

## Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 5. Probable hybrid origin of *Amazilia distans* Wetmore & Phelps

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*Abstract.*—*Amazilia distans* Wetmore & Phelps, 1956, is believed to be a hybrid between *Hylocharis cyanus* and *Amazilia fimbriata*. The hybrid, collected in Estado Táchira, Venezuela, exhibits a blended mosaic of plumage characters of the parental species. External measurements of the hybrid fall between the character means of the parental species which overlap in size.

The unique holotype of *Amazilia distans* Wetmore & Phelps, 1956 was collected by Ramón Urbano at "El Salao" (300 m) near Burgua, Estado Táchira, Venezuela, on 17 July 1954. Originally deposited in the Colección Ornitológica Phelps (No. 60790), Caracas, the type was cataloged on 9 October 1956, in the National Museum of Natural History (USNM 461695), Smithsonian Institution. Collar et al.'s (1992) report of a second specimen in the Colección Phelps was based on a misreading of the Phelps card catalog (fide M. Lentino, N. Collar). References treat *A. distans* as a valid species (e.g., Morony et al. 1975, Meyer de Schauensee & Phelps 1978, Hilty & Brown 1986, Sibley & Monroe 1990, Collar et al. 1992). Analyses reported here suggest that it represents a hybrid between *Hylocharis cyanus* and *Amazilia fimbriata*. I provide a detailed hybrid diagnosis employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990).

### Materials and Methods

The holotype of *Amazilia distans* was sexed as male (testes drawn on original label). The unstriated maxillary ramphotheca (see Ortiz-Crespo 1972) and brilliant plumage of the specimen indicate that it is an adult in definitive plumage (Figs. 1, 2). The unique appearance of *A. distans* cannot be

attributed to mutation or developmental variation of any known taxon. Nor does it seem to represent a morphologically distinctive or geographically isolated population of another species of *Amazilia*. Consequently, *A. distans* appears either to be a valid species or a hybrid. As hybrids have no standing in zoological nomenclature, the burden of proof lies with the taxonomist to reject conclusively the hybrid origin of *A. distans* before bestowing species status on it. I was unable to reject the hypothesis of hybridity.

Hybridization between species from different subfamilies, Phaethornithinae and Trochilinae, is unknown (Graves 1990). Assuming a hybrid origin for *A. distans*, the pool of potential parental species (=geographic pool) can be limited to the species of trochiline hummingbirds ( $n = 23$ ; see Appendix 1) that occur regularly below 1000 m elevation in the region immediately south and east of the Andes in Estado Táchira and Estado Apure, Venezuela (Phelps & Phelps 1958, Meyer de Schauensee & Phelps 1978, Hilty & Brown 1986). I compared *A. distans* directly with specimens of all hummingbird species in the collections of the National Museum of Natural History, Smithsonian Institution, paying particular attention to those listed in Appendix 1. Notes, photographs, and videotape of the holotype were compared with the extensive

Table 1.—Ranges and means ( $\pm$  one standard deviation) of measurements (mm) of representative specimens (adult male) of *Hylocharis cyanus*, *Amazilia fimbriata*, and the hybrid, *Hylocharis cyanus*  $\times$  *Amazilia fimbriata* (= *Amazilia distans* Wetmore & Phelps, 1956; USNM 461695).

	<i>cyanus</i> (n = 12 <sup>a</sup> )	<i>fimbriata</i> (n = 16 <sup>b</sup> )	Hybrid
Wing chord	47.1–53.0 49.8 $\pm$ 1.5	52.4–56.5 54.7 $\pm$ 1.4	51.0
Bill length	14.8–18.5 16.9 $\pm$ 1.1	17.3–22.0 19.8 $\pm$ 1.3	18.6
Rectrix 1	24.1–27.4 25.9 $\pm$ 1.2	26.2–30.1 28.8 $\pm$ 1.0	26.6
Rectrix 5	25.1–28.1 26.7 $\pm$ 1.0	27.7–32.5 30.6 $\pm$ 1.4	27.4

<sup>a</sup> Colombia (n = 5), Venezuela (n = 4), Guyana (n = 3).

