

Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 6. An intergeneric hybrid, *Agelaiocercus kingi* × *Metallura tyrianthina*, from Venezuela

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Abstract.—An intergeneric hybrid hummingbird, *Agelaiocercus kingi* × *Metallura tyrianthina*, is described. External measurements of the hybrid are intermediate of those of the parental species. Back plumage iridescence is bluer (511 nm) in the hybrid than in either of the parental species (553–571 nm). This color shift is thought to be caused by a developmental aberrancy or mutation which affects melanin granules that produce iridescence in feather keratins.

Under certain circumstances, interspecific hybridization may be an important source of genetic exchange among avian lineages that may create favorable conditions for rapid and significant evolutionary change (Grant & Grant 1992). From an analysis of data in Panov's (1989) catalog of avian hybrids, Grant & Grant (1992) reported that 19.1% (61 of 319) of hummingbird species has hybridized in nature. A surprising 69.2% (36 of 52) of the hybridizing pairs is intergeneric (taxonomy of Sibley & Monroe 1990), a finding consistent with Prager & Wilson's (1975) thesis that interspecific hybridization potential is slowly lost during avian evolution. The true extent of hybridization among hummingbirds, however, is imperfectly known. Panov's (1989) compilation includes numerous poorly documented or erroneous records, as did its antecedent (Gray 1958). Moreover, many new hybrid combinations have been reported recently (e.g., Graves 1990, 1996a, 1998a; Graves & Zusi 1990; Hinkelmann 1996; Weller & Schuchmann 1997). A definitive analysis of hybridization and phyletic reticulation must await a robust phylogeny and a systematic survey of purported hybrids, type specimens, and museum collections.

Here I describe an intergeneric hybrid combination, *Agelaiocercus kingi* × *Metallura tyrianthina*.

Materials and Methods

The unsexed specimen (American Museum of Natural History [AMNH] 146645) was collected by S. Gabaldon in Estado Mérida, Venezuela. The exact locality, elevation, and date of collection are unknown. The specimen appears to be a male in sub-definitive plumage as evidenced by the faint striations on the maxillary ramphotheca (see Ortiz-Crespo 1972) and by its elongated tail (Fig. 1 & 2). Five different identifications have been written in ink and pencil (in quotations below) on the two attached AMNH labels since the specimen was cataloged in 1927 (in probable order of occurrence): (a) "*Cyanolesbia*" [= *Agelaiocercus*]; (b) "*Agelaiocercus* ?*caudata*" [= *Agelaiocercus kingi caudatus*]; (c) "*Metallura purpureicauda*" [= *Chalcostigma purpureicauda*]; (d) "?Hybrid?, *Agelaiocercus caudata* × *Ramphomicron*" [= *Agelaiocercus kingi caudatus* × *Ramphomicron microrhynchum*]; and (e) "*Agelaiocercus emmae caudata*, (melanistic aberration),

