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.

1 Running head: *Aulacorhynchus* toucanets
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4 **AN EXAMINATION OF SPECIES LIMITS IN THE**
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6 ***AULACORHYNCHUS "PRASINUS"* TOUCANET COMPLEX (AVES: RAMPHASTIDAE)**
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29   *Abstract.*–The number of species recognized in *Aulacorhynchus* toucanets has varied

30   tremendously over the past century. Revisors seem to disagree on whether head and bill

31   coloration are useful indicators of species limits, especially in the *A. "prasinus"* complex. Using

32   morphometrics, I tested the hypothesis that the major color-based subspecific groups of *A.*

33   *"prasinus" sensu lato* are simply "cookie-cutter" (i.e., morphologically nearly identical)

34   toucanets with different head and bill colorations. Univariate and multivariate analyses show that

35   they are not simply morphological replicates of different colors: a complex array of

36   morphometric similarities and dissimilarities occur between the major subspecific groups, and

37   these variations differ between the sexes. Latitude and longitude had a small but significant

38   association with female (but not male) PC1 and PC2. Hybridization and intergradation were also

39   considered using plumage and bill characters as a surrogate to infer gene flow. Hybridization as

40   indicated by phenotype appears to be substantial between *A. "p." cyanolaemus* and *A. "p."*

41   *atrogularis* and nonexistent between other major groups, although from genetic evidence it is

42   likely rare between *A. "p." albivitta* and *A. "p." cyanolaemus*. The congruence and complexities

43   of the morphological and color changes occurring among these groups suggest that ecological

44   adaptation (through natural selection) and social selection have co-occurred among these groups

45   and that species limits are involved. Further, hybridization is not evident at key places, despite in

46   many cases (hypothetical) opportunity for gene flow. Consequently, I recommend that this

47   complex be recognized as comprising five biological species: *A. wagleri, prasinus,*

48   *caeruleogularis, albivitta,* and *atrogularis*. Four of these also have valid subspecies within them,

49   and additional work may eventually support elevation of some of these subspecies to full species.

50   Species limits in South America especially need more study.

53   INTRODUCTION

54   In spite of ongoing advances in the description and recognition of biodiversity, few

55   genera can offer such an incongruous history as *Aulacorhynchus* Gould (Aves: Piciformes:

56   Ramphastidae). The *Aulacorhynchus* toucanets inhabit montane forests from Mexico to Guyana

57   and Bolivia, and there are many allopatric taxa. Although generic limits have been generally

58   consistent during the past century, the number of species within the genus has been a matter of

59   considerable disagreement.

60   **Taxonomic History**

61   In the second edition of his monograph on the Ramphastidae, Gould (1854) recognized

62   10 species in the genus *Aulacorhamphus* (now *Aulacorhynchus* by priority), but several taxa

63   remained undescribed at that time. Between them, Salvin & Godman (1896) and Brabourne &

64   Chubb (1912) recognized 15 species in the genus. Ridgway (1914) followed this treatment. Cory

65   (1919) considered one of these species (*A. erythrognathus*) to be only a subspecies, and he

66   treated the genus as having 14 species. Although a new species was described in 1933 (*A.*

67   *huallagae*, Carriker, 1933), Peters (1948) reduced many of the formerly recognized species to

68   subspecific status and presented the species-level diversity of the genus as just seven taxa. Haffer

69   (1974) followed Peters (1948), except that he reduced one species (*A. calorhynchus*) to

70   subspecies status (after Schwartz, 1972), leaving just six. Sibley & Monroe (1990) followed this

71   treatment, but they presented a further reduction of the apparent diversity by mentioning only

72   two subspecific groups below the species level. Although more comprehensive subspecific

73   inclusion and discussion were given by Short & Horne (2001, 2002), six full species were

74   retained. The treatment of this genus since 1891 is summarized in Table 1.

75   The massive lumping of Peters (1948) proceeded with neither the presentation of data nor

76 with discussion. Careful study of one taxon, *A. calorhynchus*, by Schwartz (1972) supported the

77 single species-level change that was made between Peters (1948) and Haffer (1974), and

78 Haffer's (1974) important work has been cited to support maintaining a broad *A. prasinus* (*sensu*

79 *lato*; AOU, 1998). Haffer (1974) and Short & Horne (2001, 2002) used evidence of hybridization

80 and intergradation to support their conclusions that the whole *A. "prasinus"* complex

81 represented one biological species with many subspecies (14 and 13 subspecies, respectively); at

82 the species level across the genus Short & Horne's (2001, 2002) treatment reflected that of

83 Dickinson & Remsen (2013) in Table 1 except that they considered *A. whitelianus* a subspecies

84 of *A. derbianus*, as Peters (1948) did. Presumably similar reasoning was behind Peters (1948).

85 But subspecies, even those distinctive enough to have been considered full species for a century,

86 can get lost in the shuffle. For example, oversimplification of subspecific variation led Sibley &

87 Monroe (1990) and the American Ornithologists' Union (AOU, 1983, 1998) to completely omit

88 mention of the very distinct form *A. "prasinus" wagleri* from southwestern Mexico. The AOU

89 (1983, 1998) considered Middle American diversity in the genus as being just two subspecific

90 groups of a single species, *A. prasinus*.

91   Renewed interest in this complex (Navarro et al., 2001; Puebla-Olivares et al., 2008;

92 Bonaccorso et al., 2011; del Hoyo & Collar, 2014) is beginning to rectify the absence of data, but

93 the ensuing taxonomic changes recommended have either been based on a different species

94 concept (Bonaccorso et al., 2011) or have inadequately considered the hybridization and

95 intergradation (e.g., Navarro et al., 2001; Puebla-Olivares et al., 2008; del Hoyo & Collar, 2014)

96 that have been integral to supporting the "post-Peters" taxonomy. These latter works have

97 recommended elevation of numerous *A. "prasinus"* taxa to species status (Table 1), but they did

98 not address the reasons for lumping in the first place: evidence of hybridization. There has also

99 been heavy reliance on a single molecular marker (mtDNA) for species delimitation in *A.*

100 "*prasinus*" (Puebla-Olivares et al., 2008; Bonaccorso et al., 2011). This is problematic because

101 mtDNA can be misleading about species limits and relationships between populations due to

102 gene-tree/species-tree mismatches and because genetic distance is not a reliable indicator of

103 species limits (Avise & Wollenberg, 1997; Irwin, 2002; Funk & Omland, 2003; Degnan &

104 Rosenberg, 2006; Cheviron & Brumfield, 2009; Galtier et al., 2009; Ribeiro et al., 2011; Toews

105 & Brelsford, 2012; Pavlova et al., 2013; Peters et al., 2014; Dolman & Joseph, 2015; Morales et

106 al., 2015). Thus, species limits in the group remain uncertain (Table 1). Most disagreement has

107 been in the *A. "prasinus"* complex, and it is on this group that I focus.

108   *The* A. "prasinus" *complex.*—As currently treated (e.g., Table 1, Dickinson & Remsen,

109 2013; del Hoyo & Collar, 2014), *A. "prasinus"* either is a widely distributed and highly variable

110 biological species or it comprises multiple species (Fig. 1). So far as is known, *Aulacorhynchus*

111 toucanets are nonmigratory (AOU, 1998), but as O'Neill & Gardner (1974) and Navarro et al.

112 (2001) noted, members of the genus can wander widely during the nonbreeding season. Short &

113 Horne (2001) considered Central American forms from Mexico to Panama to be partially

114 migratory, with downslope movements to lowlands also occurring during the nonbreeding season

115 (but less commonly) throughout the *A. "prasinus"* range. The sexes are alike by plumage

116 (sexually monochromatic), but sexual size dimorphism is apparent in all taxa examined.