<sup>b</sup> Colombia (n = 8), Venezuela (n = 8).

series of *Amazilia* and *Hylocharis* in the American Museum of Natural History, New York.

Color descriptions were made under Exanolites (MacBeth). Measurements of wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of the central rectrices to the tip of central and outermost rectrices) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 1). Measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Wilkinson 1989).

The hybrid diagnosis was approached in a hierarchical manner. The presumed parental species of *A. distans* were hypothesized through the comparative analysis of plumage pattern and color, feather shape, and bill color. As a second step, the restrictive hypothesis was tested with the quantitative analysis of size and external proportions. Concordance of results is regarded as strong support for the hypothesis (Graves 1990, 1993a, 1993b, 1996a; Graves & Zusi 1990). Atavism or hybrid luxuriance has not been demonstrated in hybrid hummingbirds (Banks & Johnson 1961, Graves 1990). For brevity, *A. distans* will be re-

ferred to as a hybrid in the remainder of this paper.

## Results and Discussion

Several characters of the hybrid permit its parental species to be identified: (a) bill red tipped with black in life; (b) base of bill conspicuously swollen, nasal flanges unfeathered and exposed; (c) crown glittering bluish-green; (d) throat glittering bluish-green, chin and upper throat streaked with white; (e) indistinct white pectoral spot; (f) abdomen gray along midline; and (g) rectrices black, innermost and outermost about the same length (Appendix 2; Fig. 1, 2; Table 1). None of the potential parental species considered one at a time exhibits this suite of character states in definitive or sub-definitive plumage.

The red bill of the hybrid appears to be the most useful character for initially narrowing the field of potential parental species. Adult males of several species in Appendix 1 have pink or red mandibular (lower jaw) ramphothecae (*Lophornis delattrei*, *L. stictolophus*, *Chrysuronia oenone*, *Hylocharis cyanus*, *Amazilia versicolor*, *A. fimbriata*, and *A. viridigaster*), and some specimens of *A. fimbriata* have pinkish-brown maxillary ramphothecae (upper jaw). However, bright red maxillary ramphothecae are found in only three species, *L. delattrei*, *L. stictolophus*, and *Hylocharis cyanus*. *Lophornis* can be eliminated as possible parents of *A. distans* because they possess elongated rufous crests and predominately rufous rectrices, which would almost certainly be expressed in a hybrid. *Hylocharis cyanus* is thus identified as the parental contributor of the red maxillary ramphotheca of the hybrid.

Identifying the second parental species is most easily accomplished by focusing on the plumage characters of the hybrid that are lacking in *Hylocharis cyanus*. Plumage of the head, chin, throat and upper breast of *H. cyanus* is glittering purple. The inheritance of iridescence in hybrid hum-

