiple regression showed that only longitude was significantly associated
with PC1 in females ($F = 7.56$, $P = 0.007$, $R^2 = 0.039$); neither variable by itself was significantly
associated with PC2. Thus, there is no evidence that Bergmann’s rule is affecting this complex as
a whole.

Hybridization.—Because members of the genus are known to wander rather widely
during the nonbreeding season, the opportunity for gene flow does exist between these largely
allopatrically breeding groups. Among the six major subgroups I examined there are
theoretically five pairwise instances of possible gene flow between any two of the groups,
particularly across some of the narrower zones of separation, A. “prasinus” prasinus-wagleri
(Oaxaca, Mexico), A. “p.” caeruleogularis-albivitta (in W Colombia), A. “p.” albivitta-
cyanolaemus (Ecuador), and A. “p.” cyanolaemus-atrogularis (Peru); the fifth, prasinus-
caeruleogularis (in Nicaragua), is a larger distance, on the order of about 240 km. Note that
closest approach distances are not accurate in Fig. 2, which is based on the specimens I
examined; ranges given by other sources (e.g., Haffer, 1974; Hilty & Brown, 1986; Binford,
1989; Howell & Webb, 1995; Short & Horne, 2001; Ridgely & Greenfield, 2001; Restall,
Rodner & Lentino, 2006; Schulenberg et al., 2007) include more records (including sight
Specimens were examined carefully for phenotypic evidence (i.e., intermediate phenotypes in plumage and bill coloration) of hybridization between these major groups, but it was found to occur in just one of these pairwise comparisons: between *A. “prasinus” cyanolaemus* and *A. “p.” atrogularis* in Peru. Four specimens representing possible F_1 hybrids (due to intermediacy of characters) were found; one from La Libertad, Utcubamba (25 October 1979, D. Wiedenfeld, LSUMNS 92029; Fig. 3), and three from La Lejía in NE Peru (11 & 19 March, 16 April 1925, H. Watkins, AMNH 234533, 234532, and 234535). All four specimens show obvious intergradation between these two taxa, particularly in bill coloration (see Fig. 3 and Haffer, 1974, figure 16.8), and all four are males (these individuals were not included in the morphometric analyses). In addition, there are another five specimens that seem to show evidence of intergradation to a lesser degree, two females that are phenotypically mostly *A. “p.” cyanolaemus* (both H. Watkins: La Lejía, 19 March 1925, AMNH 234534; and Uscho, Dept. Amazonas, 3 October 1925, AMNH 234531), and three males that are phenotypically *A. “p.” atrogularis* but seem to have some *A. “p.” cyanolaemus* influence (e.g., primaries edged in russet). These latter three birds are from three localities: Divisoria, Cordillera Azul, Dept. Huanuco (17 August 1967, J. P. O’Neill, LSUMNS 62227), Huanhuachayo, Dept. Ayacucho (6 May 1971, J. P. O’Neill, LSUMNS 69410), and Abra Divisiona, Dept. Loreto (14 Aug 1977, J. W. Eley, LSUMNS 84550). It is of interest that this evidence of hybridization occurs between the subspecific pair with the fewest morphometric differences (Table 4) and close genetic affinity (Puebla-Olivares et al., 2008).

*Morphometrics and hybridization in a genetic context.*—While divergent selection should produce phenotypic differences between species, this observation makes predictions neither in
direction nor degree as far as morphometrics are concerned (i.e., it only predicts accumulating
differences). Nevertheless, where differences occur between groups on a phylogeny, and the
genetic distances involved, might be of further aid in inferring species limits—qualified, of
course, by the many known ways in which mtDNA can be misleading about species limits
(Avise & Wollenberg, 1997; Irwin, 2002; Funk & Omland, 2003; Degnan & Rosenberg, 2006;
Cheviron & Brumfield, 2009; Galtier et al., 2009; Ribeiro et al., 2011; Toews & Brelsford, 2012;
Pavlova et al., 2013; Peters et al., 2014; Dolman & Joseph, 2015; Morales et al., 2015). The
mtDNA topology of the phylogenetic relationships among the six major subspecific groups is
given in Fig. 4 (after Puebla-Olivares et al., 2008). To examine the results of my study in relation
to what is presently known about relationships among and genetic distances between the groups
examined, I downloaded the mtDNA data of Puebla-Olivares et al. (2008) from GenBank,
concatenated and aligned the sequences using Geneious (ver. 7.1; Kearse et al., 2012), and
calculated genetic distances between the groups for which I made pairwise comparisons using
MEGA (ver. 6; Tamura et al., 2004 & 2013). Three of these groups are not monophyletic in their
mtDNA (not uncommon; see Funk & Omland, 2003), but I treated the haplotypes of *A. "p." atrogularis* that have introgressed into *A. "p." albivitta* (see discussion below) as *A. "p." atrogularis* for the calculation of genetic distances.

Phenotypic evidence of hybridization occurs only between the most closely related pair
on this tree, but the presence of *A. "p." atrogularis* mtDNA in birds that are phenotypically *A.
"p." albivitta* with no outward evidence of hybrid characteristics indicate that gene flow can
occur between groups that are on average 4.2% divergent (Fig. 4, bottom clade). Contrasting the
number of morphometric differences that have accumulated between the pairwise comparisons
of major groups that might hybridize due to proximity (Table 4, excluding *albivitta-atrogularis*)
with genetic distance reveals a positive correlation (linear regression, $F = 6.07$, $P = 0.04$, $R^2 = 0.67$; Fig. 5).

**DISCUSSION**

My results show that a complex array of morphometric similarities and dissimilarities occur between the major subspecific groups of *A. “prasinus.”* Moreover, these variations differ between the sexes. The morphometric data (Tables 3, 4, and 5) clearly show that these taxa are not simply “cookie-cutter” renditions of a green toucanet bearing different head and bill colors.

It might be argued that morphological change among the major subspecific groups of *A. “prasinus”* are to be expected: that Bergmann’s rule of increased body size with latitude (and elevation; Mayr 1963) would apply to populations of *Aulacorhynchus “prasinus”* and predispose this examination to finding morphometric differences. Analyses showed no association between male principal components and either latitude or longitude. Further, while female principal components showed a small but significant effect from latitude and longitude, only longitude by itself showed a significant association with PC1, leaving no evidence for Bergmann’s rule operating among these taxa as a group. The absence of any geographic effect in males suggests that some other factor, perhaps sexual selection, overcomes the relatively small geographic effect that otherwise occurs in females.