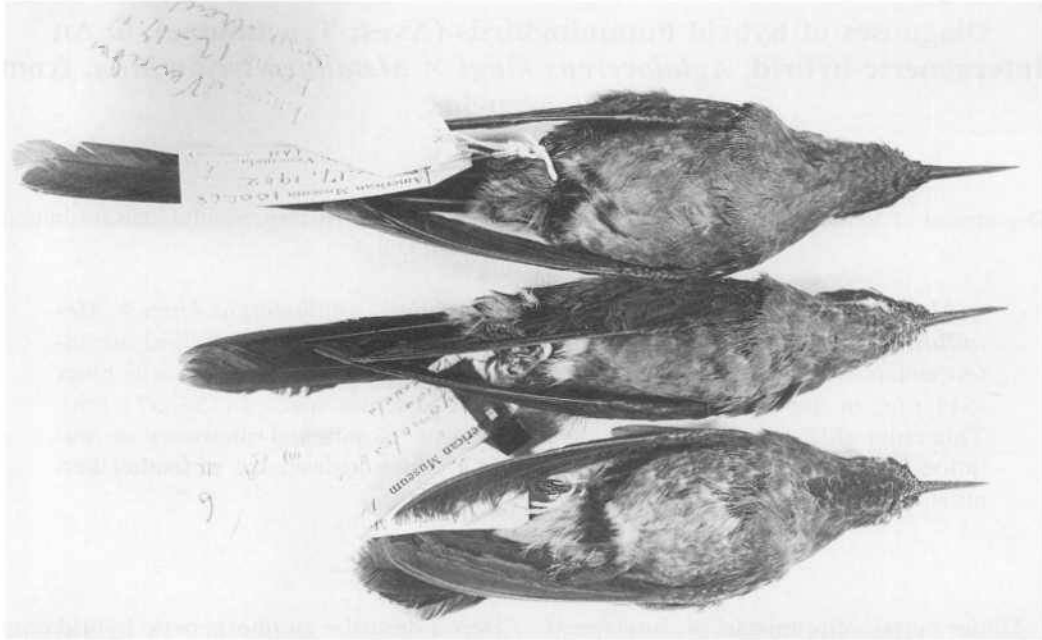


Fig. 1. Ventral views of male *Aglaiocercus kingi caudatus* (top), *Metallura tyrianthina oreopola* (bottom), and a probable hybrid, *A. kingi caudatus* \times *M. tyrianthina oreopola* (AMNH 146645).



Fig. 2. Probable hybrid, *Aglaiocercus kingi caudatus* \times *Metallura tyrianthina oreopola* (AMNH 146645).

fide J. Berlioz, Apr. 1975" [= *Agelaiocercus kingi caudatus*].

I compared the oft-identified specimen with series of all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997), in the collections of the American Museum of Natural History and the National Museum of Natural History (USNM), Smithsonian Institution. For the purpose of hybrid diagnosis, I considered all hummingbirds (Trochilinae; taxonomy of Sibley & Monroe 1990) that occur in Estado Mérida as potential parental species (Phelps & Phelps 1958, Meyer de Schauensee & Phelps 1978) (Appendix 1). In addition, I compared the specimens directly with the holotypes of *Chalcostigma purpureicauda* (AMNH 483931), *Lesbia ortoni* (AMNH 156651), *Zodalia thaumasta* (USNM 173911), and *Aeronympha prozantis* (Field Museum of Natural History, FMNH 11852), and with notes, photographs, and videotape of the holotype of *Heliangelus zusii* (Academy of Natural Sciences of Philadelphia, ANSP 159261).

Color descriptions given in Appendix 2 were made under natural light. I evaluated the color of dorsal plumage (center of back) and the ventral surfaces of the rectrices with a reflectance spectrophotometer equipped with a 11.0 mm aperture (Color Mate Colorimeter, Milton Roy). The colorimetric characters were described in terms of opponent-color coordinates (L , a , b) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), red-green (a), and yellow-blue (b). The rationale is that a color cannot be red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value a , which is positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by b for yellows and $-b$ for blues. The third coordinate L , ranging from 0 to 100, describes the "lightness" of color; low val-

ues are dark, high values are light. In other words, the more light reflected from the plumage the higher the L value will be. It should be noted that visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans. The relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. Dominant wavelengths reflected from plumage surfaces are listed for comparison. Data in Table 1 were compiled from the averages of five independent measurements (specimen moved from aperture between trials) for each plumage area per specimen.

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 each rectrix) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 2). Measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Wilkinson 1989).

There are three alternatives to consider—the specimen represents an aberrant color morph of *A. kingi* or some other species, a hybrid, or an undescribed species. The specimen differs significantly in size and shape from all species in Appendix 1. In particular, the rectrices of the specimen are considerably wider, flatter in cross section, and more iridescent on the ventral surfaces than in *A. kingi*, indicating that it is not simply a melanistic example of that species as suggested by Berlioz on the specimen label. Because hybrids have no standing in zoological nomenclature, the burden of proof rests on the investigator to refute this possibility before bestowing species status on a unique specimen. Because the evidence points to hybridization, I refer to the specimen as a hybrid in the remainder of the paper.