117   In past work there has been too little discussion of the fact that different levels of

118 differentiation occur among the subspecies of *A. prasinus, sensu lato*. All of the named forms do

119 not represent equally differentiated populations; there are major subspecific groups of one or

120 more described subspecies. Objectively determining what these groups are can be done by

121 following taxonomic history, coupled as it is with a color-based clustering. Cory (1919)

122   recognized eight species that were later lumped by Peters (1948) into *A. prasinus* (Table 1). It

123   seems that four of these (*A. wagleri, lautus, cyanolaemus,* and *dimidiatus*) were not available for

124   Cory (1919) to examine, however (he noted which taxa were in the Field Museum of Natural

125   History at that time). Two of these taxa, *A. lautus* and *A. dimidiatus*, may have been included as

126   full species through intertia. This was not uncommon: Ridgway (1914) considered that the genus

127   had 15 species, but he was uncertain because he had only been able to examine seven of them.

128   The subsequent rediscovery and examination of *A. dimidiatus* (O'Neill & Gardner, 1974) showed

129   intergradation with *A. "prasinus" atrogularis*, and the Santa Marta isolate *A. "prasinus" lautus*

130   is, by plumage, clearly a relatively minor derivative of the *A. "p." albivitta* group. These

131   considerations reduce the number of major, color-based subspecific groups in the *A. "prasinus"*

132   complex to six (*A. "p." wagleri, prasinus, caeruleogularis, albivitta, cyanolaemus*, and

133   *atrogularis*).

134   The rather pronounced differences among these major groups are illustrated in Fig. 1,

135   together with examples of some of the less-pronounced variation (though still between named

136   subspecies) occurring within two of these groups. Del Hoyo & Collar (2014) presented an

137   analysis of colors that reaffirms this approach, coming back to the same six color-based

138   subspecific groups and treating them as full biological species. Diagnostic characters of these six

139   groups are given in Table 2. It is these six groups that form the basis for my comparisons. They

140   are the color-based groupings that have been recognized by students of the birds themselves.

141   The troubled taxonomic history of *Aulacorhynchus* (especially *A. prasinus, sensu lato*)

142   reflects disagreement among revisors over the ability of plumage and bill colors and patterns to

143   represent species limits. Members of the *A. "prasinus"* group in particular are effectively

144   ecologically similar geographic replacements (Mallet, 2007), and where named taxa have been

145   found to come together hybridization has been described (e.g., Haffer, 1974; Short & Horne,

146   2001). Given evidence of hybridization, it is unclear how the birds themselves perceive these

147   differences. Is this group (*A. "prasinus"sensu lato*) really one in which head and bill colors and

148   patterns are very plastic, resulting in species that include a high degree of color variation? Or are

149   full species being overlooked? If bill and head color characteristics are plastic and not indicative

150   of species limits, as many treatments since 1948 suggest, then strikingly color-based taxa, most

151   of Cory's (1919) species and the six of del Hoyo & Collar (2014), would not likely show a great

152   deal of morphometric distinctiveness. If, on the other hand, substantial, concordant

153   morphological changes are also occurring, then perhaps the concept of ecologically similar

154   geographic replacements, which seems broadly applicable to *A. prasinus, sensu lato*, is masking

155   important group-specific evolutionary adaptations that go beyond the existing color changes, the

156   latter of which likely reflect social selection. Such morphological differences might suggest

157   adaptive changes among groups that would make immigrants and hybrids less fit (Price, 2008).

158   My question then is simple: Are these color-based subspecific groups just "cookie-cutter" (i.e.,

159   morphologically nearly identical) toucanets bearing different throat and bill colorations, or are

160   there also significant morphological changes occurring among them? If substantial morphometric

161   changes occur concurrently with dramatic color changes, then species limits should probably be

162   reconsidered, as several have suggested (Navarro et al., 2001; Puebla-Olivares et al., 2008;

163   Bonaccorso et al., 2011; del Hoyo and Collar, 2014).

164   Morphometrics alone are unlikely to be important components of species limits in forms

165   like these where colors are obviously important, and this is not meant as a study of how

166   morphology varies within the group independently of color-based clustering. Navarro et al.

167   (2001) did a morphological analysis based on 17 allopatric groupings, and this is not meant to

168 repeat those analyses. Geography alone can affect morphology (e.g., Bergmann's rule; Mayr,

169 1963), and my analyses account for this. In this study I will 1) test for univariate differences

170 between pairwise groups that are geographically closest to each other; 2) compare these groups

171 in multivariate, principal component space (because univariate measures can be correlated with

172 each other); and 3) visually examine specimens for evidence of hybridization because such

173 evidence has been historically important in the taxonomy of the group.

METHODS AND RESULTS

175   I used morphometrics to examine how body characteristics vary among the major, color-

176 based subspecific groups in the *Aulacorhynchus "prasinus"* complex (Fig. 1, Table 2). Museum

177 specimens (institutions listed in Acknowledgments) were visually examined and measurements

178 of wing chord, tail, tarsometatarsus, bill, bill height, and bill width (all three bill measures from

179 anterior edge of nares) were made to the nearest 0.1 mm using vernier calipers following

180 Baldwin, Oberholser & Worley (1931). Wing tip (length of longest primary to first secondary)

181 was also measured to the nearest 0.1 mm using vernier calipers. Although Navarro et al. (2001)

182 raised the possibility that bill growth in this group might be indeterminate, with my larger sample

183 size of 98 male *A. prasinus sensu stricto* (see Appendix) I found that bill length had a normal

184 distribution, so it is retained in my analyses. Morphometric geographic variation within these six

185 major subspecific groups was not examined, because that is not related to the hypothesis being

186 tested, i.e., are morphological changes occurring concurrently with color-based changes (see also

187 Navarro, 2001). However, the effects of geography upon the data are examined after the main

188 questions posed are addressed. Some of these major subspecific "groups" have named subspecies

189 within them. *Aulacorhynchus prasinus* has four (*prasinus, warneri, virescens, volcanius*), *A.*

190 *"p." caeruleogularis* two (*caeruleogularis, cognatus*), *A. "p." albivitta* four (*lautus,*

191 *griseigularis, phaeolaemus, albivitta*), and *A. "p." atrogularis* two (*atrogularis, dimidiatus*); the

192 other two major subspecific groups (*wagleri,* and *cyanolaemus*) have no named subspecies

193 within them (Appendix). Color differences formed the basis for the majority of characters used

194 to describe all of these named subspecies, with size being mentioned (in addition to color) in just

195 three of 14 cases. Within-group variation is accounted for in the standard statistical manner (e.g.,

196 Table 3). Immature individuals were not measured.

197   I examined and measured 578 specimens of the six major subspecific groups of *A.*

198 "*prasinus.*" The distributions of these groups (Fig. 2) were found to be allopatric or parapatric, as

199 others have depicted (e.g., Haffer, 1974; Short & Horne, 2001; Ridgely & Greenfield, 2001;

200 Restall, Rodner & Lentino, 2006). Morphometric data exhibited male-biased sexual size

201 dimorphism (Table 3), so all analyses were performed separately for each sex.

202   Univariate mensural characteristics (Table 3) were visually examined to determine

203 whether it was warranted to apply statistical testing for differences. This was done to reduce the

204 overall number of tests made, which enhances the power of individual tests when applying

205 multiple-test corrections. No statistical tests were done on mass (due to small sample sizes), and

206 tests were applied in a pairwise manner between groups most proximate to each other (except for

207 *A. "prasinus" albivitta-atrogularis*). The Bonferroni-style of multiple-test correction is highly

208 conservative, so I did not use it; in controlling for table-wide Type I error (rejecting the null

209 hypothesis when it is true), it raises the likelihood of Type II error (incorrectly accepting the null

210 hypothesis) at the level of the single test (Sokal & Rohlf, 1995; Whitlock & Schluter, 2009).

211 While false discoveries will accrue with multiple testing, determining whether there are

212 differences at the individual test level is very important for a study of this type. I used an

213 approach more commensurate with this need, one that controls for the expected proportion of

214   falsely rejected null hypotheses, the "false discovery rate" (Benjamini & Hochberg, 1995). I

215   report both aspects (uncorrected and corrected), because future investigators of subsets of these

216   taxa should focus on characteristics that differ between them and not be distracted by the

217   additional statistical gyrations that I needed to perform to reduce table-wide error when making

218   so many tests (60 tests for Table 4 and 24 for Table 5).