Another possibility is that differences occur not due to genetic disjunctions among locally adapted lineages, but rather to environmental variables affecting development (e.g., James, 1983; West-Eberhard, 2003). If we consider these allopatric forms as a series of natural experiments in differentiation, I suggest that we can consider group-specific morphological evolutionary adaptation as a more likely basis for the observed differences than the possibility of developmental plasticity (although the latter is itself subject to selection; West-Eberhard, 2003),
especially because they are coupled with color changes that are not attributable to developmental plasticity. Several clear patterns emerge from the data to suggest that a simple change in environment is not the cause of the morphological differences occurring among these major groups. These patterns include sexually different morphometric changes between groups (Table 4), a large-small-large pattern going from northern Middle America to South America (Table 4), and discordant changes between PC1 and PC2 (Table 5). Nor are the differences among them simply differences in size, as Bergmann’s rule would predict; indeed there is a minimal influence of geography alone (latitude and longitude; (Tables 4 and 5). If between-group differences were driven by developmental plasticity, I would expect more evidence of underlying predictable patterns, such as sexually similar responses. Instead, heterogeneity is the hallmark of the differences observed, and ecological adaptation is (hypothetically) a reasonable explanation (see also Mayr, 1963; Price, 2008).

Thus, in *A. prasinus sensu lato* we have complex morphometric changes occurring in conjunction with a series of additional complex phenotypic changes, for example: paedomorphic basal bill encrustations retained and enhanced in adult *A. “prasinus” wagleri* (an important character that alone among these examples is not simply one of color); chestnut coloration in the bill of *A. “p.” albivitta*; changes in coloration at the base of the bill among the groups, and a double leapfrog pattern in throat colors (light-dark-light-dark; Fig. 1). 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 all of the evidence available.
Haffer (1974), who measured 66 *A. prasinus* (*sensu lato*), treated all forms as subspecies. Given evidence of hybridization in two cases in the *A. “prasinus”* complex, he concluded that differences would probably not prevent interbreeding; he thus retained the post-Peters (1948) taxonomy for this group. The evidence of intergradation occurs between *A. “p.” atrogularis* and *A. “p.” cyanolaemus* in Peru (a dataset that I have expanded upon above) and seemingly rather widespread intergradation among *A. “p.” albivitta* forms (*A. “p.” albivitta, phaeolaemus, and griseigularis*). Probably to simplify his survey of the entire family, Haffer (1974) generally treated all subspecies as equivalent in degree of differentiation, not making distinctions between minor and major variants. Thus, his correct observation of apparently pronounced gene flow among *A. “p.” albivitta* forms may have overshadowed the comparative rarity of gene flow among the major forms.

Short & Horne (2001) also pointed to intergradation among subspecies and noted (p. 326) that “differences in colour of head and of the bill seem ineffective in preventing interbreeding, e.g. in NW South America; allopatric taxa are no more distinctive in features than are the interbreeding forms (the entire complex ought to be studied carefully before any one taxon is elevated to the status of species).” It is likely that the evidence of hybridization discussed by Haffer (1974) and Short & Horne (2001) formed the basis for Peters’ (1948) massive lumping, although he gave no reasoning.

Navarro et al. (2001) studied the phenotype of the *A. “prasinus”* complex, examining 247 specimens from Middle America and 58 from South America. Unlike my study, they included in their analyses patterns and colors of the head and bill. They sidestepped the issue of hybridization and concluded that there were four species in Middle America (*A. wagleri, prasinus, caeruleogularis*, and *cognatus*) and three more in South America (*A. lautus, albivitta, albivitta,
and *atrogularis* (“nigrogularis” in their abstract is an error)).

Puebla-Olivares et al. (2008) provided the first genetic data for the *A. “prasinus”* complex. My conclusions, which I will detail below, are mostly congruent with theirs, but there are also key differences (Table 1). These differences stem mainly from how we choose to interpret the genetic data and morphological diagnosability. For example, Puebla-Olivares et al. (2008) relied heavily on genetic distance, reciprocal monophyly, and inferred gene flow using relatively small population samples and a single locus (mtDNA). Although the evolutionary hypothesis that their data provides for this group is likely to be mostly accurate, the power of these data for determining species limits is not high, particularly in a group in which hybridization has played a pivotal role in determining taxonomy. Moreover, if we set aside genetic distance for a moment, there are other named, allopatric forms that are morphologically diagnosable and reciprocally monophyletic in their data that they did not highlight as being likely species (e.g., the subspecies *A. prasinus warneri, volcanius*, and *chiapensis* within *prasinus, sensu stricto*). Further, Puebla-Olivares et al. (2008) showed two *A. “p.” albivitta* from NE Ecuador in their *A. “p.” “atrogularis”* clade with no discussion (contrast their table 1 locality 22 with their figures 1 and 2; *A. “p.” albivitta* is the form that occurs in NE Ecuador, not *A. “p.” atrogularis*, given incorrectly in their figure 1 but correctly in their table 1). This is a clear mismatch of morphology and genetics: two individuals that are phenotypically *A. “p.” albivitta* (catalogued as such and verified by me from photographs) have mtDNA haplotypes more closely related to *A. “p.” atrogularis* and *cyanolaemus*. (The vouchers are ANSP 185,312 for tissue 4837 and ANSP 185,311 for tissue 4799; only tissue numbers are given for these birds by Puebla-Olivares et al. [2008].) This produces a paraphyletic *A. “p.” albivitta* and suggests that there has been historical gene flow between forms that are quite different.
While these data are important, using them to determine species limits is problematic.

And considering morphology, their observation (Puebla-Olivares et al., 2008:47) that the diagnostic morphological attributes of their focal clades “could facilitate reproductive isolation” is unduly optimistic given evidence to the contrary (e.g., their own unremarked A. “p.” albivitta results and the quote of Short & Horne [2001] above). Genetic distance is not a reliable indicator of species limits in birds (Price, 2008; Winker, 2009). A better indicator is how the birds themselves interact when in contact (Mayr, 1969; Mayr & Ashlock, 1991). And when examining gene flow, sample sizes and geographic coverage become critically important (Winker, 2010), especially in groups, such as the A. “prasinus” complex, whose taxonomy has been so affected by evidence of hybridization.

Hybridization.—Fortunately, with respect to gene flow we do have larger sample sizes if we use diagnostic morphological attributes as a surrogate (i.e., the plumage and bill characteristics upon which the named forms have been based). Despite what is likely to be ample opportunity for gene flow through dispersal across the five zones of contact or “nearest approach,” evidence of hybridization among the major groups in the A. “prasinus” complex presently exists in just two cases: between A. “prasinus” atrogularis and cyanolaemus (phenotypic only, as detailed above), and in the genetic results of Puebla-Olivares et al. (2008), which showed two A. “p.” albivitta specimens from NE Ecuador with mtDNA more closely related to A. “p.” cyanolaemus/atrogularis. This latter case suggests that historical crossing may have occurred across this zone, although morphological evidence of this is not yet evident.