The diagnosis was approached in a hierarchical manner. The presumed parental species of the hybrid first were hypothesized through the comparative analysis of plumage pattern, as well as from feather

Table 1.—Ranges and means (\pm standard deviation) of opponent color coordinates (L , a , b) and dominant wavelength reflected from dorsal plumage (center of back) and the ventral surface of rectrices in male *Agelaiocercus kingi caudatus*, *Metallura tyrianthina oreopola*, and their probable hybrid (AMNH 146645).

Variables		<i>A. kingi</i> ($n = 12$)	<i>M. tyrianthina</i> ($n = 12$)	Hybrid
Back plumage				
L (Lightness)	(L)	23.6–30.1 27.1 \pm 1.8	21.5–26.6 24.2 \pm 1.4	24.1
a (Red [+]/Green [-])	(a)	-14.8–(-6.6) -10.9 \pm 2.9	-7.1–(-0.6) -3.7 \pm 1.8	-7.9
b (Yellow [+]/Blue [-])	(b)	15.4–20.2 17.8 \pm 1.4	12.6–20.9 17.3 \pm 2.3	2.9
Dominant Wavelength (nm)		553.1–563.8 557.8 \pm 3.5	562.8–570.5 566.7 \pm 2.6	511.3
Ventral surface of rectrices				
L (Lightness)	(L)	18.8–21.1 20.1 \pm 0.7	20.3–23.9 21.7 \pm 1.0	20.6
a (Red [+]/Green [-])	(a)	3.8–5.9 4.9 \pm 0.6	11.5–17.0 14.6 \pm 1.6	10.6
b (Yellow [+]/Blue [-])	(b)	-4.3–1.5 -0.9 \pm 1.9	5.5–14.9 9.5 \pm 2.9	-7.1
Dominant Wavelength (nm)		487.2–652.1 520.7 \pm 47.7	588.9–622.7 602.5 \pm 11.2	541.0

and bill shape. The restrictive hypothesis then was tested with a quantitative analysis of size and external proportions. Concordance of results is regarded as strong sup-

port for the hypothesis (Graves 1990, Graves & Zusi 1990).

Results and Discussion

Plumage characters.—Salient characters of the hybrid that permit its parental species to be identified include: (a) moderately elongated outer rectrices (fork depth = 23.7 mm), nearly flat in cross section; (b) unmarked rectrices exhibiting metallic iridescence on the dorsal and ventral surfaces; (c) short tibial plumes (not extending to hallux); and (d) short straight bill (11.1 mm). Two species in the pool of potential parental species (Appendix 1) possess elongated tails (length of rectrix 5 > 55 mm): *Ocreatus underwoodii* and *Agelaiocercus kingi*. *Ocreatus* can be deleted from the list of possibilities because the hybrid lacks evidence of spatulate rectrices or lengthened tibial plumes. *Agelaiocercus kingi* is thus identified as one of the parental species.

Determination of the other parental species is equally straightforward. The intensity of the metallic iridescence reflected

Table 2.—Ranges and means (\pm standard deviation) of measurements (mm) of males of *Agelaiocercus kingi caudatus* (subdefinitive plumage, see Appendix 2), *Metallura tyrianthina oreopola*, and their presumed hybrid (AMNH 146645).