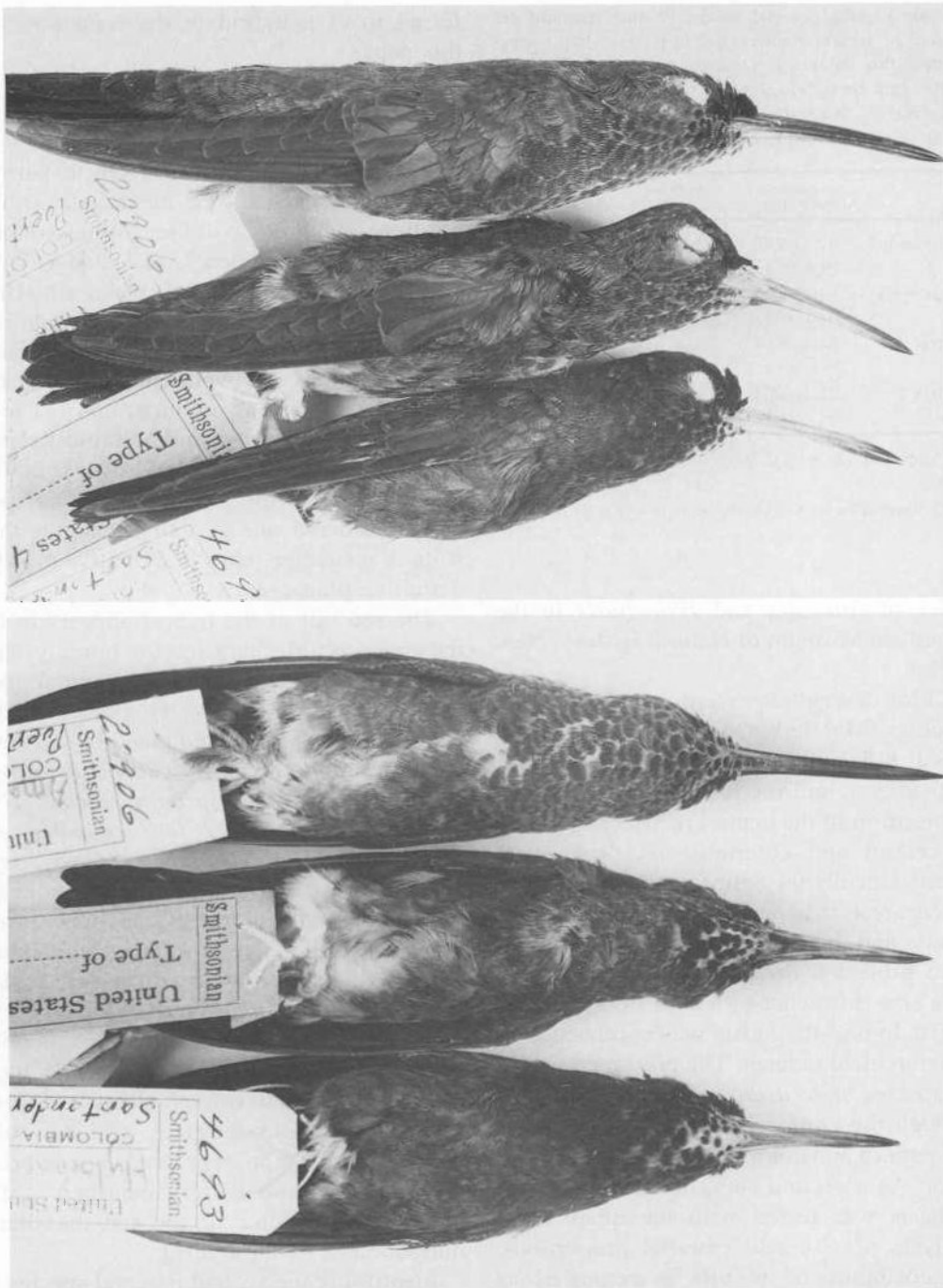


Fig. 1. Lateral and ventral views of male *Amazilia fimbriata* (top), *Hylocharis cyanus* (bottom), and their putative hybrid, *A. distans* Wetmore & Phelps (USNM 461695).