Aulacorhynchus “prasinus” is uncommon in this region, and the ranges of A. “p.” albivitta and cyanolaemus are not known to come into contact (Ridgely & Greenfield, 2001; Restall, Rodner & Lentino, 2006). These two A. “p.” albivitta specimens also demonstrate that phenotypic
evidence of hybridization, which does occur and has been useful in past evaluations in A.

“prasinus,” can be absent despite gene flow (but even nuclear genomic evidence of hybridization
can disappear over a few generations of backcrossing; Lavretsky et al., 2016).

From this dataset, therefore, we know that hybridization in toucanets can be visible and
invisible, the latter probably after repeated backcrossings to one parent taxon. We might,
however, consider the visible hybrids to be roughly indicative of a hybridization rate. Current
evidence thus suggests that hybridization between A. “p.” albivitta and cyanolaemus is rare. In
the case of A. “p.” cyanolaemus and atrogularis, however, my results expand the scope of
hybridization recognized, both in number of possible F_1 specimens (those most intermediate in
characters) and in the broader distribution of specimens likely exhibiting intergradation (and note
that it is bi-directional). The fact that all four putative F_1 specimens are males suggests the
possibility that the two forms are sufficiently divergent that genetic incompatibilities are
preventing viability of the heterogametic sex, which is the female in birds (Haldane’s rule; Price,
2008). However, this is not a significant departure from the sex ratio of the rest of the A.

“prasinus” sample I examined (P = 0.13, Fisher’s exact test), and the two forms are not very
divergent genetically in mtDNA (< 1%; Fig. 4 and Puebla-Olivares et al., 2008). The matrilineal
passage of A. “p.” cyanolaemus/atrogularis mtDNA into A. “p.” albivitta in NE Ecuador
(Puebla-Olivares et al., 2008) also suggests that Haldane’s rule is not operating among major
subspecific groups in South America. In the case of A. “p.” cyanolaemus and A. “p.” atrogularis,
hybrids and intergrades represented a substantial percentage of the specimens I was
able to examine of these taxa (as many as 10 specimens, with remaining sample sizes of 19 each
of cyanolaemus and atrogularis). Given the small sample, it remains unclear whether this
reflects the true incidence of hybrids between these taxa, but given present evidence it is
Species limits.—Despite considerable combined evidence from coloration, morphometrics, and mtDNA data, comprehensive and accurate species limits for this group remain elusive, no matter what species concept one chooses to use. 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). Further study could raise this number (e.g., by splitting *A. atrogularis cyanolaemus* from *atrogularis* again).

Under a phylogenetic species concept (PSC), one could probably raise every allopatric population in *A. “prasinus”* to the species level, resulting in at least 12 taxa using morphology alone. So how many species of toucanets are there in the *A. “prasinus”* complex?

Historically, evidence of hybridization has often driven taxonomic decisions under the biological species concept (BSC), as has apparently occurred in this case. My interpretation of the taxonomic history of *Aulacorhynchus “prasinus”* is that evidence of hybridization and intergradation between named forms (among forms of the *A. “p.” albivitta* group and between *A. “p.” albivitta* and *cyanolaemus*) caused all named forms to be lumped together as one species (Peters, 1948). But hybridization is not uncommon between full species (Grant & Grant, 1992), and avian taxonomists have used a working definition of the BSC that recognizes this (e.g., Short, 1969; Johnson, Remsen & Cicero 1999; Winker et al., 2007). Gene flow, reproductive isolating mechanisms, and lineage reticulation remain fundamentally important evolutionary phenomena affecting species diversity and the process of evolutionary divergence, and thus they require consideration. 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).

Classic systematics and taxonomy (Mayr, 1969; Mayr & Ashlock, 1991) uses a
comparative approach to determine species limits among allopatric taxa, examining what occurs
at contact zones (if available) and/or what occurs in similar cases in closely related taxa. In
previous work on *A. “prasinus”* taxonomy I do not think enough credit has been given to the
dispersal abilities of these birds. And yet despite that ability there is a lack of evidence for gene
flow (using phenotype as an indicator) between five of the major subspecific groups (*A.
prasinus*-wagleri, prasinus-caeruleogularis, caeruleogularis-albivitta, albivitta-cyanolaemus).

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). 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. 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 (Fig. 1, Table 2).

The populational processes of lineage divergence and the hierarchical nature of differentiation that accrues as gene flow decreases and divergent selection produces increasingly different phenotypes (anagenesis) have produced gradations of differentiation in the genus *Aulacorhynchus*. This is seen from population-level differences of little significance (e.g., among some questionably recognizable subspecies; see Appendix), to diagnosable isolated populations within biological species, to full biological species, to a recognizable subgeneric group (members of *A. “prasinus” sensu lato*). Genetic data also support this subgeneric group (Puebla-Olivares et al., 2008), and the name *Ramphoxanthus*, which is particularly fitting (i.e., yellow-bills), is available for it (Bonaparte, 1854). This group diverged from other members of the genus during the Miocene (approximately 6-9 million years ago; Bonaccorso & Guayasamin, 2013). Within the five groups comprising *A. “prasinus”* that I consider full biological species (*A. wagleri, prasinus, caeruleogularis, albivitta, and atrogularis*) there are a number of diagnosable subspecific taxa that are clearly evolutionarily significant units, and some, being 100% diagnosable, could be called phylogenetic species (e.g., *A. p. warneri, A. c. cognatus, A. albivitta lautus*). These, however, do not represent major phenotypic differences, and I consider this
continued lumping to be warranted given present evidence, which includes hybridization and
intergradation between other subspecies with similar degrees of differentiation within the major
subspecific A. “prasinus” groups (e.g., A. p. prasinus-virescens, A. albivitta phaeolaemus-
griseigularis; Short & Horne, 2001, and personal observation).

Voice has not diverged among these five groups as much as it has in other species in the
genus (Schwartz, 1972; Short & Horne, 2001). Indeed, Short & Horne (2001:327) related that
“Calls of forms in Peru, Venezuela, Panama, Costa Rica and Mexico are much alike...”

However, more work is warranted in this area. For example, A. wagleri has a slower pace to its
vocalizations than A. prasinus (from www.xeno-canto.org, 4 A. wagleri average 1.85 calls/sec
while 6 A. prasinus average 2.13 calls/sec; XC 274798, 219401-2, and 177515 vs. XC 96724,
256673, 256311, 233097, and 138132-3). Other differences may be apparent with increased
sample sizes.