Character	<i>A. kingi</i> ($n = 21$)	<i>M. tyrianthina</i> ($n = 20$)	Hybrid
Wing chord	59.7–63.6 61.8 \pm 1.0	54.0–61.5 57.7 \pm 2.2	61.4
Bill	11.0–13.6 12.3 \pm 0.7	9.1–10.6 9.9 \pm 0.4	11.1
Rectrix 1	22.8–25.3 24.1 \pm 0.8	33.7–38.9 36.1 \pm 1.6	32.1
Rectrix 2	29.0–33.6 31.3 \pm 1.2	34.3–41.3 37.9 \pm 1.8	36.9
Rectrix 3	38.9–46.7 42.8 \pm 1.9	36.0–43.6 39.9 \pm 1.8	43.1
Rectrix 4	53.7–61.5 58.0 \pm 2.2	38.4–45.3 41.5 \pm 2.1	49.0
Rectrix 5	67.5–102.7 81.5 \pm 8.7	37.9–46.3 42.2 \pm 2.7	55.8

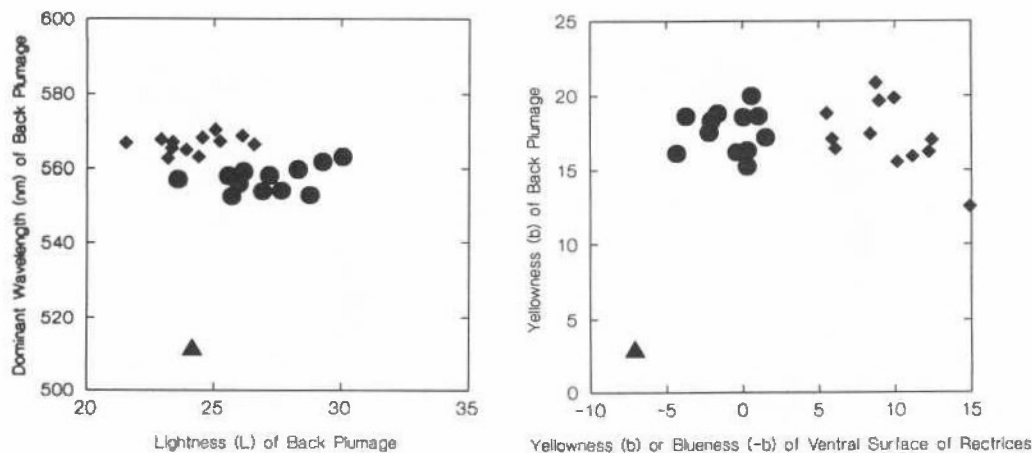


Fig. 3. Bivariate plots of spectrophotometric data from male hummingbirds: *Aglaiocercus kingi caudatus* (circles); *Metallura tyrianthina oreopola* (diamonds); and a probable hybrid, *A. kingi caudatus* \times *M. tyrianthina oreopola* (triangle; AMNH 146645).

from the ventral surfaces of the hybrid's rectrices is matched or exceeded only in *Metallura tyrianthina*. Details of plumage pattern and feather shape are sufficient to suggest that the parentage of the hybrid is *Aglaiocercus kingi* \times *Metallura tyrianthina* (see Appendix 2). None of the other species in Appendix 1, considered two at a time, can account for the characters observed in the hybrid. In particular, the ventral rectricial surfaces of the hybrid are metallic reddish-purple as opposed to dull black or purplish-black in both *Ramphomicron micro-rhynchum* and *A. kingi*, effectively eliminating this pair of species from contention.

The question of plumage color.—Iridescence in hummingbirds is caused by the interference of light reflected from the upper and lower surfaces of gas-filled vacuoles in melanin granules in the keratin of feather barbules, which are compactly stacked in 7–15 layers in the barbule keratins (Dorst 1951; Greenewalt et al. 1960a, 1960b; Lucas & Stettenheim 1972). Carotenoid pigments have not been extracted from iridescent feathers. Employing transmission electron microscopy and micro-spectrophotometry, Greenewalt et al. (1960a, 1960b) found melanin granules to be elliptical in shape, about 2.5μ long, 1.5μ wide, and

0.15μ thick. Briefly summarized, they found that granules contain a fairly uniform layer of gas-filled vacuoles that resemble a monolayered foam. The melanin matrix and gas-filled vacuoles have refractive indices of ~ 2.0 and 1.0 , respectively. The color of iridescence varies according to the thickness of the granule and the amount of gas in the vacuoles. Iridescent colors change from blue to green to orange and finally to red, as the effective refractive index of granules advances from 1.45 to 1.90 (figure 4 of Greenewalt et al. 1960a). Melanin granules in noniridescent parts of feathers lack vacuoles.