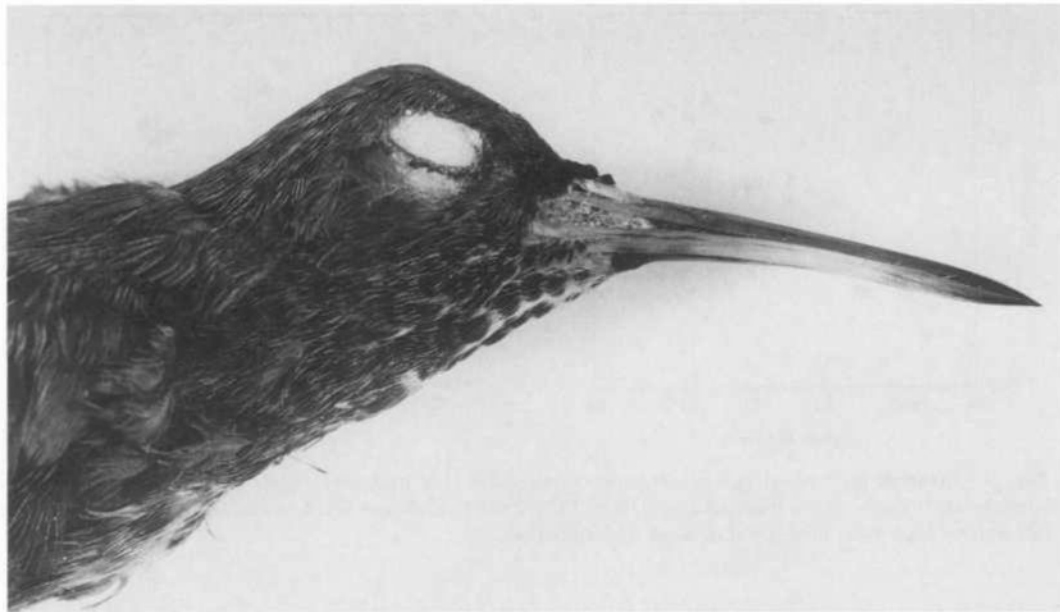


Fig. 2. Lateral view of head and bill of the type of *Amazilia distans* Wetmore & Phelps (USNM 461695).

mingbirds is poorly understood (Graves 1990, Graves & Zusi 1990). In this case, however, I assume that hybridization between two purple-crowned species would not result in offspring with a bluish-green crown. The glittering bluish-green crown and throat of the hybrid suggest that the second parental species has iridescent green plumage in these areas, ruling out *Klais guimeti* (purple chin and upper throat) as a parental species. In another example, the rectrices of *Chrysuronia oenone* are shining coppery-gold on both dorsal and ventral surfaces, whereas the rectrices of the hybrid are black, similar to those of *H. cyanus* (bluish-black). Hybridization of *C. oenone* and *H. cyanus* would likely produce offspring with bronze-colored or dark brown rectrices that are significantly paler, less melanized, than those of the hybrid. In a similar fashion, *Campylopterus falcatus* (chestnut rectrices, thickened primary rachises), *Colibri thalassinus* and *C. coruscans* (purple auricular tufts, banded rectrices), *Chlorostilbon poortmani* (shining golden-green tail), *Chlorestes notatus* (brilliant bluish-green plumage from breast to

undertail coverts), *Chalybura buffonii* (lengthened silky-white undertail coverts), *Helimaster longirostris* (tail spots, brilliant magenta gorget), *Thalurania furcata* (purple lower breast, deeply forked tail), *Heliodoxa leadbeateri* (violet crown patch), *Sternoclyta cyanopectus* (violet breast patch, white-tipped rectrices, heavy curved bill), *Coeligena coeligena* (brown plumage), *Ocreatus underwoodii* (racket-tipped rectrices, tibial "puffs"), *Agelaiocercus kingi* (greatly elongated rectrices with metallic bluish-green dorsal surfaces), and *Chaetocercus jourdani* (rufous shafts of rectrices, rose throat), can be removed from the list of potential parental species because they exhibit plumage characters not expressed in the hybrid. By the process of elimination, the second parental species appears to be one of three species of *Amazilia* that are sympatric with *Hylocharis cyanus* in Táchira, Venezuela (Appendix 1).

Wetmore & Phelps (1956:4) noted that the type of *A. distans* had the general appearance of *Amazilia fimbriata*, differing from that species "in the glittering blue foreneck and upper breast, and in possess-