219   Significant univariate mensural differences were found among the six groups in both

220   sexes (Tables 3 and 4). The number of significant differences was highest when *A. "prasinus"*

221   *caeruleogularis* was compared with *A. "p." prasinus* to the north and west (8 differences) and *A.*

222   *"p." albivitta* to the south and east (11 differences; Table 4). After multiple-test correction

223   (which only affected *A. "p." cyanolaemus* comparisons in Table 4), the fewest differences

224   occurred when *A. "p." cyanoleamus* was compared with *A. "p." albivitta* to the north (3

225   differences) and *A. "p." atrogularis* to the south (2 differences), although small sample sizes

226   were likely to be at least partially responsible for this. I included a pairwise comparison between

227   *A. "p." albivitta* and *A. "p." atrogularis* because of the uncertain taxonomic status of

228   (major/minor group or species/subspecies; Table 1), and small sample sizes available for, *A. "p."*

229   *cyanolaemus*. Intermediate levels of univariate differences occurred between *A. "p." prasinus*

230   and *A. "p." wagleri* (7 differences) and *A. "p." albivitta* and *A. "p." atrogularis* (6 differences).

231   Wingtip, bill width, and tarsometatarsus showed the fewest significant differences between

232   groups, whereas wing chord and tail lengths showed the most (Table 4). A pronounced large-

233   small-large pattern was revealed among *A. "p." prasinus-caeruleogularis-albivitta* (Tables 3 and

234   4). The characteristics exhibiting significant differences between taxon pairs varied among pairs

235   and, in most cases, between sexes (Table 4). In other words, significant mensural differences

236   were decidedly inconsistent between groups.

237   Morphometric relationships between groups (within sexes) were further explored using

238   principal components analyses (PCA). Two analyses were performed. For each sex, all

239   individuals of all groups were run through a single analysis, and the first two principal

240   components (PC1 and PC2) were extracted from the variance-covariance matrix of the log-

241   transformed data. PC1 and PC2 explained 45.0% and 32.4% of the variance among males and

242   48.0% and 31.1% among females, respectively. For each of the two sex-specific analyses,

243   principal components scores were generated for each individual on PC1 and PC2, and these

244   individual scores were then compared between the major subspecific groups using *t*-tests. These

245   tests were done to determine whether, on a multivariate basis, morphometric differences between

246   taxon pairs were as heterogeneous as suggested by univariate analyses (Tables 3 and 4). Results

247   suggest that they were; again, differences between groups varied in an unpredicatable manner

248   between the sexes and between the two independent multivariate dimensions (PC1 and PC2;

249   Table 5). Of the multivariate pairwise comparisons, only *A. "prasinus" albivitta-cyanolaemus*

250   showed no significant differences (Table 5), although several univariate differences were found

251   (Table 4). These results may reflect the small sample size in *A. "p." cyanolaemus*. After

252   multiple-test correction, contrasts within the South American forms (the last three rows in Table

253   5) yielded no significant differences at the table-wide level. Again, while smaller sample sizes

254   likely affected these last results, a "cookie-cutter" effect is not apparent among the major

255   subspecific groups of the *A. "prasinus"* complex, either in univariate or in multivariate

256   morphometric space (Tables 4 and 5).

257   The major, color-based subspecific groups of *A. "prasinus"* do show considerable

258   morphometric differences between them, but are these differences just an expected result from

259   changes of size with latitude under Bergmann's rule (Mayr, 1963) or otherwise geographically

260 driven? Variation in the two sex-specific principal components was examined in two multiple

261 regressions for each sex (PC1 & PC2) against the variables latitude and longitude. Neither

262 regression was significant in males, but both were in females ($F > 4.0$, $P < 0.02$). However, only

263 a small proportion of female variation was explained by latitude and longitude, 4% for PC1 ($R^2 =$

264 0.04) and 6% for PC2 ($R^2 = 0.06$). Thus, geography has a small but significant influence in 5 of

265 the 11 differences denoted in Table 5, perhaps contributing to the higher significance levels

266 found in females there. Finally, in considering the individual effects of these two geographic

267 variables, stepwise multiple regression showed that only longitude was significantly associated

268 with PC1 in females ($F = 7.56$, $P = 0.007$, $R^2 = 0.039$); neither variable by itself was significantly

269 associated with PC2. Thus, there is no evidence that Bergmann's rule is affecting this complex as

270 a whole.

271   *Hybridization*.—Because members of the genus are known to wander rather widely

272 during the nonbreeding season, the opportunity for gene flow does exist between these largely

273 allopatrically breeding groups. Among the six major subgroups I examined there are

274 theoretically five pairwise instances of possible gene flow between any two of the groups,

275 particularly across some of the narrower zones of separation, *A. "prasinus" prasinus-wagleri*

276 (Oaxaca, Mexico), *A. "p." caeruleogularis-albivitta* (in W Colombia), *A. "p." albivitta-*

277 *cyanolaemus* (Ecuador), and *A. "p." cyanolaemus-atrogularis* (Peru); the fifth, *prasinus-*

278 *caeruleogularis* (in Nicaragua), is a larger distance, on the order of about 240 km. Note that

279 closest approach distances are not accurate in Fig. 2, which is based on the specimens I

280 examined; ranges given by other sources (e.g., Haffer, 1974; Hilty & Brown, 1986; Binford,

281 1989; Howell & Webb, 1995; Short & Horne, 2001; Ridgely & Greenfield, 2001; Restall,

282 Rodner & Lentino, 2006; Schulenberg et al., 2007) include more records (including sight

283   records) and are more accurate.

284   Specimens were examined carefully for phenotypic evidence (i.e., intermediate

285   phenotypes in plumage and bill coloration) of hybridization between these major groups, but it

286   was found to occur in just one of these pairwise comparisons: between *A. "prasinus"*

287   *cyanolaemus* and *A. "p." atrogularis* in Peru. Four specimens representing possible F_1 hybrids

288   (due to intermediacy of characters) were found; one from La Libertad, Utcubamba (25 October

289   1979, D. Wiedenfeld, LSUMNS 92029; Fig. 3), and three from La Lejía in NE Peru (11 & 19

290   March, 16 April 1925, H. Watkins, AMNH 234533, 234532, and 234535). All four specimens

291   show obvious intergradation between these two taxa, particularly in bill coloration (see Fig. 3

292   and Haffer, 1974, figure 16.8), and all four are males (these individuals were not included in the

293   morphometric analyses). In addition, there are another five specimens that seem to show

294   evidence of intergradation to a lesser degree, two females that are phenotypically mostly *A. "p."*

295   *cyanolaemus* (both H. Watkins: La Lejía, 19 March 1925, AMNH 234534; and Uscho, Dept.

296   Amazonas, 3 October 1925, AMNH 234531), and three males that are phenotypically *A. "p."*

297   *atrogularis* but seem to have some *A. "p." cyanolaemus* influence (e.g., primaries edged in

298   russet). These latter three birds are from three localities: Divisoria, Cordillera Azul, Dept.

299   Huanuco (17 August 1967, J. P. O'Neill, LSUMNS 62227), Huanhuachayo, Dept. Ayacucho (6

300   May 1971, J. P. O'Neill, LSUMNS 69410), and Abra Divisiona, Dept. Loreto (14 Aug 1977, J.

301   W. Eley, LSUMNS 84550). It is of interest that this evidence of hybridization occurs between

302   the subspecific pair with the fewest morphometric differences (Table 4) and close genetic

303   affinity (Puebla-Olivares et al., 2008).