The pattern of bluish-green iridescence in the hybrid corresponds precisely to that of green iridescence in the parental species, suggesting a single mutational or developmental aberrancy that affects plumage color. The dominant wavelength reflected from dorsal plumage is shorter in the hybrid (511 nm) than in the parental species: *Aglaiocercus kingi* (553 – 564 nm) and *Metallura tyrianthina* (563 – 571 nm) (Table 1, Fig. 3). The premise that "hybridization produces no traits characteristic of genera or species other than those involved in the particular cross" (Banks & Johnson 1961:3) was extended to spectrophotometric measures of

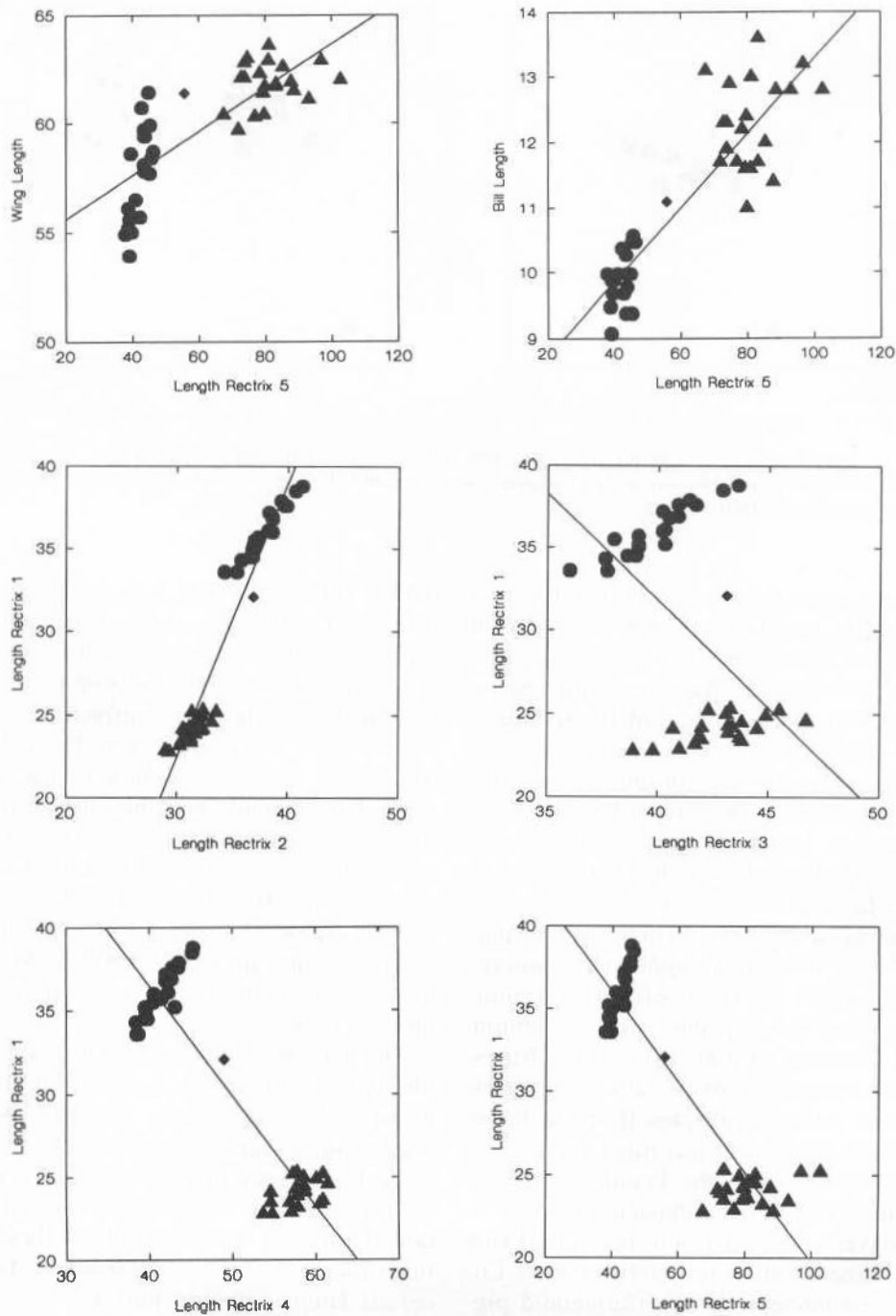


Fig. 4. Bivariate plots of mensural characters of male hummingbirds: *Agelaiocercus kingi caudatus* (triangles); *Metallura tyrianthina oreopola* (circles); and a probable hybrid, *A. kingi caudatus* \times *M. tyrianthina oreopola* (diamond; AMNH 146645). Least squares regression lines are projected for comparison.

plumage color (Graves 1996b). Both assumptions are violated in the present example.

Elucidation of the micro-structure and spectrophotometric properties of melanin granules in *Agelaiocercus kingi*, *Metallura tyrianthina*, and the hybrid is beyond the scope of this paper. Several observations on hummingbird plumages, however, are worth noting. A variety of plumage aberrations, unassociated with hybridization, has been observed in hummingbirds, including leucism, albinism, schizochroism, erythrisms, and melanism (Salvin 1892, Banks & Medina 1963, Greenway 1978, Graves 1998b). Subtle within-population variation in iridescent color is commonly observed whenever large series of species are assembled. Although post-mortem effects may be partially responsible in some cases (Graves 1986, 1991), most of the observed variation in iridescence among individuals, factoring out the effects of sex and age (see Bleiweiss 1992), is due to genetic and developmental factors. Pronounced color shifts of the magnitude observed in this hybrid are rare but not unknown (e.g., Salvin 1892, Greenway 1978). The example described here seems to be the first in which a hybrid hummingbird exhibits a major plumage aberrancy.