Considering my suggested taxonomy (Appendix) in relation to the mtDNA tree of
Puebla-Olivares et al. (2008), there are two paraphyletic species (Fig. 4). First, A. albivitta is
paraphyletic with respect to A. atrogularis-cyanolaemus. Second, my treatment of A.
caeruleogularis is paraphyletic with respect to A. prasinus and A. wagleri because it includes A.
“p. ” cognatus; that has been the norm since its description, only Navarro et al. (2001) and
Puebla-Olivares et al. (2008) have treated it as a full species thus far. Paraphyletic species are not
uncommon (Funk & Omland, 2003; Oyler-McCance, St. John & Quinn, 2010), but there is
clearly work remaining to be done on species limits in this complex, especially in South
America. For example, the distributions of A. atrogularis cyanolaemus, A. a. atrogularis, and the
hybrid zone between them warrant further study, as does the apparently rare instance of crossing
between A. albivitta and A. atrogularis cyanolaemus in Ecuador (mtDNA evidence of Puebla-
Also, the relationship between *A. c. caeruleogularis* and *A. c. cognatus* in Panama bears further investigation; they are phenotypically relatively similar (Short & Horne, 2001:325 also noted their close resemblance) in contrast to, e.g., *A. a. atrogularis* and *cyanolaemus*. Larger sample sizes, more loci, coverage of hybrid zones, and continued recognition that there are relatively major and minor phenotypic variants among these named taxa will be needed to finally and fully resolve species limits in this group.

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**LITERATURE CITED**

American Ornithologists’ Union (AOU). 1983. *Check-list of North American birds* (6th ed). Lawrence, Kansas: American Ornithologists’ Union.

American Ornithologists’ Union (AOU). 1998. *Check-list of North American birds* (7th ed).
Washington, D. C.: American Ornithologists’ Union.

Avise J, Wollenberg K. 1997. Phylogenetics and the origin of species. *Proceedings of the National Academy of Sciences USA* 94:7748-7755.

Baldwin SP, Oberholser HC, Worley LG. 1931. Measurements of birds. *Scientific Publications of the Cleveland Museum of Natural History* 2:1-165.

Bangs, O. 1898. On some birds from the Sierra Nevada de Santa Marta, Colombia. *Proceedings of the Biological Society of Washington* 12:171-182.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* 57:289-300.

Binford L.C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. *Ornithological Monographs* 43:1-418.

Boissonneau M. 1840. Oiseaux nouveaux de Santa-Fé de Bogota. *Revue Zoologique* 1840:66-71.

Bonaparte CL. 1854. Conspectus volucrum zygodactylorum. *Ateneo Italiano* 1(8):116-129.

Bonaccorso E, Guayasamin JM, Peterson AT, Navarro-Sigüenza AG. 2011. Molecular phylogeny and systematics of Neotropical toucanets in the genus *Aulacorhynchus*. *Zoologica Scripta* 40:336-349.

Bonaccorso E, Guayasamin JM. 2013. On the origin of Pantepui montane biotas: A perspective based on the phylogeny of *Aulacorhynchus* toucanets. *PLoS ONE* 8:e67321.

Brodkorb P. 1940. New birds from southern Mexico. *Auk* 57:542-549.

Brabourne L, Chubb C. 1912. *The birds of South America. Vol. I*. London: Taylor and Francis.

Carriker MA Jr. 1933. Descriptions of new birds from Peru, with notes on other little-known species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 85:1-38.

Chapman FM. 1915. Diagnoses of apparently new Colombian birds. IV. *Bulletin of the American Museum of Natural History* 34:635-662.

Chapman FM. 1917. The distribution of bird-life in Colombia: A contribution to a biological survey of South America. *Bulletin of the American Museum of Natural History* 36:1-729.

Cheviron ZA, Brumfield RT. 2009. Migration-selection balance and local adaptation of mitochondrial haplotypes in rufous-collared sparrows (*Zonotrichia capensis*) along an elevational gradient. *Evolution* 63: 1593–1605.
Cory CB. 1919. Catalogue of birds of the Americas. Part II, No. 2. *Field Museum of Natural History Zoological Series* 13:317-607.

Degnan JH, Rosenberg NA. 2006. Discordance of species trees with their most likely gene trees. *PLoS Genetics* 2:e68.

del Hoyo J, Collar NJ. 2014. *HBW and BirdLife International Illustrated Checklist of the Birds of the World, Volume 1, Non-passerines*. Barcelona: Lynx Edicions.

"D. W. M." 1853. Proceedings of the Zoological Society [being a report of two meetings in February of this year]. *Zoologist* 1853:3860-3861.

Dickey DR, van Rossem AJ. 1930. Geographic variation in *Aulacorhynchus prasinus* (Gould). *Ibis* 1930:48-55.

Dickinson EC, and Remsen JV Jr. (Eds.) 2013. *The Howard and Moore Complete Checklist of the Birds of the World, 4th ed., Volume 1 Non-Passerines*. Eastbourne, U. K.: Aves Press.

Dolman G, Joseph L. 2015. Evolutionary history of birds across southern Australia: structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species. *Emu* 115:35-48.

Funk DJ, Omland K. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology Evolution and Systematics* 34: 397-423.

Galtier N, Nabholz B, Glemin S, Hurst GDD. 2009. Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Molecular Ecology* 18: 4541–4550.

Gould J. 1833. *A Monograph of the Ramphastidae, or Family of Toucans (part 1)*. London: The author.

Gould J. 1841-47. *Monographie der Ramphastiden*. Nuremburg.

Gould J. 1854. Description of a new species of *Aulcorhamphus*. *Proceedings of the Zoological Society of London* 1853:45.

Gould J. 1866. Description of a new species of toucan belonging to the genus *Aulcororamphus*. *Proceedings of the Zoological Society of London* 1866:24.

Gould J. 1874. On three new species of toucans pertaining to the genus *Aulcorhamphus*. *Annals & Magazine of Natural History (4)* 14:183-4.

Grant PR, Grant BP. 1992. Hybridization in bird species. *Science* 256:193-197.

Griscom L. 1924. Descriptions of new birds from Panama and Costa Rica. *American Museum
Novitates 141:1-12.

Haffer J. 1974. Avian speciation in tropical South America. Publications of the Nuttall Ornithological Club 14:1-390.

Hellmayr CE. 1911. A contribution to the ornithology of western Colombia. Proceedings of the Zoological Society of London 1911:1084-1213.

Hilty SL, Brown WL. 1986. A guide to the birds of Colombia. Princeton, New Jersey: Princeton University Press.