304   *Morphometrics and hybridization in a genetic context.*—While divergent selection should

305   produce phenotypic differences between species, this observation makes predictions neither in

306   direction nor degree as far as morphometrics are concerned (i.e., it only predicts accumulating

307   differences). Nevertheless, where differences occur between groups on a phylogeny, and the

308   genetic distances involved, might be of further aid in inferring species limits—qualified, of

309   course, by the many known ways in which mtDNA can be misleading about species limits

310   (Avise & Wollenberg, 1997; Irwin, 2002; Funk & Omland, 2003; Degnan & Rosenberg, 2006;

311   Cheviron & Brumfield, 2009; Galtier et al., 2009; Ribeiro et al., 2011; Toews & Brelsford, 2012;

312   Pavlova et al., 2013; Peters et al., 2014; Dolman & Joseph, 2015; Morales et al., 2015). The

313   mtDNA topology of the phylogenetic relationships among the six major subspecific groups is

314   given in Fig. 4 (after Puebla-Olivares et al., 2008). To examine the results of my study in relation

315   to what is presently known about relationships among and genetic distances between the groups

316   examined, I downloaded the mtDNA data of Puebla-Olivares et al. (2008) from GenBank,

317   concatenated and aligned the sequences using Geneious (ver. 7.1; Kearse et al., 2012), and

318   calculated genetic distances between the groups for which I made pairwise comparisons using

319   MEGA (ver. 6; Tamura et al., 2004 & 2013). Three of these groups are not monophyletic in their

320   mtDNA (not uncommon; see Funk & Omland, 2003), but I treated the haplotypes of *A. "p."*

321   *atrogularis* that have introgressed into *A. "p." albivitta* (see discussion below) as *A. "p."*

322   *atrogularis* for the calculation of genetic distances.

323   Phenotypic evidence of hybridization occurs only between the most closely related pair

324   on this tree, but the presence of *A. "p." atrogularis* mtDNA in birds that are phenotypically *A.*

325   *"p." albivitta* with no outward evidence of hybrid characteristics indicate that gene flow can

326   occur between groups that are on average 4.2% divergent (Fig. 4, bottom clade). Contrasting the

327   number of morphometric differences that have accumulated between the pairwise comparisons

328   of major groups that might hybridize due to proximity (Table 4, excluding *albivitta-atrogularis*)

329   with genetic distance reveals a positive correlation (linear regression, $F = 6.07$, $P = 0.04$, $R^2 =$

330   0.67; Fig. 5).

DISCUSSION

332   My results show that a complex array of morphometric similarities and dissimilarities

333   occur between the major subspecific groups of *A. "prasinus."* Moreover, these variations differ

334   between the sexes. The morphometric data (Tables 3, 4, and 5) clearly show that these taxa are

335   not simply "cookie-cutter" renditions of a green toucanet bearing different head and bill colors.

336   It might be argued that morphological change among the major subspecific groups of *A.*

337   *"prasinus"* are to be expected: that Bergmann's rule of increased body size with latitude (and

338   elevation; Mayr 1963) would apply to populations of *Aulacorhynchus "prasinus"* and predispose

339   this examination to finding morphometric differences. Analyses showed no association between

340   male principal components and either latitude or longitude. Further, while female principal

341   components showed a small but significant effect from latitude and longitude, only longitude by

342   itself showed a significant association with PC1, leaving no evidence for Bergmann's rule

343   operating among these taxa as a group. The absence of any geographic effect in males suggests

344   that some other factor, perhaps sexual selection, overcomes the relatively small geographic effect

345   that otherwise occurs in females.

346   Another possibility is that differences occur not due to genetic disjunctions among locally

347   adapted lineages, but rather to environmental variables affecting development (e.g., James, 1983

348   1991; West-Eberhard, 2003). If we consider these allopatric forms as a series of natural

349   experiments in differentiation, I suggest that we can consider group-specific morphological

350   evolutionary adaptation as a more likely basis for the observed differences than the possibility of

351   developmental plasticity (although the latter is itself subject to selection; West-Eberhard, 2003),

352 especially because they are coupled with color changes that are not attributable to developmental

353 plasticity. Several clear patterns emerge from the data to suggest that a simple change in

354 environment is not the cause of the morphological differences occurring among these major

355 groups. These patterns include sexually different morphometric changes between groups (Table

356 4), a large-small-large pattern going from northern Middle America to South America (Table 4),

357 and discordant changes between PC1 and PC2 (Table 5). Nor are the differences among them

358 simply differences in size, as Bergmann's rule would predict; indeed there is a minimal influence

359 of geography alone (latitude and longitude; (Tables 4 and 5). If between-group differences were

360 driven by developmental plasticity, I would expect more evidence of underlying predictable

361 patterns, such as sexually similar responses. Instead, heterogeneity is the hallmark of the

362 differences observed, and ecological adaptation is (hypothetically) a reasonable explanation (see

363 also Mayr, 1963; Price, 2008).

364   Thus, in *A. prasinus sensu lato* we have complex morphometric changes occurring in

365 conjunction with a series of additional complex phenotypic changes, for example: paedomorphic

366 basal bill encrustations retained and enhanced in adult *A. "prasinus" wagleri* (an important

367 character that alone among these examples is not simply one of color); chestnut coloration in the

368 bill of *A. "p." albivitta*; changes in coloration at the base of the bill among the groups, and a

369 double leapfrog pattern in throat colors (light-dark-light-dark; Fig. 1). Concordant shifts in suites

370 of mensural and other morphological characters are precisely what we would predict to occur

371 between individuals representing genetically disjunct, locally adapted gene pools. Consequently,

372 this evidence suggests that this is what they are, and at these levels of morphological

373 differentiation (morphometrics, coloration, and pattern) we would usually consider these groups

374 to be full biological species. But that conclusion does not include all of the evidence available.

375   Haffer (1974), who measured 66 *A. prasinus* (*sensu lato*), treated all forms as subspecies.

376   Given evidence of hybridization in two cases in the *A. "prasinus"* complex, he concluded that

377   differences would probably not prevent interbreeding; he thus retained the post-Peters (1948)

378   taxonomy for this group. The evidence of intergradation occurs between *A. "p." atrogularis* and

379   *A. "p." cyanolaemus* in Peru (a dataset that I have expanded upon above) and seemingly rather

380   widespread intergradation among *A. "p." albivitta* forms (*A. "p." albivitta, phaeolaemus*, and

381   *griseigularis*). Probably to simplify his survey of the entire family, Haffer (1974) generally

382   treated all subspecies as equivalent in degree of differentiation, not making distinctions between

383   minor and major variants. Thus, his correct observation of apparently pronounced gene flow

384   among *A. "p." albivitta* forms may have overshadowed the comparative rarity of gene flow

385   among the major forms.

386   Short & Horne (2001) also pointed to intergradation among subspecies and noted (p. 326)

387   that "differences in colour of head and of the bill seem ineffective in preventing interbreeding,

388   e.g. in NW South America; allopatric taxa are no more distinctive in features than are the

389   interbreeding forms (the entire complex ought to be studied carefully before any one taxon is

390   elevated to the status of species)." It is likely that the evidence of hybridization discussed by

391   Haffer (1974) and Short & Horne (2001) formed the basis for Peters' (1948) massive lumping,

392   although he gave no reasoning.

393   Navarro et al. (2001) studied the phenotype of the *A. "prasinus"* complex, examining 247

394   specimens from Middle America and 58 from South America. Unlike my study, they included in

395   their analyses patterns and colors of the head and bill. They sidestepped the issue of

396   hybridization and concluded that there were four species in Middle America (*A. wagleri,*

397   *prasinus, caeruleogularis,* and *cognatus*) and three more in South America (*A. lautus, albivitta,*

398   and *atrogularis* ["*nigrogularis*" in their abstract is an error]).

399   Puebla-Olivares et al. (2008) provided the first genetic data for the *A.* "*prasinus*"

400   complex. My conclusions, which I will detail below, are mostly congruent with theirs, but there

401   are also key differences (Table 1). These differences stem mainly from how we choose to

402   interpret the genetic data and morphological diagnosability. For example, Puebla-Olivares et al.