External measurements.—One of the guiding principles of hybrid diagnosis is that hybrids are not larger or smaller than their parental species (Graves 1990). Morphological luxuriance or dwarfism in hybrid hummingbirds has not been recorded. Male *Agelaiocercus kingi* and *Metallura tyrianthina* are similar in bill length (cumulative range, 9.1–13.6 mm) and wing chord (cumulative range, 54.0–63.6 mm), but differ markedly in tail size and shape (Table 2, Fig. 4). Bivariate plots of rectrix length of the parental species exhibit positive (1 vs. 2) or negative (1 vs. 3, 1 vs. 4, 1 vs. 5) allometry. Except for rectrix 3, measurements of the hybrid fall between the character means for *A. kingi* and *M. tyrianthina*, and, in several cases, approximate the val-

ues predicted by least squares regression on bivariate plots (Table 2, Fig. 4). In summary, plumage pattern, distribution and intensity of iridescence, rectrix shape, and mensural characters provide strong support for the hypothesis of hybridity (*Agelaiocercus kingi* × *Metallura tyrianthina*).

Previous records.—A hybrid of *Agelaiocercus kingi* and *Metallura tyrianthina* was reported once before by Meyer de Schauensee (1947:108), who described a specimen (No. 134) obtained in Bogotá, circa 1909, from the Brother Nicéforo María collection:

“... fore-crown glittering brassy green, hind crown and back dark bluish green, rump and upper tail coverts bluer; chin dusky, throat patch shaped as in *Metallura tyrianthina* but blue instead of green; breast dark bluish green, bases and edges of the feathers buffy; belly dark green, the bases of the feathers white, showing through and giving a somewhat barred appearance; tail purple, deeply forked, the outermost tail feathers 50 mm., the central ones 30 mm., wing 61 mm., culmen 12.5 mm.”