Howell SNG, Webb S. 1995. A guide to the birds of Mexico and northern Central America. Oxford: Oxford University Press.

Irwin D J. 2002. Phylogeographic breaks without geographic barriers to gene flow. Evolution 56: 2383-2394.

James FC. 1983. Environmental component of morphological differentiation in birds. Science 221:184-186.

James FC. 1991. Complementary descriptive and experimental studies of clinal variation in birds. American Zoologist 31:694-706.

Johnson NK, Remsen JV Jr, Cicero C. 1999. Resolution of the debate over species concepts in ornithology: A new comprehensive biologic species concept. Pages 1470-1482 in Proceedings of the 22nd International Ornithological Congress (Adams NJ, Slotow RH, eds.). Johannesburg: BirdLife South Africa.

Jones HL. 2003. Birds of Belize. Austin: University of Texas Press.

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647-1649.

Mayr E. 1963. Animal Species and Evolution. Cambridge, Massachusetts: Belknap Press.

Mayr E. 1969. Principles of Systematic Zoology. New York: McGraw-Hill Book Company.

Mayr E, Ashlock PD. 1991. Principles of Systematic Zoology (2nd ed). New York: McGraw-Hill, Inc.

Land H. 1970. Birds of Guatemala. Wynnewood, Pennsylvania: Livingston Publishing Company.
Mallet J. 2007. Subspecies, semispecies, superspecies. In Levin, S.A. (ed.) Encyclopedia of Biodiversity. Elsevier Inc., Oxford. Online update1, pp. 1-5.

Morales HE, Pavlova A, Joseph L, Sunnucks P. 2015. Positive and purifying selection in mitochondrial genomes of a bird with mitonuclear discordance. Molecular Ecology 24:2820-2837.

Lavretsky P, Peters JL, Bahn V, Kulikova I, Zhuravlev YN, Wilson R, Barger C, Winker K, Gurney K, Clark B, Breault A, Slattery S, McCracken KG. 2016. Becoming pure: identifying generational classes of admixed individuals within lesser an greater scaup populations. Molecular Ecology 25:661-674.

Monroe BL Jr. 1968. A distributional survey of the birds of Honduras. Ornithological Monographs 7:1-458.

Navarro S AG, Peterson AT, López-Medrano E, Benítez-Díaz H. 2001. Species limits in Mesoamerican Aulacorhynchus toucans. Wilson Bulletin 113:363-372.

Nelson EW. 1912. Descriptions of new genera, species and subspecies of birds from Panama, Colombia and Ecuador. Smithsonian Miscellaneous Collections 60:1-26.

Olson SL. 1997. [Review of] John Gould the Bird Man. Auk 114:540-541.

O’Neill JP, Gardner AL. 1974. Rediscovery of Aulacorhynchus dimidiatus (Ridgway). Auk 91:700-704.

Oyler-McCance SJ, St. John J, Quinn TW. 2010. Rapid evolution in lekking grouse: Implications for taxonomic definitions. Ornithological Monographs 67:114-122.

Pavlova A, Amos JN, Joseph L, Loynes K, Austin J, Keogh JS, Stone GN, Nicholls JA, Sunnucks P. 2013. Perched at the mito-nuclear crossroads: divergent mitochondrial lineages correlate with environment in the face of ongoing nuclear gene flow in an Australian bird. Evolution 67:3412–3428.

Peters JL. 1948. Check-list of birds of the world, Vol. VI. Cambridge, Massachusetts: Harvard University Press.

Peters J L, Winker K, Millam KC, Lavretsky P, Kulikova I, Wilson RE, Zhuravlev YN, McCracken KG. 2014. Mito-nuclear discord in six congeneric lineages of Holarctic ducks (genus Anas). Molecular Ecology 23:2961–2974.

Price, T. 2008. Speciation in Birds. Greenwood Village, Colorado: Roberts and Company.

Puebla-Olivares F, Bonaccorso E, Espinosa de los Monteros A, Omland KE, Llorente-Bosquets JE, Peterson AT, Navarro-Sigüenza AG. 2008. Speciation in the emerald toucanet
(Aulacorhynchus prasinus) complex. *Auk* **125**:39-50.

Remsen JV Jr, Areta JI, Cadena CD, Jaramillo A, Nores M, Pacheco JF, Pérez-Emán J, Robbins MB, Stiles FG, Stotz DF, Zimmer KJ. Version 14 April 2016. A classification of the bird species of South America. American Ornithologists’ Union. www.museum.lsu.edu/~Remsen/SACCBaseline.html

Restall R, Rodner C, Lentino M. 2006. *Birds of Northern South America: An identification guide*. New Haven, Connecticut: Yale University Press.

Ribeiro AM, Lloyd P, Bowie RCK. 2011. A tight balance between natural selection and gene flow in a southern African arid-zone endemic bird. *Evolution* **65**:3499–3514.

Ridgely RS, Greenfield PJ. 2001. *The Birds of Ecuador, Vol. II*. Ithaca, New York: Comstock Publishing Associates.

Ridgway R. 1886. Descriptions of some new species of birds supposed to be from the interior of Venezuela. *Proceedings of the U. S. National Museum* **9**:92-94.

Ridgway R. 1912. Descriptions of some new species and subspecies of birds from tropical America. *Proceedings of the Biological Society of Washington* **25**:87-92.

Ridgway R. 1914. The Birds of North and Middle America, Part VI. *Bulletin of the U. S. National Museum* **50(6)**:1-882.

Salvin O, Godman FD. 1896. *Biologia Centrali-Americana, Aves. Vol. II*. London: Taylor and Francis.

Schwartz P. 1972. On the taxonomic rank of the Yellow-billed Toucanet. *Boletín Sociedad Venezolana Ciencias Naturales* **29**:459-476.

Schulenberg TA, Stotz DF, Lane DF, O’Neill JP, Parker TA III. 2007. *Birds of Peru*. Princeton, New Jersey: Princeton University Press.

Sclater PL. 1891. Family Rhamphastidae, pp. 122-160 in *Catalogue of the Birds in the British Museum, Volume XIX*. London: British Museum (Natural History).

Short LL. 1969. Taxonomic aspects of avian hybridization. *Auk* **86**:84-105.

Short LL., Horne JFM. 2001. *Toucans, barbets, and honeyguides*. Oxford: Oxford University Press.

Short LL., Horne JFM. 2002. Family Ramphastidae (toucans). Pp. 220-272 in *Handbook of the Birds of the World, Volume 7* (del Hoyo J, Elliott A, Sargatal J, eds.). Barcelona: Lynx Edicions.