403   (2008) relied heavily on genetic distance, reciprocal monophyly, and inferred gene flow using

404   relatively small population samples and a single locus (mtDNA). Although the evolutionary

405   hypothesis that their data provides for this group is likely to be mostly accurate, the power of

406   these data for determining species limits is not high, particularly in a group in which

407   hybridization has played a pivotal role in determining taxonomy. Moreover, if we set aside

408   genetic distance for a moment, there are other named, allopatric forms that are morphologically

409   diagnosable and reciprocally monophyletic in their data that they did not highlight as being likely

410   species (e.g., the subspecies *A. prasinus warneri*, *volcanius*, and *chiapensis* within *prasinus,*

411   *sensu stricto*). Further, Puebla-Olivares et al. (2008) showed two *A. "p." albivitta* from NE

412   Ecuador in their *A. "p." "atrogularis"* clade with no discussion (contrast their table 1 locality 22

413   with their figures 1 and 2; *A. "p." albivitta* is the form that occurs in NE Ecuador, not *A. "p."*

414   *atrogularis*, given incorrectly in their figure 1 but correctly in their table 1). This is a clear

415   mismatch of morphology and genetics: two individuals that are phenotypically *A. "p." albivitta*

416   (catalogued as such and verified by me from photographs) have mtDNA haplotypes more closely

417   related to *A. "p." atrogularis* and *cyanolaemus*. (The vouchers are ANSP 185,312 for tissue

418   4837 and ANSP 185,311 for tissue 4799; only tissue numbers are given for these birds by

419   Puebla-Olivares et al. [2008].) This produces a paraphyletic *A. "p." albivitta* and suggests that

420   there has been historical gene flow between forms that are quite different.

421   While these data are important, using them to determine species limits is problematic.

422 And considering morphology, their observation (Puebla-Olivares et al., 2008:47) that the

423 diagnostic morphological attributes of their focal clades "could facilitate reproductive isolation"

424 is unduly optimistic given evidence to the contrary (e.g., their own unremarked *A. "p." albivitta*

425 results and the quote of Short & Horne [2001] above). Genetic distance is not a reliable indicator

426 of species limits in birds (Price, 2008; Winker, 2009). A better indicator is how the birds

427 themselves interact when in contact (Mayr, 1969; Mayr & Ashlock, 1991). And when examining

428 gene flow, sample sizes and geographic coverage become critically important (Winker, 2010),

429 especially in groups, such as the *A. "prasinus"* complex, whose taxonomy has been so affected

430 by evidence of hybridization.

431   *Hybridization.*—Fortunately, with respect to gene flow we do have larger sample sizes if

432 we use diagnostic morphological attributes as a surrogate (i.e., the plumage and bill

433 characteristics upon which the named forms have been based). Despite what is likely to be ample

434 opportunity for gene flow through dispersal across the five zones of contact or "nearest

435 approach," evidence of hybridization among the major groups in the *A. "prasinus"* complex

436 presently exists in just two cases: between *A. "prasinus" atrogularis* and *cyanolaemus*

437 (phenotypic only, as detailed above), and in the genetic results of Puebla-Olivares et al. (2008),

438 which showed two *A. "p." albivitta* specimens from NE Ecuador with mtDNA more closely

439 related to *A. "p." cyanolaemus/atrogularis.* This latter case suggests that historical crossing may

440 have occurred across this zone, although morphological evidence of this is not yet evident.

441 *Aulacorhynchus "prasinus"* is uncommon in this region, and the ranges of *A. "p." albivitta* and

442 *cyanolaemus* are not known to come into contact (Ridgely & Greenfield, 2001; Restall, Rodner

443 & Lentino, 2006). These two *A. "p." albivitta* specimens also demonstrate that phenotypic

444   evidence of hybridization, which does occur and has been useful in past evaluations in *A.*

445   "*prasinus*," can be absent despite gene flow (but even nuclear genomic evidence of hybridization

446   can disappear over a few generations of backcrossing; Lavretsky et al., 2016).

447   From this dataset, therefore, we know that hybridization in toucanets can be visible and

448   invisible, the latter probably after repeated backcrossings to one parent taxon. We might,

449   however, consider the visible hybrids to be roughly indicative of a hybridization rate. Current

450   evidence thus suggests that hybridization between *A. "p." albivitta* and *cyanolaemus* is rare. In

451   the case of *A. "p." cyanolaemus* and *atrogularis*, however, my results expand the scope of

452   hybridization recognized, both in number of possible F_1 specimens (those most intermediate in

453   characters) and in the broader distribution of specimens likely exhibiting intergradation (and note

454   that it is bi-directional). The fact that all four putative F_1 specimens are males suggests the

455   possibility that the two forms are sufficiently divergent that genetic incompatibilities are

456   preventing viability of the heterogametic sex, which is the female in birds (Haldane's rule; Price,

457   2008). However, this is not a significant departure from the sex ratio of the rest of the *A.*

458   "*prasinus*" sample I examined ($P = 0.13$, Fisher's exact test), and the two forms are not very

459   divergent genetically in mtDNA ($< 1\%$; Fig. 4 and Puebla-Olivares et al., 2008). The matrilineal

460   passage of *A. "p." cyanolaemus/atrogularis* mtDNA into *A. "p." albivitta* in NE Ecuador

461   (Puebla-Olivares et al., 2008) also suggests that Haldane's rule is not operating among major

462   subspecific groups in South America. In the case of *A. "p." cyanolaemus* and *A. "p."*

463   *atrogularis*, hybrids and intergrades represented a substantial percentage of the specimens I was

464   able to examine of these taxa (as many as 10 specimens, with remaining sample sizes of 19 each

465   of *cyanolaemus* and *atrogularis*). Given the small sample, it remains unclear whether this

466   reflects the true incidence of hybrids between these taxa, but given present evidence it is

467   substantial.

468   *Species limits*.—Despite considerable combined evidence from coloration,

469   morphometrics, and mtDNA data, comprehensive and accurate species limits for this group

470   remain elusive, no matter what species concept one chooses to use. Using the biological species

471   concept, I suggest that consideration of all of the available evidence indicates that we should

472   recognize five species in the *A.* "*prasinus*" complex (*A. wagleri, prasinus, caeruleogularis*,

473   *albivitta*, and *atrogularis*), each with any associated named subspecies (Appendix). Further study

474   could raise this number (e.g., by splitting *A. atrogularis cyanolaemus* from *atrogularis* again).

475   Under a phylogenetic species concept (PSC), one could probably raise every allopatric

476   population in *A.* "*prasinus*" to the species level, resulting in at least 12 taxa using morphology

477   alone. So how many species of toucanets are there in the *A.* "*prasinus*" complex?

478   Historically, evidence of hybridization has often driven taxonomic decisions under the

479   biological species concept (BSC), as has apparently occurred in this case. My interpretation of

480   the taxonomic history of *Aulacorhynchus "prasinus"* is that evidence of hybridization and

481   intergradation between named forms (among forms of the *A. "p." albivitta* group and between *A.*

482   *"p." albivitta* and *cyanolaemus*) caused all named forms to be lumped together as one species

483   (Peters, 1948). But hybridization is not uncommon between full species (Grant & Grant, 1992),

484   and avian taxonomists have used a working definition of the BSC that recognizes this (e.g.,

485   Short, 1969; Johnson, Remsen & Cicero 1999; Winker et al., 2007). Gene flow, reproductive

486   isolating mechanisms, and lineage reticulation remain fundamentally important evolutionary

487   phenomena affecting species diversity and the process of evolutionary divergence, and thus they

488   require consideration. Effective lineage reticulation requires that hybrid offspring have equal or

489   greater fitness than offspring of pure parental forms. Also, gene flow must occur frequently

490   enough to overcome the differentiating selective factors likely to be operating on largely

491   allopatric populations (and this relationship is nonlinear; see Winker, 2010 for discussion). The

492   more differences there are between populations in morphology, the more differences there are

493   likely to be in selective factors operating on these populations and the more difficult effective

494   gene flow is likely to be between populations; at larger scales this results in the general

495   correlation between morphological difference and reproductive isolation (Mayr, 1963; Price,

496   2008).