The brief description of Nicéforo's specimen differs in minor details from the Venezuelan specimen (AMNH 146645). The two specimens are similar in size. Nicéforo's specimen possesses a bluish gorget as might be expected in an adult male hybrid of *Metallura t. tyrianthina* and *Agelaiocercus k. kingi* from the Cordillera Oriental of the Colombian Andes. Whereas I characterized the back color of the Venezuelan specimen as “greenish-blue,” Meyer de Schauensee used the term “bluish-green” for Nicéforo's specimen. This and other discrepancies might reflect semantics or real differences in color. Unfortunately, the whereabouts of Nicéforo's specimen is unknown, although another mentioned in Meyer de Schauensee's paper was deposited in the Academy of Natural Sciences of Philadelphia (Nicéforo no. 148, now ANSP 159261; Graves 1993).

Acknowledgments

I thank Richard Banks, Robert Bleiweiss, Kenneth C. Parkes, and Richard Zusi for critiques of the manuscript. I thank the cu-

rators and staffs of the American Museum of Natural History, New York, the Field Museum of Natural History, Chicago, and the Academy of Natural Sciences of Philadelphia, for permitting me to examine specimens in their care and for specimen loans. Photographic prints were provided by Smithsonian photographic services. Museum work was supported by the Alexander Wetmore Fund and the Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution.

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Appendix 1

Species of hummingbirds that occur in Estado Mérida, Venezuela: *Campylorhynchus fuscatus*, *Colibri thalassinus*, *C. coruscans*, *Klais guimeti*, *Lophornis delatrei*, *L. stictolophus*, *Chlorestes notatus*, *Chlorostilbon mellisugus*, *C. poortmani*, *Thalurania furcata*, *Hylacharix cyanus*, *Chrysoronia oenone*, *Amazilia versicolor*, *A. fimbriata*, *A. viridigaster*, *Chalybura buffonii*, *Heliodoxa leadbeateri*, *Sternoclyta cyanopectus*, *Coeligena coeligena*, *Ocreatus underwoodii*, *Aglaiocercus kingi*, *Hellomaster longirostris*, *Chaetocercus jordanii*.

Appendix 2

Comparative description of plumages of male *Aglaiocercus kingi caudatus*, *Metallura tyrianthina oropala*, and their presumed hybrid, AMNH 146645. The molts and plumages of male *Aglaiocercus* spp. are incompletely known. Young males (>6 months?) acquire a plumage that differs from the definitive plumage of adult males. This subdefinitive plumage is characterized by shorter outer rectrices, an incompletely developed crown patch (8 of 20 examined), and remnants of a white rump patch (see Zimmer 1952). One quarter (5 of 20) of the males in subdefinitive plumage

retain a few striations on the maxillary ramphothecum, a character usually interpreted as a sign of immaturity (Ortiz-Crespo 1972). The descriptions of *Aglaiocercus kingi* given below refer to the subdefinitive plumage.

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 dark bluish-green crown of young *kingi* is replaced (from anterior to posterior) by an ovate crown patch composed of brilliant bluish-green feathers. The hindneck, back, and rump are dark green; feathers are gray, tipped with green. Upper-tail coverts are bluish-green. A few white feathers form an indistinct patch on the lower hack.

The dorsal plumage of *tyrianthina* is dark dusky green, brighter on the crown, and with coppery highlights on the lower hack and rump. Feathers are gray, hued subterminally with coppery-green, and tipped broadly with dark green. When viewed head-on in direct light, plumage posterior to the midcrown region appears sooty black. Immature *tyrianthina* lack a contrasting rump patch.

Under a diffuse light source, the dorsum of the hybrid is a rich greenish-blue (paler on the crown), a color that is distinctly different from that of the presumed parental species. Feathers on the left side of the forehead are discolored, possibly by a preservative chemical. Dorsal feathers are dark gray, tipped with greenish-blue. Crown feathers are not modified as in adult *kingi*. When light is reflected obliquely (>90° from the observer), the dorsal plumage appears purple; when viewed head-on the hindcrown, hack, and rump appear black. A few rump feathers are tipped with buff.