Sibley CG, Monroe BL Jr. 1990. *Distribution and taxonomy of birds of the world*. New Haven,
Sokal RR., Rohlf FJ. 1995. *Biometry (3rd ed)*. New York: W. H. Freeman and Company.

Tamura K, Nei M, Kumar 2. 2004. Prospects for inferring very large phylogenies by using the neighbor-joining method. *Proceedings of the National Academy of Sciences USA* 101:11030-11035.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30:2725-2729.

Toews DP, Brelsford A. 2012. The biogeography of mitochondrial and nuclear discordance in animals. *Molecular Ecology* 21:3907–3930.

Wetmore A. 1968. *The birds of the Republic of Panama. Part 2. Columbidae (pigeons) to Picidae (woodpeckers)*. Washington, D. C.: Smithsonian Institution Press.

West-Eberhard MJ. 2003. *Developmental Plasticity and Evolution*. New York: Oxford University Press.

Whitlock MC, Schluter D. 2009. *The Analysis of Biological Data*. Greenwood Village, Colorado: Roberts and Company Publishers.

Winker K. 2000. A new subspecies of toucanet (*Aulacorhynchus prasinus*) from Veracruz, Mexico. *Ornitología Neotropical* 11:253-257.

Winker K. 2009. Reuniting genotype and phenotype in biodiversity research. *BioScience* 59:657-665.

Winker K. 2010. Subspecies represent geographically partitioned variation, a goldmine of evolutionary biology, and a challenge for conservation. *Ornithological Monographs* 67:6-23.

Winker K, Rocque D, Braile TM, Pruett CL. 2007. Vainly beating the air: Species concept debates need not impede science and conservation. *Ornithological Monographs* 63:30-44.

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.

Figure 2. Distributions of the specimens of Aulacorhynchus “prasinus” examined in this study with the focal six major subspecific groups labeled. Neither all specimens in existence nor observation records are included, so ranges are not complete. Red stars indicate evidence of hybridization; the top-most one, in Ecuador, is from the study of Puebla-Olivares et al. (2008).

Figure 3. An example of a hybrid A. “p.” atrogularis × A. “p.” cyanolaemus. A) a pure A. “p.” cyanolaemus (LSU 87627); B) a hybrid (LSU 92029); and C) a pure A. “p.” atrogularis (LSU 73933).

Figure 4. 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.

Figure 5. The relationship between genetic distance (Figure 4) and the accumulation of morphometric differences (Table 4) between the major subspecific groups that might hybridize due to proximity. The positive correlation is that predicted by the processes of anagenesis and speciation.
Appendix

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,
(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, Chiriqui; 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-Fè 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).
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.

| Taxon | Treatment |
|-------|-----------|
| prasinus | X         |
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 | Cory (1919) | Peters (1948) | Sibley & Monroe (1990) | Short & Horne (2001) | B. et al. (2011)g | Nav. et al. (2001)g | P-O et al. (2008)g | Dickinson & Remsen (2013)/ | del Hoyo & Collar (2014) | this article |
|------------------|----------------|---------------|-------------|---------------|-----------------------|---------------------|-------------------|---------------------|---------------------|--------------------------|--------------------------|--------------|
| *A. sulcatus*    | ×              | ×             | ×           | ×             | ×                     | ×                   | ×                 | ×                   | ×                   | ×                        | ×                        | ×            |
| *A. erythrognathus* | ×              | ×             | ×           | ssp. of sulcatus | ssp. of sulcatus | 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 | ssp. of sulcatus | ssp. of sulcatus | ssp. of sulcatus | ×            |
| *A. derbianus*   | ×              | ×             | ×           | ×             | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ×            |
| *A. whitelanius* | ×              | ×             | ×           | ssp. of sulcatus | ssp. of sulcatus | ssp. of sulcatus | ssp. of sulcatus | ssp. of sulcatus | ssp. of sulcatus | ssp. of sulcatus | ssp. of sulcatus | ×            |
| *A. haematopygus*| ×              | ×             | ×           | ×             | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ssp. of derbianus | ×            |
| *A. prasinus*    | ×              | ×             | ×           | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. wagleri*     | ×              | ×             | ×           | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. caeruleogularis* | ×              | ×             | ×           | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. cognatus*    | – d            | – d           | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. albivitta*   | ×              | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. griseigularis* | ×              | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. dauers*      | ×              | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. cyanolaemus* | ×              | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. dimidiatus*  | ×              | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. atrogularis* | ×              | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. auwagleri*   | – f            | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ×            |
| *A. cyanolaemus* | ×              | ×             | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | ssp. of prasinus | 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).

h – though not included in either study.

i – Treatment matches the South American Classification Committee (Remsen et al. 2016).
Table 2. Color and pattern-based diagnostic characteristics of the six major subspecific groups of *Aulacorhynchus “prasinus”* (based on specimens and del Hoyo and Collar 2014). Middle American forms are at left; South American forms are at right.
Table 2. Color and pattern-based diagnostic characteristics of the six major subspecific groups of *Aulacorhynchus* “prasinus” (based on specimens and del Hoyo and Collar 2014). Middle American forms are at left; South American forms are at right.

| Subspecies | Characteristics |
|------------|-----------------|
| *A. “p.” wagleri* (monotypic) | greatly enhanced orange, paedomorphic bill encrustations at the very base of upper mandible; orange band at base of lower mandible; broad black base of upper mandible; yellowish-white forehead grading to olive crown; pale bluish-green underparts. |
| *A. “p.” albivitta* (incl. subsp. *A. “p.” lautus, griseigularis, phaeolaemus, and albivitta*): yellowish skin surrounds more than half the eye; variable chin and throat (white, grayish, pale gray-blue); chestnut at base of lower mandible in most. |
| *A. p. prasinus* (incl. subsp. *A. p. prasinus, warneri, virescens, and volcanius*): upper mandible broadly yellow to base; black patches at nares; bright yellow stripe at base of mandible; white cheeks below eye. |
| *A. “p.” cyanolaemus* (monotypic): upper mandible mostly black; pinkish skin around part of eye; deep blue-gray chin and upper throat with little to none on cheek. |
| *A. “p.” caeruleogularis* (incl. subsp. *A. “p.” caeruleogularis and cognatus*): deep rich blue chin, throat, and cheek; rich olive crown and nape in absence of pale throat. |
| *A. “p.” atrogularis* (incl. subsp. *A. “p.” atrogularis and dimidiatus*): strongly bi-colored, orange-yellow vs. white basal bill stripe going from upper to lower mandibles; black chin, throat, and cheek; dark skin around eye (only one of group in South America). |
Table 3. Mensural characteristics of both sexes among six major groups of the *Aulacorhynchus “prasinus”* complex. Units are mm except for mass (g) and sample size (N).
Table 3. Mensural characteristics of both sexes among six major groups of the *Aulacorhynchus “prasinus”* complex. Units are mm except for mass (g) and sample size (N).