497   Classic systematics and taxonomy (Mayr, 1969; Mayr & Ashlock, 1991) uses a

498   comparative approach to determine species limits among allopatric taxa, examining what occurs

499   at contact zones (if available) and/or what occurs in similar cases in closely related taxa. In

500   previous work on *A. "prasinus"* taxonomy I do not think enough credit has been given to the

501   dispersal abilities of these birds. And yet despite that ability there is a lack of evidence for gene

502   flow (using phenotype as an indicator) between five of the major subspecific groups (*A.*

503   *prasinus-wagleri, prasinus-caeruleogularis, caeruleogularis-albivitta, albivitta-cyanolaemus*).

504   For example, in south-central Mexico (Oaxaca), *A. prasinus* and *A. wagleri* breed within about

505   100 km of each other, a distance that *A. prasinus* individuals appear to move routinely away

506   from their breeding areas, e.g., at the base of the Yucatan Peninsula (e.g., Land, 1970; Jones,

507   2003), which does not seem unusual for an arboreal frugivore (see also discussions in O'Neill &

508   Gardner, 1974, and Navarro et al., 2001). Hybridization *per se* is not sufficient evidence for

509   conspecificity, and in this group I find the lack of hybrids at most zones of potential crossing of

510   major subspecific groups to be more compelling in the determination of species limits than its

511   clear and seemingly routine presence at one—particularly in light of the repeated evidence of

512   varying suites of morphological characters changing abruptly across these zones. However, I do

513   consider that the apparent frequency of hybridization between *A. atrogularis cyanolaemus* and *A.*

514   *a. atrogularis* warrants a conservative approach to their separation at the species level, and thus I

515   do not recommend doing so without more evidence. In short, morphologically there is no

516   evidence for hybridization between five of the major subspecific groups, despite likely

517   opportunity, especially in northern Middle America. This is coupled with pronounced

518   morphometric differences between these groups, suggesting group-specific ecological adaptation

519   in addition to whatever social selection factors have likely caused the rather dramatic head and

520   bill color differences (Fig. 1, Table 2).

521   The populational processes of lineage divergence and the hierarchical nature of

522   differentiation that accrues as gene flow decreases and divergent selection produces increasingly

523   different phenotypes (anagenesis) have produced gradations of differentiation in the genus

524   *Aulacorhynchus*. This is seen from population-level differences of little significance (e.g., among

525   some questionably recognizable subspecies; see Appendix), to diagnosable isolated populations

526   within biological species, to full biological species, to a recognizable subgeneric group (members

527   of *A. "prasinus" sensu lato*). Genetic data also support this subgeneric group (Puebla-Olivares et

528   al., 2008), and the name *Ramphoxanthus*, which is particularly fitting (i.e., yellow-bills), is

529   available for it (Bonaparte, 1854). This group diverged from other members of the genus during

530   the Miocene (approximately 6-9 million years ago; Bonaccorso & Guayasamin, 2013). Within

531   the five groups comprising *A. "prasinus"* that I consider full biological species (*A. wagleri,*

532   *prasinus, caeruleogularis, albivitta,* and *atrogularis*) there are a number of diagnosable

533   subspecific taxa that are clearly evolutionarily significant units, and some, being 100%

534   diagnosable, could be called phylogenetic species (e.g., *A. p. warneri, A. c. cognatus, A. albivitta*

535   *lautus*). These, however, do not represent major phenotypic differences, and I consider this

536   continued lumping to be warranted given present evidence, which includes hybridization and

537   intergradation between other subspecies with similar degrees of differentiation within the major

538   subspecific *A. "prasinus"* groups (e.g., *A. p. prasinus-virescens*, *A. albivitta phaeolaemus-*

539   *griseigularis*; Short & Horne, 2001, and personal observation).

540   Voice has not diverged among these five groups as much as it has in other species in the

541   genus (Schwartz, 1972; Short & Horne, 2001). Indeed, Short & Horne (2001:327) related that

542   "Calls of forms in Peru, Venezuela, Panama, Costa Rica and Mexico are much alike..."

543   However, more work is warranted in this area. For example, *A. wagleri* has a slower pace to its

544   vocalizations than *A. prasinus* (from www.xeno-canto.org, 4 *A. wagleri* average 1.85 calls/sec

545   while 6 *A. prasinus* average 2.13 calls/sec; XC 274798, 219401-2, and 177515 vs. XC 96724,

546   256673, 256311, 233097, and 138132-3). Other differences may be apparent with increased

547   sample sizes.

548   Considering my suggested taxonomy (Appendix) in relation to the mtDNA tree of

549   Puebla-Olivares et al. (2008), there are two paraphyletic species (Fig. 4). First, *A. albivitta* is

550   paraphyletic with respect to *A. atrogularis-cyanolaemus*. Second, my treatment of *A.*

551   *caeruleogularis* is paraphyletic with respect to *A. prasinus* and *A. wagleri* because it includes *A.*

552   *"p." cognatus*; that has been the norm since its description, only Navarro et al. (2001) and

553   Puebla-Olivares et al. (2008) have treated it as a full species thus far. Paraphyletic species are not

554   uncommon (Funk & Omland, 2003; Oyler-McCance, St. John & Quinn, 2010), but there is

555   clearly work remaining to be done on species limits in this complex, especially in South

556   America. For example, the distributions of *A. atrogularis cyanolaemus*, *A. a. atrogularis*, and the

557   hybrid zone between them warrant further study, as does the apparently rare instance of crossing

558   between *A. albivitta* and *A. atrogularis cyanolaemus* in Ecuador (mtDNA evidence of Puebla-

559   Olivares et al,. 2008). Also, the relationship between *A. c. caeruleogularis* and *A. c. cognatus* in

560   Panama bears further investigation; they are phenotypically relatively similar (Short & Horne,

561   2001:325 also noted their close resemblance) in contrast to, e.g., *A. a. atrogularis* and

562   *cyanolaemus*. Larger sample sizes, more loci, coverage of hybrid zones, and continued

563   recognition that there are relatively major and minor phenotypic variants among these named

564   taxa will be needed to finally and fully resolve species limits in this group.

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847

848

849   Figure 1. The six major, color-based taxonomic groups of the *Aulacorhynchus "prasinus"*

850   species complex, from top to bottom: A) *wagleri*; B) *prasinus* (nominate *prasinus* and *warneri*,

851   the full-bodied bird, are portrayed): C) *caeruleogularis*; D) *albivitta* (*griseigularis* and nominate

852 *albivitta* are portrayed); E) *cyanolaemus* (yellow-tipped bill); and F) *atrogularis*.

853

854
855 Figure 2. Distributions of the specimens of *Aulacorhynchus "prasinus"* examined in this study

856 with the focal six major subspecific groups labeled. Neither all specimens in existence nor

857 observation records are included, so ranges are not complete. Red stars indicate evidence of

858 hybridization; the top-most one, in Ecuador, is from the study of Puebla-Olivares et al. (2008).

859

860 Figure 3. An example of a hybrid *A. "p." atrogularis × A. "p." cyanolaemus*. A) a pure *A. "p."*

861 *cyanolaemus* (LSU 87627); B) a hybrid (LSU 92029); and C) a pure *A. "p." atrogularis* (LSU

862 73933).

863

864 Figure 4. The mtDNA topology of the relationships among the six major subspecific groups,

865 following Puebla-Olivares et al. (2008). Taxa labeled with a "(+)" are non-monophyletic in

866 mtDNA. Values between the major subspecific groups are the between-group mean genetic

867 distances between them.

868

869 Figure 5. The relationship between genetic distance (Figure 4) and the accumulation of

870 morphometric differences (Table 4) between the major subspecific groups that might hybridize

871 due to proximity. The positive correlation is that predicted by the processes of anagenesis and

872 speciation.

