

Diagnoses of hybrid hummingbirds (Aves: Trochilidae).
11. Documentation of an intergeneric woodstar hybrid,
Calliphlox mitchellii × *Chaetocercus mulsant*

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Abstract.—A specimen in the Museum Alexander Koenig collected in Colombia is shown to be a hybrid between *Calliphlox mitchellii* and *Chaetocercus mulsant*. This is the first known example of intergeneric hybridization between species in these presumably closely related genera. External measurements of the hybrids are consistent with the proposed parental hypothesis.

As far as I am aware, the sole reference to intergeneric hybridization between miniature woodstars currently placed in *Chaetocercus* and *Calliphlox* (sensu Schuchmann 1999) is buried in the published catalog of the Otto Kleinschmidt Collection, which is now deposited in the Museum Alexander Koenig, Bonn, Germany (Kleinschmidt 1943:226):

“*Chaetocercus*—? 9837 ♂ ohne Orig.-Etik., wohl CC, höchst interessanter Vogel, Zwischenglied oder Mischung bzw. Bastard zwischen *Chaetocercus mulsanti* und *Calliphlox mitchelli*. Schwerlich Aberration von *mulsanti*. *C. harterti* scheint ähnlich, ist aber kleiner.”

Kleinschmidt's brief entry was accompanied by an inked drawing of the rectrices of the specimen and those of its proposed parental species. This record was overlooked in subsequent catalogs of hummingbird hybrids (Meyer de Schauensee 1949, Gray 1958, Panov 1989, Schuchmann 1999). In any case, Kleinschmidt's presentation was insufficient to determine the taxonomic status of the specimen or to make a convincing case for a particular hybrid combination. Here I provide an assessment of the specimen employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990), as modified by the findings of Graves (1998, 1999).

Methods

The specimen (Museum Alexander Koenig 9837) was obtained by the Fassel brothers in Colombia, possibly from the Cordillera Central, but little else is known about its provenance except that Anton and Eduard Fassel collected natural history specimens in Colombia from 1908 to 1911. The specimen, which was sexed as ♂ on one of the three attached labels (November 2001), appears to be in definitive plumage as judged by the absence of striations on the maxillary ramphotheca, the absence of distinctive buffy feather tips on the dorsal plumage or white spots in the rectrices, and the presence of a strongly iridescent gorget. Descriptions in this paper refer to definitive male plumage.

I compared the specimen with all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997), deposited in the Museum Alexander Koenig. Color photographs of the specimen were compared with all trochiline species in the National Museum of Natural History, Smithsonian Institution. The diminutive specimen was similar in size and general appearance to several of the small woodstars. For assessing the possibility of hybridization, I considered all species cur-

Table 1.—Ranges (mean \pm standard deviation) of measurements (mm) of wing chord, bill length, and rectrix length (R1–R5) of adult males of *Calliphlox mitchellii*, *Chaetocercus amethystina*, *Chaetocercus mulsant*, and a probable hybrid, *Calliphlox mitchellii* \times *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

Character	<i>Calliphlox mitchellii</i> (N = 13–15)	<i>Calliphlox amethystina</i> ^a (N = 10–11)	<i>Chaetocercus mulsant</i> (N = 18–19)	Hybrid
Wing	34.3–37.2 (35.6 \pm 0.6)	30.4–33.1 (32.0 \pm 0.4)	37.6–40.6 (39.3 \pm 0.9)	38.9
Bill	12.9–14.3 (13.7 \pm 0.4)	11.4–13.6 (12.5 \pm 0.8)	15.5–17.3 (16.3 \pm 0.4)	16.2
R1	11.9–13.1 (12.5 \pm 0.4)	13.3–15.1 (14.2 \pm 0.6)	14.4–17.2 (15.8 \pm 0.7)	15.1
R2	16.0–17.5 (16.7 \pm 0.5)	16.1–17.4 (16.9 \pm 0.5)	17.3–20.4 (19.1 \pm 0.9)	18.8
R3	23.3–27.7 (25.3 \pm 1.3)	20.8–25.0 (23.0 \pm 1.1)	22.8–27.8 (25.1 \pm 1.3)	28.3
R4	30.0–34.3 (32.0 \pm 1.3)	28.0–31.1 (29.7 \pm 0.9)	22.8–26.6 (24.7 \pm 0.9)	31.2
R5	29.9–33.1 (31.6 \pm 1.0)	32.2–36.9 (33.8 \pm 1.4)	19.3–22.2 (20.4 \pm 0.8)	27.5

^a Bahia (n = 1), "Brazil" (n = 3), Minas Gerais (n = 3), Rio de Janeiro (n = 4).

rently placed by Schuchmann (1999) in *Calliphlox* (*mitchellii*, *amethystina*) and *Chaetocercus* (*mulsant*, *bombus*, *heliodor*, *astreans*, *jourdanii*) that occur in Colombia (Hilty & Brown 1986) as potential parental species (see Graves 1997).

Measurements were taken with digital calipers and rounded to the nearest 0.1 mm: 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) (Table 1). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5). Scatter plots of measurements were used to illustrate size differences among specimens.

General color descriptions presented in Appendix 1 were made under natural light. I evaluated crown color with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even

lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the rectrix surface without depressing it. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements.

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 perceived as 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 coded as 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 values are dark, high values are light. The more light reflected from the plumage, the higher the L value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans and the relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. In any case, the L, a, b color system permits plumage color to be unambiguously characterized for taxonomic purposes.