|          | prasinus | wagleri | caeruleogularis | albivitta | cyanolaemus | atrogularis |
|----------|----------|---------|-----------------|-----------|-------------|-------------|
|          | M        | F       | M               | F         | M           | F           |
| Mass (g) | mean     | 186.6   | 171.2           | 169.7     | 152.8       | 158.5       | 176.7       | 158.8       | 158.1       | 112.5       |
|          | s.d.     | 20.98   | 24.78           | 14.10     | 24.67       | 5.72        | 23.57       | 28.53       | 25.23       | 2.50        |
|          | min      | 153.6   | 135             | 145       | 118         | 154         | 160         | 130         | 124         | 110         |
|          | max      | 239.2   | 229.6           | 200       | 184         | 166.6       | 210         | 210         | 188         | 115         |
|          | N        | 13      | 11              | 13        | 14          | 8           | 3           | 3           | 5           | 8           |
| Wing chord (WCH) | mean | 124.1   | 119.6           | 125.9     | 120.0       | 116.5       | 128.1       | 125.5       | 127.1       | 125.0       | 122.4       | 118.0       |
|          | s.d.     | 4.58    | 4.95            | 3.80      | 3.64        | 4.90        | 4.38        | 4.26        | 3.24        | 5.78        | 3.62        | 6.07        | 7.00        |
|          | min      | 113.1   | 106.4           | 117.4     | 117.4       | 103.5       | 104.0       | 118.6       | 117.7       | 114.0       | 119.9       | 108.1       | 105.5       |
|          | max      | 135.0   | 130.7           | 136.7     | 132.3       | 133.1       | 125.6       | 139.5       | 132.4       | 137.8       | 131.2       | 133.6       | 129.6       |
|          | N        | 98      | 74              | 28        | 26          | 105         | 50          | 86          | 57          | 9           | 10          | 17          | 11          |
| Tail (TL) | mean | 109.7   | 105.0           | 113.1     | 111.8       | 98.4        | 94.6        | 109.8       | 106.4       | 106.8       | 109.1       | 112.2       | 106.3       |
|          | s.d.     | 6.01    | 6.48            | 5.15      | 4.42        | 5.04        | 4.60        | 6.90        | 5.90        | 2.14        | 6.92        | 4.89        | 7.62        |
|          | min      | 95.9    | 90.8            | 101.8     | 103.8       | 84.3        | 85.1        | 92.1        | 91.5        | 102.1       | 96.4        | 102.9       | 94.1        |
|      | max  | 124.4 | 119.0 | 122.7 | 121.9 | 116.1 | 106.9 | 127.0 | 120.5 | 109.2 | 118.6 | 119.8 | 118.0 |
|------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|      |      |       |       |       |       |       |       |       |       |       |       |       |       |
| N    | 94   | 71    | 28    | 25    | 99    | 48    | 84    | 57    | 8     | 10    | 16    | 11    |       |
| Tarso-|      | mean  | 32.4  | 31.5  | 32.5  | 31.7  | 32.3  | 31.3  | 32.9  | 32.0  | 32.8  | 31.5  | 31.4  | 29.8  |
| (TS) | s.d. | 1.45  | 1.44  | 0.99  | 0.99  | 1.33  | 1.24  | 1.29  | 1.18  | 1.26  | 1.46  | 2.19  | 1.95  |       |
|      |      | min   | 28.1  | 27.9  | 29.0  | 29.7  | 29.2  | 29.0  | 29.4  | 28.7  | 31.1  | 28.8  | 26.8  | 26.7  |
|      |      | max   | 35.8  | 35.1  | 34.6  | 33.4  | 35.7  | 34.8  | 35.5  | 35.2  | 35.0  | 34.2  | 35.6  | 33.6  |
| N    | 98   | 75    | 28    | 26    | 105   | 50    | 86    | 57    | 9     | 10    | 17    | 11    |       |
|      |      |       |       |       |       |       |       |       |       |       |       |       |       |
|      |      | mean  | 71.2  | 57.9  | 71.4  | 61.2  | 58.8  | 48.6  | 64.5  | 52.9  | 65.4  | 54.8  | 68.0  | 54.9  |
| (BL) | s.d. | 5.75  | 4.62  | 4.70  | 3.77  | 3.82  | 3.97  | 4.96  | 4.29  | 5.18  | 2.15  | 5.57  | 6.45  |       |
|      |      | min   | 58.4  | 49.1  | 64.0  | 55.2  | 45.2  | 42.1  | 54.3  | 43.8  | 55.1  | 50.8  | 59.9  | 46.7  |
|      |      | max   | 84.7  | 71.9  | 84.6  | 69.7  | 69.2  | 68.1  | 73.3  | 68.0  | 75.1  | 59.4  | 79.8  | 69.2  |
| N    | 98   | 75    | 28    | 26    | 105   | 50    | 86    | 57    | 9     | 10    | 17    | 11    |       |
|      |      |       |       |       |       |       |       |       |       |       |       |       |       |
|      |      | mean  | 24.2  | 22.7  | 23.3  | 22.6  | 22.3  | 20.9  | 23.3  | 21.7  | 23.1  | 22.4  | 24.7  | 22.5  |
| (BLH)| s.d. | 1.13  | 1.18  | 0.99  | 0.89  | 1.00  | 0.99  | 1.05  | 1.04  | 1.95  | 0.65  | 2.28  | 1.78  |       |
|      |      | min   | 20.8  | 20.7  | 20.9  | 21.3  | 19.6  | 19.1  | 20.2  | 19.3  | 18.9  | 21.2  | 22.9  | 20.0  |
|      |      | max   | 26.7  | 25.1  | 25.7  | 25.0  | 25.2  | 23.6  | 25.7  | 24.2  | 25.0  | 23.5  | 33.1  | 26.2  |
| N    | 97   | 75    | 28    | 26    | 104   | 50    | 86    | 57    | 9     | 10    | 17    | 11    |       |
|       | Bill width | mean | 21.1 | 20.1 | 21.3 | 21.1 | 21.0 | 20.2 | 21.5 | 20.4 | 20.4 | 19.5 | 21.3 | 19.7 |
|-------|-----------|------|------|------|------|------|------|------|------|------|------|------|------|------|
|       | (BLW) s.d.|      | 1.01 | 0.99 | 0.72 | 0.94 | 1.06 | 1.07 | 1.06 | 1.03 | 1.13 | 0.77 | 1.06 | 1.50 |
|       | min       |      | 18.7 | 17.7 | 20.0 | 19.0 | 17.8 | 18.2 | 19.0 | 17.7 | 18.3 | 18.5 | 19.2 | 17.4 |
|       | max       |      | 23.4 | 23.5 | 22.7 | 23.4 | 23.5 | 24.0 | 24.4 | 22.9 | 22.4 | 21.1 | 22.8 | 22.8 |
|       | N         |      | 98   | 75   | 28   | 26   | 105  | 50   | 86   | 57   | 9    | 10   | 17   | 11   |
| Wing tip | mean    |      | 16.9 | 16.7 | 18.2 | 17.9 | 16.8 | 16.4 | 16.6 | 15.9 | 16.7 | 16.6 | 17.0 | 16.5 |
|       | (WGTP) s.d.|    | 2.56 | 2.78 | 2.15 | 1.94 | 2.06 | 2.37 | 2.24 | 1.87 | 1.32 | 1.77 | 3.02 | 2.13 |
|       | min       |      | 11.4 | 9.9  | 13.2 | 13.3 | 10.8 | 9.7  | 11.5 | 12.1 | 14.3 | 14.3 | 11.2 | 11.4 |
|       | max       |      | 24.0 | 23.0 | 22.8 | 21.3 | 22.8 | 21.9 | 22.5 | 20.0 | 18.1 | 19.4 | 22.6 | 19.2 |
|       | N         |      | 95   | 69   | 28   | 26   | 104  | 49   | 86   | 57   | 9    | 10   | 17   | 11   |
Table 4