873   **Appendix**

874   *Suggested taxonomy*.—Because I have examined all of the described taxa in the complex,

875   this revision includes subspecies (although quantitative analyses were not undertaken below the

876   level of the six major groups). Given below are species, subspecies, authors of original

877   descriptions, type localities, and notes pertaining to each species. Distribution is not included,

878   because I did not examine all existing specimens and can add little of substance to distributions

879   set forth by the authors cited herein. The species sequence given follows the relationships in the

880   mtDNA tree of Puebla-Olivares et al. (2008) but with the two major clades flipped to better

881   accommodate the group's geographic distribution (as I have also done in Fig. 4).

882

883   Genus *Aulacorhynchus* (green toucanets), subgenus *Ramphoxanthus*

884

885   *Aulacorhynchus wagleri* (Sturm *in* Gould, 1841:pl. 16 (heft 2, pl. 6)). Wagler's Toucanet.

886   no type loc. [= Guerrero and Oaxaca, Mexico].

887

888   *Aulacorhynchus prasinus* (Gould, 1833). Northern Emerald Toucanet.

889   *A. p. prasinus* (Gould, 1833). Mexico [= Valle Real, Oaxaca].

890   *A. p. warneri* Winker (2000). Volcán San Martín, Sierra de Los Tuxtlas, Veracruz,

891   Mexico.

892   *A. p. virescens* Ridgway (1912:88). Chasniguas, Honduras.

893   *A. p. volcanius* Dickey and van Rossem (1930:53). Volcán de San Miguel, Dept. San

894   Miguel, El Salvador.

895   **Notes:** *A. p. stenorhabdus* (Dickey and van Rossem, 1930:52) and *A. p. chiapensis* (Brodkorb,

896   1940) are considered synonyms of *A. p. virescens*; variation among them appears to be clinal

897   (see also Monroe, 1968). Wetmore (1941, notes in USNM) considered *chiapensis* as "doubtfully

898   separable," but recognized *stenorhabdus*. See notes under *A. albivitta* regarding the English

899   common name.

900   ***Aulacorhynchus caeruleogularis*** (Gould, 1854:45). Blue-throated Toucanet.

901   ***A. c. caeruleogularis*** (Gould, 1854:45). Veragua [, Panama] [= Boquete, Chiriquí; Wetmore

902   1968:508].

903   ***A. c. cognatus*** (Nelson, 1912:4). Mount Pirri (at 5,000 feet altitude) head of Rio Limon,

904   eastern Panama.

905   **Notes:** *A. c. maxillaris* (Griscom, 1924:2) is considered a synonym of *A. c. caeruleogularis* (cf.

906   Wetmore 1968:509). See Wetmore (1968) for citation of the name *caeruleogularis* appearing

907   first in the Zoologist in 1853; no description appears there, however, the reference being a report

908   of what occurred at two meetings in February 1853 ("D.W.M.", 1853). Olson (1997) provided

909   more notes on these occurrences in relation to Gould.

910

911   ***Aulacorhynchus albivitta*** (Boissonneau, 1840:70). Southern Emerald Toucanet.

912   ***A. a. lautus*** (Bangs, 1898:173). San Miguel [, Sierra Nevada de Santa Marta], Colombia.

913   ***A. a. griseigularis*** Chapman (1915:639). Santa Elena (alt. 9000 ft.), Cen. Andes,

914   Antioquia, Col.

915   ***A. a. phaeolaemus*** Gould (1874:184). Concordia, in Columbia [sic], and Merida, in

916   Venezuela [= Concordia, Antioquia, western Colombia; Hellmayr, 1911:1213].

917   ***A. a. albivitta*** (Boissonneau, 1840:70). Santa-Fé de Bogota [, Colombia].

918   **Notes:** Chapman (1917) inexplicably omitted the occurrence of the species (endemic subsp.

919 *lautus*) in the Santa Marta region. More detailed study is needed to resolve problems in the

920 status, relationship, distributions, and nomenclature of *phaeolaemus* and *griseigularis* (see

921 Chapman, 1917; Haffer, 1974). The English name for this species given by Cory (1919:377),

922 White-throated Toucanet, is only appropriate for the subspecies *albivitta*, and thus is more

923 appropriate at the species level for *A. prasinus* (*sensu stricto*, though not used there). The other

924 subspecies of *albivitta* are all grayish or grayish-blue on the throat. Del Hoyo and Collar (2014)

925 suggested Grayish-throated, but this overlooks both white-throated birds and those with blue in

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

927 *prasinus*.

928

929 ***Aulacorhynchus atrogularis*** (Sturm *in* Gould, 1841:heft 2, pl.2 & text). Black-throated

930   Toucanet.

931   ***A. a. cyanolaemus*** (Gould, 1866:24). Loxa [=Loja] in Ecuador.

932   ***A. a. atrogularis*** (Sturm *in* Gould, 1841:heft 2, pl.2 & text). Andes of Peru

933   [=Chunchamayo, central Peru; Cory, 1919:380).

934   ***A. a. dimidiatus*** (Ridgway, 1886:93). No loc.; suggested by O'Neill and Gardner

935   (1974:703) to be along the eastern foothills of the Andes of central southern Peru.

936 **Note:** Recognition of *A. a. dimidiatus* follows O'Neill and Gardner (1974). *A. a. cyanolaemus* is
937 blue-throated (Fig. 1).

Treatments of species-level diversity in the genus *Aulacorhynchus*.

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.

1   Table 1. Treatments of species-level diversity in the genus *Aulacorhynchus*. Taxa historically recognized only as subspecies are not

2   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

3   treated yet, and a blank indicates that the taxon was not considered.

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

5   a – Salvin & Godman (1896) treated only Middle American *Aulacorhynchus*, which at the time were considered *Aulacorhamphus*.

6   b – Brabourne and Chubb (1912) treated South American members of the genus (then considered *Aulacorhamphus*).

7   c – *huallagae* was described by Carriker (1933).

8   d – *cognatus* was described as a subspecies by Nelson (1912).

9   e – *griseigularis* was described as a subspecies by Chapman (1915).

10   f – *lautus* was described by Bangs (1898).

11   h – though not included in either study.

12   i – Treatment matches the South American Classification Committee (Remsen et al. 2016).

Color and pattern-based diagnostic characteristics

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.

1 Table 2. Color and pattern-based diagnostic characteristics of the six major subspecific groups of

2 *Aulacorhynchus "prasinus"* (based on specimens and del Hoyo and Collar 2014). Middle

3 American forms are at left; South American forms are at right.

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. subspp. *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. subspp. *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. subspp. *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. subspp. *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).

Mensural characteristics of both sexes among six major groups of the *Aulacorhynchus "prasinus"* complex

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*).

1 Table 3. Mensural characteristics of both sexes among six major groups of the *Aulacorhynchus "prasinus"* complex. Units are mm except for

2 mass (g) and sample size (*N*).

		prasinus		*wagleri*		*caeruleogularis*		*albivitta*		*cyanolaemus*		*atrogularis*	
		M	F	M	F	M	F	M	F	M	F	M	F
Mass (g)	mean	186.6	171.2	169.7	172.0	152.8	158.5	-	-	176.7	158.8	158.1	112.5
	s.d.	20.98	24.78	14.10	15.94	24.67	5.72	-	-	23.57	28.53	25.23	2.50
	min	153.6	135	145	127	118	154	-	-	160	130	124	110
	max	239.2	229.6	200	189.3	184	166.6	-	-	210	210	188	115
	N	13	11	13	14	8	3	-	-	3	5	8	2
Wing chord	mean	124.1	119.6	125.9	123.3	120.0	116.5	128.1	125.5	127.1	125.0	122.4	118.0
(WCH)	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	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
(TL)	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

22		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
23		N	94	71	28	25	99	48	84	57	8	10	16	11
24														
25	Tarso-													
26	metatarsus	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
27	(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
28		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
29		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
30		N	98	75	28	26	105	50	86	57	9	10	17	11
31														
32	Bill	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
33	(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
34		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
35		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
36		N	98	75	28	26	105	50	86	57	9	10	17	11
37														
38	Bill height	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
39	(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
40		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
41		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
42		N	97	75	28	26	104	50	86	57	9	10	17	11
43														

44	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
45	(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
46		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
47		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
48		N	98	75	28	26	105	50	86	57	9	10	17	11
49														
50	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
51	(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
52		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
53		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
54		N	95	69	28	26	104	49	86	57	9	10	17	11

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.