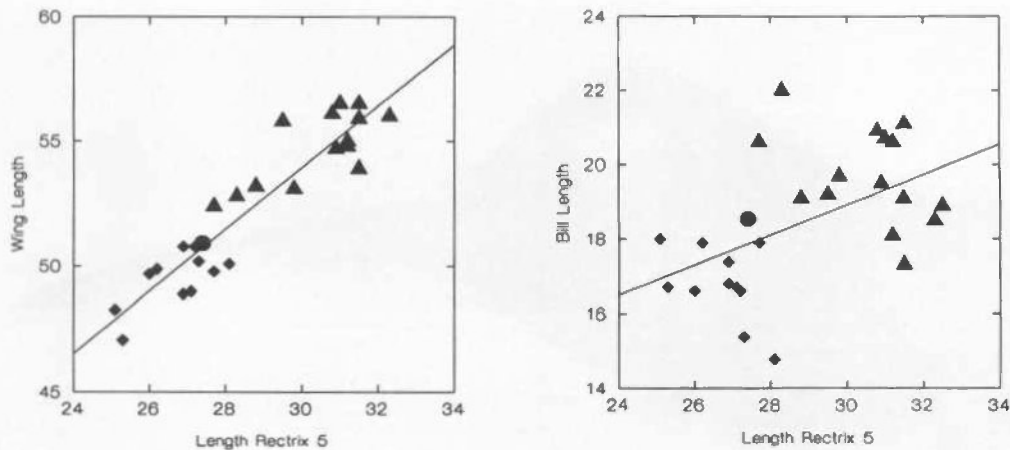


Fig. 3. Bivariate plots of selected measurements (see Table 1) of male *Hylocharis cyanus* (diamonds), *Amazilia fimbriata* (triangles), and their putative hybrid (filled circle), *A. distans* Wetmore & Phelps (USNM 461695). Least squares regression lines are illustrated for comparison.

ing a crown spot differing in color from the rest of the head . . . the appearance of the specimen is so distinct from that of other species of the genus [*Amazilia*] that we have no hesitation in describing it as representing a new species." I concur with Wetmore and Phelps that *A. fimbriata* bears more than a fleeting resemblance to *Amazilia distans* in plumage pattern. In fact, the hybrid is nearly intermediate in appearance between *Hylocharis cyanus* and *Amazilia fimbriata*. Significantly, the hybrid lacks plumage traits that characterize *A. versicolor* (e.g., dark subterminal band on the outermost rectrices) and *A. viridigaster* (e.g., brown or buff undertail coverts). In conclusion, evidence gleaned from bill and plumage characters suggest that *A. distans* represents a hybrid of *Hylocharis cyanus* and *Amazilia fimbriata*.

*External measurements.*—Measurements of avian hybrids fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (see Buckley 1982). External measurements of adult male *Hylocharis cyanus* and *Amazilia fimbriata* overlap and the difference in character means (larger species divided by smaller) is modest: wing chord (9.8%) bill length (17.2%); rectrix 1

(11.2%); and rectrix 5 (14.6%). Consistent with the hypothesis derived from plumage color and pattern, measurements of the hybrid fall between the character means of the parental species (Table 1, Fig. 3). Had the hybrid's measurements fallen outside the range of those of *Hylocharis cyanus* and *Amazilia fimbriata*, this particular hybrid hypothesis would have been rejected.

In summary, both plumage and morphological data are consistent with the hypothesis that *Amazilia distans* represents a hybrid between *Hylocharis cyanus* and *Amazilia fimbriata*. These species overlap extensively in Amazonia. For taxonomic purposes the *Amazilia distans* Wetmore & Phelps is available only for the purpose of homonymy.

Berlioz (1929) described a supposed hybrid specimen, *Hylocharis cyanus* × *Amazilia fimbriata*, prepared in the "Bahia" style and presumably collected in Brazil. Unfortunately, he failed to report the specimen's registration number or in what museum the specimen was deposited. Later, he (Berlioz 1951:287 equivocated in his identification, suggesting that the specimen might represent *Hylocharis pyropygia* (Salvin & Godman 1881), poorly-known and

somewhat doubtful species from Bahia, Brazil (see Sibley & Monroe 1990):

"D'ailleurs, faute de connaître alors des *Hyl. pyropygia* authentiques, j'avais primitivement décrit ce spécimen . . . comme étant probablement un hybride: *Agyrtrina* [*Amazilia*] *fimbriata nigricauda* X *Hylocharis cyanus*. Sans rejeter définitivement cette hypothèse, très justifiable par l'apparence de l'Oiseau, il me semble pourtant plausible, maintenant que l'identification, comme espèce distincte, d'*Hyl. pyropygia* s'est affirmée par l'existence de plusieurs spécimens identiques, de considérer dubitativement cet Oiseau comme référable aussi à cette dernière espèce."