The ventral plumage of *kingi* is medium green exhibiting subdued iridescence. A few small shining green disks occur on the throat of more mature individuals. The barbs of ventral feathers are narrowly tipped with buff or grayish-buff, especially along the midline of the abdomen. Some males in juvenile and subdefinitive plumage (e.g., AMNH 484067) have a white or buffy-white line extending from the base of the bill posterior to below the eye. Downy vent feathers are dark gray tipped with white or pale gray. Undertail coverts are dark green broadly edged with buff. Tihial feathers are short (extending half way to the hallux from the tibiotarsal joint), dark olive-gray and narrowly tipped with scattered grayish-buff barbs.

The venter of *tyrianthina* is dark dull green; feathers are tipped with buff or grayish-brown, especially along the midline. Feather tipping imparts a mottled appearance to the underparts. A narrow ovate gorget extends from the chin to the upper breast in *tyrianthina*. When viewed head-on in direct light, the auriculars and sides of the throat appear matte black and contrast greatly with the brilliant green gorget. Subadult males have a buffy line extending from the bill to below the eye.

Vent feathers are dark gray tipped with white or pale gray. Under-tail coverts are buff with a large broadly lanceolate spot (coppery- or bronzy-red) along the midline. Tibial feathers (dark gray tipped with buff) extend to the base of the hallux.

The venter of the hybrid is similar in pattern to *kingi*, but with the green portions replaced with bluish-green (paler than dorsum). A small brilliant feather occurs along the midline at midthroat (deep blue tip separated from the gray base by narrow blending bands of light blue and coppery-gold). A buffy-white stripe extends from the bill to below the eye (Fig. 2). Vent feathers are dark gray tipped with white. Undertail coverts are buff with a lanceolate subterminal spot (purple) near the midline. Tibial feathers (dark gray broadly tipped with buff) of the hybrid extend about halfway to the hallux, but may have been damaged by knotting of the specimen label string.

The remiges of *kingi* are brownish-black faintly tinted with purple. The outer vanes of the primary coverts and the innermost secondaries are edged with shining green or bluish-green; secondary coverts are broadly tipped with bluish-green. The remiges of *tyrianthina* are very similar in color but faintly tinted with bronze or olive. Wing coverts and the innermost secondaries are bronzy-green.

The remiges of the hybrid resemble those of *kingi*. Wing coverts and innermost secondaries are purple tipped with dark bluish-green.

The tail of *kingi* is deeply forked. The basal portions of the rectrices that are obscured in the folded tail are black. The exposed dorsal sections of the inner rectrices (1-4) are deep brilliant purple tipped with bluish-green. The outermost rectrices (5) lack bluish-green tips, are greatly elongated, narrow (5-6 mm wide, 25 mm from tip), and bowed in cross-section. Inner rectrices are smoothly tapered; rectrix 5 is bluntly tipped. Ventrally, the vanes are dull purplish-black. The rachises in *kingi* are blackish-brown dorsally, medium brown ventrally.

The tail of *tyrianthina* is shallowly forked. Rectrices are wide (10-11 mm), nearly flat in cross-section, abruptly truncate at the tip, and metallic coppery-red above and below. Rachises are dark brown above and below.

The tail of the hybrid is moderately forked. Feather size and shape are intermediate between *kingi* and *tyrianthina*. The outermost rectrices (5) are slightly bowed in cross-section (ca. 9.3 mm at widest point). Rectrices are metallic reddish-purple, above and below, the innermost (1-2) are diffusely tipped with purple. This iridescence, especially from the ventral surfaces, is similar in visual essence to that of *tyrianthina*. Rachises are dark brown above, medium brown ventrally.

Bill color is black in *kingi*, *tyrianthina*, and hybrid. In dorsal profile, the bills of both parental species are abruptly tapered, more so in *kingi*. The bill profile of the hybrid is similar to that of *tyrianthina*.