Patterns of significance from results of t-tests of mensural characters between geographic pairs of major subspecific group

Table 4. Patterns of significance from results of t-tests of mensural characters between geographic pairs of major subspecific groups of *Aulacorhynchus* “prasinus.” Positive (+) values indicate that the first named group averages larger, while negatives (-) indicate that the second is the larger. Character abbreviations follow Table 3.
Table 4. Patterns of significance from results of $t$-tests of mensural characters between geographic pairs of major subspecific groups of *Aulacorhynchus* “prasinus.” Positive (+) values indicate that the first named group averages larger, while negatives (-) indicate that the second is the larger. Character abbreviations follow Table 3.

| Pairs compared          | Sex | WCH  | TL  | TS  | BL  | BLH | BLW | WGTP | N |
|-------------------------|-----|------|-----|-----|-----|-----|-----|------|---|
| *prasinus-wagleri*      | M   | ** (-) | *** (-) | *** (+) | * (-) | 98, 28 |
|                         | F   | ** (-) | *** (-) | *** (-) | ** (-) | 75, 26 |
| *prasinus-caeruleogularis* | M   | *** (+) | *** (+) | *** (+) | *** (+) | 98, 105 |
|                         | F   | *** (+) | *** (+) | *** (+) | *** (+) | 75, 50 |
| *caeruleogularis-albivitta* | M   | *** (-) | *** (-) | ** (-) | *** (-) | 105, 86 |
|                         | F   | *** (-) | *** (-) | ** (-) | *** (-) | 50, 57 |
| *albivitta-cyanolaemus* | M   | * (+) | * (+) | * (-) | 86, 9 |
|                         | F   | * (+) | * (-) | * (+) | 57, 10 |
| *cyanolaemus-atrogularis* | M   | ** (-) | 9, 17 |
|                         | F   | * (+) | * (+) | 10, 11 |
| *albivitta-atrogularis* | M   | ** (+) | * (+) | * (-) | 86, 17 |
|                         | F   | ** (+) | ** (+) | 57, 11 |

* - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$

- Not significant after table-wide correction for false discovery rates (see text).
Table 5 (on next page)

Patterns of significance from results of $t$-tests comparing individual principal component (PC) scores

Table 5. Patterns of significance from results of $t$-tests comparing individual principal component (PC) scores between geographic pairs of major subspecific groups of *Aulacorhynchus* “prasinus.” PC scores are from the first two principal components. Individuals with missing values were excluded. Underlined asterisks indicate significance after false discovery rate correction for multiple tests.
Table 5. Patterns of significance from results of $t$-tests comparing individual principal component (PC) scores between geographic pairs of major subspecific groups of *Aulacorhynchus* “prasinus.” PC scores are from the first two principal components. Individuals with missing values were excluded. Underlined asterisks indicate significance after false discovery rate correction for multiple tests.

| Pairs compared         | Sex | PC1 | PC2 | N  |
|------------------------|-----|-----|-----|----|
| prasinus-wagleri       | M   | *   |     | 90,28 |
|                        | F   | *** | *   | 65,25 |
| prasinus-caeruleogularis | M   | **  | *** | 90,98 |
|                        | F   | *** |     | 65,48 |
| caeruleogularis-albivitta | M   | *** |     | 98,84 |
|                        | F   | *** | **  | 48,57 |
| albivitta-cyanolaemus  | M   |     |     | 84,8 |
|                        | F   |     |     | 57,10 |
| cyanolaemus-atrogularis| M   |     | *   | 8,16 |
|                        | F   |     |     | 10,11 |
| albivitta-atrogularis  | M   |     | *   | 84,16 |
|                        | F   |     |     | 57,11 |

* - $P < 0.05$

** - $P < 0.01$

*** - $P < 0.001$
Figure 1

The six major, color-based taxonomic groups of the *Aulacorhynchus “prasinus”* species complex

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*. 
Figure 2 (on next page)

Distributions of the specimens of *Aulacorhynchus “prasinus”* examined in this study

Figure 2. Distributions of the specimens of *Aulacorhynchus “prasinus”* examined in this study with the focal six major subspecific groups labeled. Neither all specimens in existence nor observation records are included, so ranges are not complete. Red stars indicate evidence of hybridization; the top-most one, in Ecuador, is from the study of Puebla-Olivares et al. (2008).
Figure 3

An example of a hybrid

Figure 3. An example of a hybrid A. “p.” atrogularis × A. “p.” cyanolaemus. A) a pure A. “p.” cyanolaemus (LSU 87627); B) a hybrid (LSU 92029); and C) a pure A. “p.” atrogularis (LSU 73933).
Figure 4

The mtDNA topology of the relationships among the six major subspecific groups, following Puebla-Olivares et al. (2008).

Figure 4. 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.
Figure 5 (on next page)

The relationship between genetic distance (Figure 3) and the accumulation of morphometric differences (Table 4)

Figure 5. The relationship between genetic distance (Figure 3) and the accumulation of morphometric differences (Table 4) between the major subspecific groups that might hybridize due to proximity. The positive correlation is that predicted by the processes of anagenesis and speciation.