To further complicate matters, Berlioz (1938) had proposed in earlier paper that *Hylocharis pyropygia* was actually a hybrid between *Chlorostilbon aureoventris* and *Hylocharis cyanus*. In any case, there appears to be no previous verified examples of the hybrid combination reported here (*Hylocharis cyanus* X *Amazilia fimbriata*).

*Sight records.*—Sight records of "*Amazilia distans*" in northwestern Venezuela and adjacent Colombia (see Hilty & Brown 1986, Collar et al. 1992) are problematic, and, to my knowledge, none is supported by diagnostic photographs. Although these sightings may refer to *Hylocharis* X *Amazilia* hybrids, they more likely represent the manifestation of imaginations fertilized by the possibility of observing a narrowly distributed endemic. Identification of hummingbird hybrids under field conditions is virtually impossible (Graves 1996b).

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#### Literature Cited

- Banks, R. C., & N. K. Johnson. 1961. A revision of North American hybrid hummingbirds.—*Condor* 63:3–28.
- Berlioz, J. 1929. Un cas nouveau d'hybridité chez les Trochilidés.—*L'Oiseau* 10:340–343.
- . 1938. Notes critiques sur des Trochilidés.—*L'Oiseau* (new series) 8:3–19.
- . 1951. Etude systématique de quelques espèces litigieuses de Trochilidés.—*L'Oiseau* 21: 278–288.
- Buckley, P. A. 1982. Avian genetics. Pp. 21–110 in M. Petrak, ed., *Diseases of cage and aviary birds*. 2nd ed. Lea and Febiger, Philadelphia, 680 pp.
- Collar, N. J., L. P. Gonzaga, N. Krabbe, A. Madroño Nieto, L. G. Naranjo, T. A. Parker, III, & D. C. Wege. 1992. Threatened birds of the Americas: The ICBP/IUCN Red Data Book, 3rd edition, part 2. International Council for Bird Preservation, Cambridge, U.K., 1150 pp.
- Graves, G. R. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—*Proceedings of the Biological Society of Washington* 103:6–25.
- . 1993a. Relic of a lost world: a new species of sunangel (Trochilidae: *Helianthus*) from "Bogota."—*Auk* 110:1–8.
- . 1993b. A new hybrid manakin (*Dixiphia pipra* X *Pipra filicauda*) (Aves: Pipridae) from the Andean foothills of eastern Ecuador.—*Proceedings of the Biological Society of Washington* 106:436–441.
- . 1996a. Hybrid wood warblers, *Dendroica striata* X *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes.—*Proceedings of the Biological Society of Washington* 109:373–390.
- . 1996b. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 1. Characterization of *Calypte anna* X *Stellula calliope* and the possible effects of egg volume on hybridization potential.—*Proceedings of the Biological Society of Washington* 109:755–763.
- , & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* X *Helianthus amethysticollis*) from northern Colombia.—*Condor* 92:754–760.
- Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, 836 pp.
- Meyer de Schauensee, R., & W. H. Phelps, Jr. 1978.

- A guide to the birds of Venezuela. Princeton University Press, 424 pp.
- Morony, J. J., Jr., W. J. Bock, & J. Farrand, Jr. 1975. Reference list of the birds of the world. American Museum of Natural History, New York, 207 pp.
- Ortiz-Crespo, F. I. 1972. A new method to separate immature and adult hummingbirds.—*Auk* 89: 851–857.
- Phelps, W. H., & W. H. Phelps, Jr. 1958. Lista de las aves de Venezuela con su distribución. Tomo 2, Parte 1. Editorial Sucre, Caracas, 317 pp.
- Salvin, O., & F. D. Godman. 1881. On some new and little-known species of Trochilidae.—*Ibis* (series 4) 5:595–597.
- Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.
- Wetmore, A., & W. H. Phelps, Jr. 1956. Further additions to the list of birds of Venezuela.—*Proceedings of the Biological Society of Washington* 69:1–10.
- Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, 822 pp.