1 Table 4. Patterns of significance from results of *t*-tests of mensural characters between

2 geographic pairs of major subspecific groups of *Aulacorhynchus "prasinus."* Positive (+) values

3 indicate that the first named group averages larger, while negatives (-) indicate that the second is

4 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					* (-)a	* (+)		57, 10
cyanolaemus-atrogularis	M		** (-)						9, 17
	F	* (+)		* (+)a					10, 11
albivitta-atrogularis	M		** (+)		* (+)	* (-)	* (-)		86, 17
	F	** (+)		** (+)					57, 11

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

a - Not significant after table-wide correction for false discovery rates (see text).

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.

1 Table 5. Patterns of significance from results of *t*-tests comparing individual principal

2 component (PC) scores between geographic pairs of major subspecific groups of

3 *Aulacorhynchus "prasinus."* PC scores are from the first two principal components. Individuals

4 with missing values were excluded. Underlined asterisks indicate significance after false

5 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*.

A

B

C

D

E

F

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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).

prasinus

wagleri

caeruleogularis

albivitta

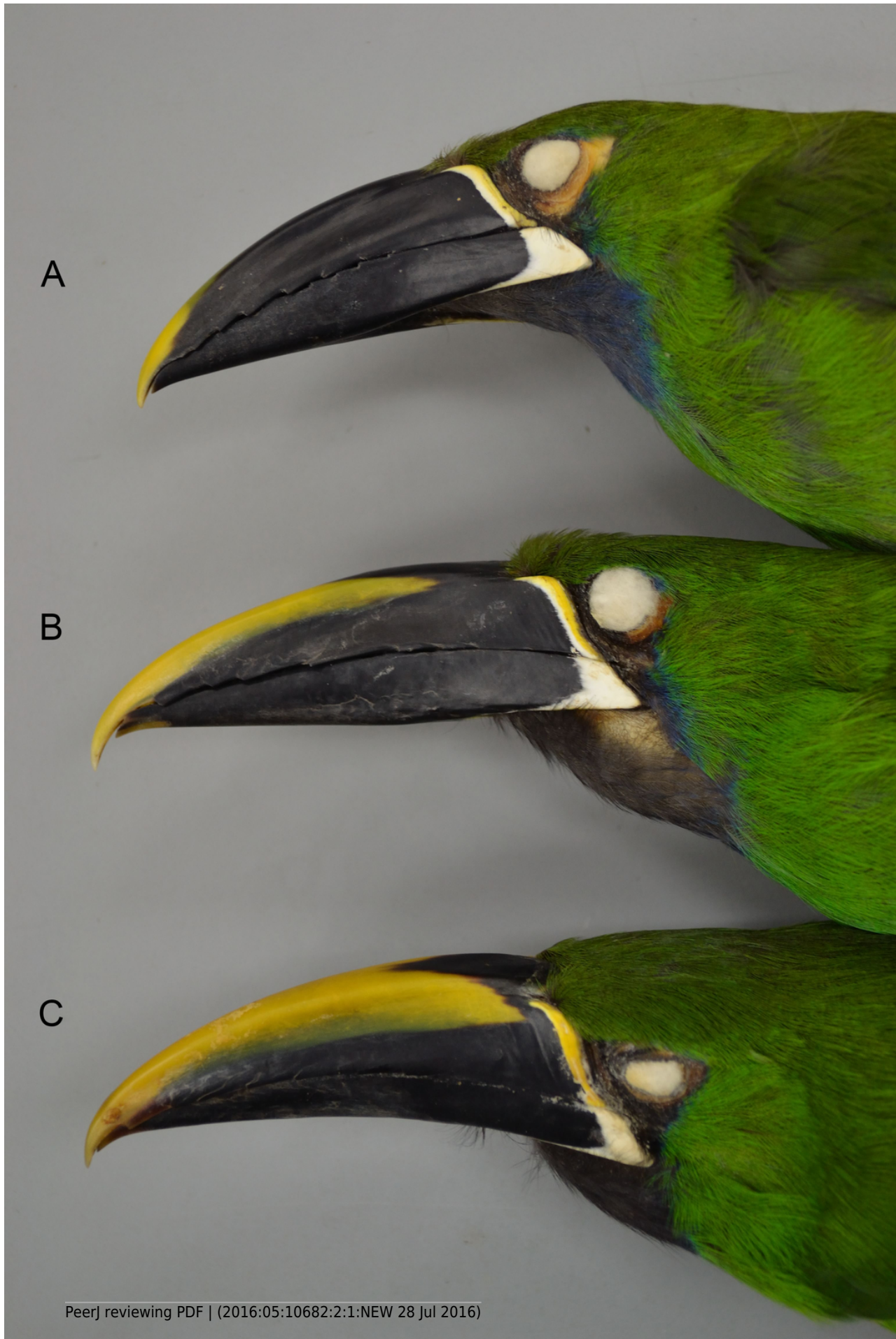
cyanolaemus

atrogularis

500 km

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).

A

B

C

Figure 4

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

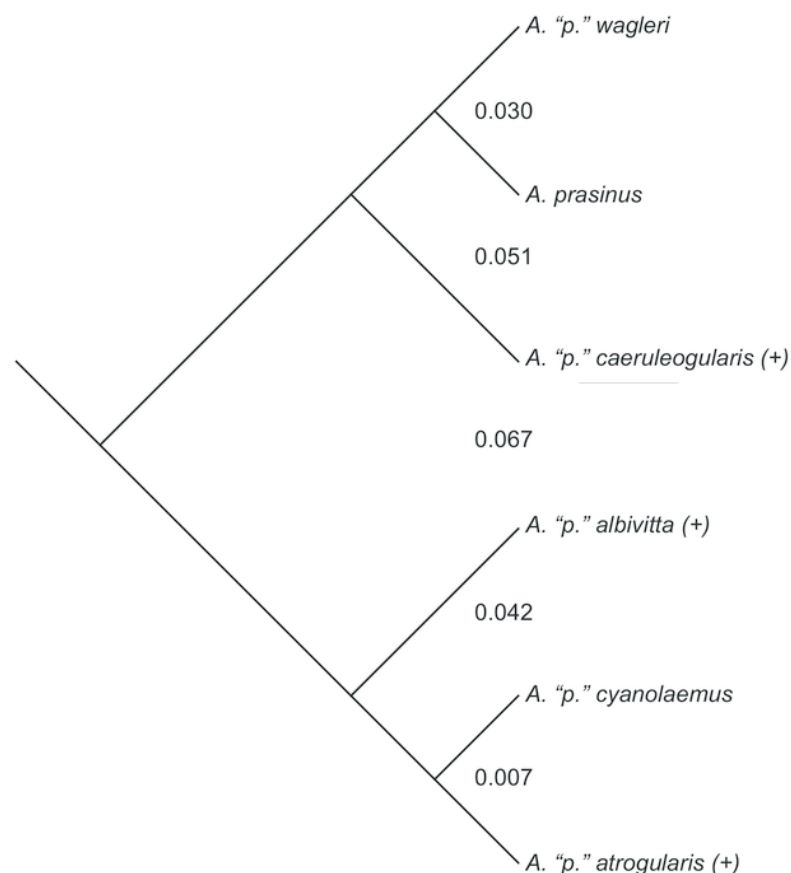
Figure 4. The mtDNA topology of the relationships among the six major subspecific groups, following Puebla-Olivares et al. (2008). Taxa labeled with a "(+)" are non-monophyletic in mtDNA. Values between the major subspecific groups are the between-group mean genetic distances between them.

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.