#### Appendix 1

Species of hummingbirds that occur regularly below 1000 m elevation in southwestern Estado Táchira and extreme western Estado Apure, Venezuela: *Campylopterus falcatus*, *Colibri thalassinus*, *C. coruscans*, *Klais guineii*, *Lophornis delatrei*, *L. stictolophus*, *Chlorestes notatus*, *Chlorostilbon mellisugus*, *C. poortmani*, *Thalurania furcata*, *Hylocharis cyanus*, *Chrysoronia oenone*, *Amazilia versicolor*, *A. fimbriata*, *A. viridigaster*, *Chalybura buffonii*, *Heliodoxa leadbeateri*, *Sternoclyta cyanopectus*, *Coeligena coeligena*, *Ocreatus underwoodii*, *Aglaiocercus kingi*, *Heliomaster longirostris*, *Chaetocercus jourdani*.

#### Appendix 2

General comparative description of definitive plumages of male *Hylocharis cyanus*, *Amazilia fimbriata*, and the hybrid, *H. cyanus* × *A. fimbriata* (= *Amazilia distans* Wetmore & Phelps, 1956; USNM 461695). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

The forecrown and crown (to a line drawn across

the crown at the rear of the orbits) of *cyanus* are glittering purple, bordered posteriorly by dark bluish-green on the hindcrown. The hindneck, upper back, and scapulars are dark green, gradually turning to bronzy green and then coppery on the lower back and rump, respectively; the upper-tail coverts are purplish black. In *fimbriata* the dorsal plumage (capitulum and spinal tracts) is primarily dark green, with bronze reflections on the crown and upper-tail coverts. The dorsum of the hybrid is intermediate in appearance between *cyanus* and *fimbriata*, but more closely resembling the latter species. The forecrown is glittering greenish-blue and the upper-tail coverts are dark bronzy green.

The sides of the head, throat, and upper breast of *cyanus* are deep glittering purple; exposed white feather bases on the chin impart a spotted or mottled appearance. Feathers of the lower breast, sides, and flanks are dark brownish-gray tipped with a dark green disc; greenish feather tips are less apparent near the midline. Vent feathers are white and the under-tail coverts are dull brownish-black (blue reflections in bright light). Feathers of the chin, throat, and upper breast of *fimbriata* have glittering green discs (when viewed head-on); feathers are white basally, narrowly fringed with white. White feather margins and a few completely white feathers form an indistinct spot near the center of the lower breast. The belly, sides, and flanks are green with an indistinct grayish-white stripe along the midline. Vent feathers are white; under-tail coverts are dark gray (with greenish reflections) moderately margined with white or pale grayish-white. The venter of the hybrid more closely resembles that of *fimbriata*. Feather discs of the chin, throat, and upper breast are bluish-green, a few are distinctly purple. Traces of the white pectoral spot of *fimbriata* are present (one completely white feather); under tail coverts are dark slate gray margined with dull white.

The tail of *cyanus* is bluish-black. In *fimbriata*, the outer rectrices (2–5) are dull bluish-black; the outer margins of rectrices 2–4 are glossed with dark green. The central rectrices (1) are dark green, becoming dull bluish-black distally. The tail of the hybrid is similar in color to that of *cyanus*, but the outer margins of rectrices 2–4 are faintly glossed with bronzy-green; the basal two-thirds of the central rectrices (1) are glossed with bronzy-green.

The maxillary ramphotheca is red, tipped with black in *cyanus*, and moderately to heavily melanized (pinkish-brown to black in life) in *fimbriata*. Ramphotheca of the hybrid exhibits an intermediate amount of melanin; the specimen tag notes that the bill was red with a black tip in life.