Results and Discussion

I considered the hypotheses that the specimen represents (i) a geographic variant or genetic color morph of a valid species; (ii) a hybrid; or (iii) an undescribed species. Hybrids lack formal standing in zoological nomenclature. Therefore, hybridity must be ruled out before species status is conferred. Because the specimen differed significantly in size and shape from all species of *Calliphlox* or *Chaetocercus*, it does not appear to represent a previously undiscovered color morph or geographic variant of a known species. All evidence is consistent with Kleinschmidt's hypothesis that the specimen represents an intergeneric hybrid, *Calliphlox mitchellii* \times *Chaetocercus mulsant*. Several characters of the hybrid facilitate the identification of its parental species (Figs. 1, 2): (a) purplish-rose gorget with a few scattered white barbs on the chin; (b) white pectoral band; (c) broad white midline from pectoral band to vent; (d) absence of rufous or buff pigmentation on the rectrices; (e) the presence of cinnamon or rufous tipping on lower flank feathers; and (f) the unusual shape of the tail (rectrix length: $R4 > R3 > R5 > R2 > R1$).

Here I present a synopsis of the critical steps of the hybrid diagnosis (see Appen-

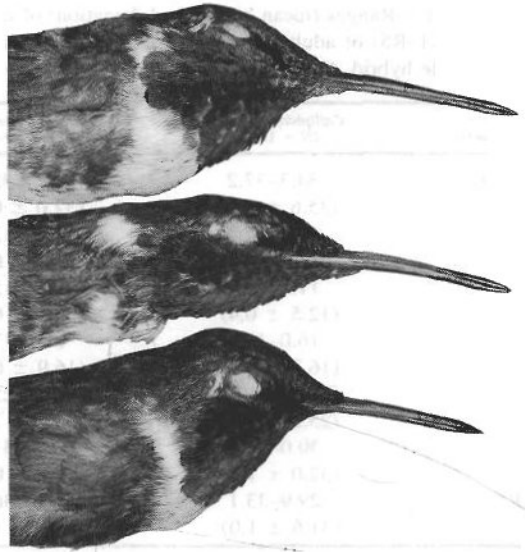


Fig. 1. Lateral views of males in definitive plumage (top to bottom): *Chaetocercus mulsant*, a probable hybrid, *Calliphlox mitchellii* \times *Chaetocercus mulsant* (Museum Alexander Koenig 9837), and *Calliphlox mitchellii*.

dix). The pool of potential parental species may first be narrowed by focusing on absence of rufous or buff pigmentation in the rectrices in the hybrid. Because brown and reddish-brown pigments appear to exhibit consistent penetrance in hummingbird hybrids (Banks & Johnson 1961, Graves & Newfield 1996), *Chaetocercus bombus* (buff pectoral band) and *C. jourdani* (rufous pigmentation on rachis and vanes of rectrices) can be eliminated from further consideration as parental species. *Chaetocercus astreans* can also be eliminated because its geographic range in the Sierra Nevada de Santa Marta does not overlap that of other potential parental species (Graves 1986) and because it possesses a dark red gorget and bluish-green dorsal plumage, neither of which is expressed in the hybrid. Similarly, *Chaetocercus heliodor* can be eliminated because hybridization between it and any of the remaining species would likely produce offspring with a grayish-white pectoral band, dark green dorsal plumage toned with



Fig. 2. Ventral view of a probable hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

bluish-green, and dark greenish flanks (Graves 1997). Based on plumage characters, the hybrid could be the product of two possible combinations of species: *Calliphlox mitchellii* × *Chaetocercus mulsant* and *Calliphlox amethystina* × *Chaetocercus mulsant*. On geographical grounds the hybrid must represent the former combination because *Calliphlox amethystina* and *Calliphlox mitchellii* have allopatric distributions east and west of the Cordillera Oriental (Hilty and Brown 1986). The hybrid was collected in the Cordillera Central (Kleinschmidt 1943). Colorimetric measurements of crown color (Table 2) are consistent with the hypothesis that the specimen represents an intergeneric hybrid between *Calliphlox mitchellii* and *Chaetocercus mulsant*.

As a second step, I tested the restrictive hypothesis with an examination of size and external proportions (Fig. 3). Measurements of trochiline hybrids fall within the mensural ranges exhibited by their parental species as a consequence of the polygenic

mode of inheritance (Banks & Johnson 1961). Measurements of *Calliphlox mitchellii* and *Chaetocercus mulsant* overlap for only two of the seven characters but the percent difference in character means (larger species divided by smaller) is moderate except for the outermost rectrix (R5): wing chord (10.4%), bill length (18.9%), R1 (26.4%), R2 (14.4%), R3 (0.8%), R4 (29.6%), and R5 (54.9%). Measurements of the hybrid fall within the cumulative range of parental measurements for six of the seven measurements. The third rectrix (R3) of the hybrid was 0.5 mm (1.8%) longer than the largest value recorded for that character in the parental species. There have been no well-documented cases of morphological luxuriance (where the size of hybrid offspring exceeds that of the parental species) among avian hybrids (Graves 1990, 1996). I suspect that the cumulative range of measurements for R3 in the parental species would overlap the hybrid value if the sample size was increased.

I note for comparative purposes that *Cal-*

Table 2.—Minima, maxima, and means (\pm standard deviation) of opponent color coordinates (L , a , b) of crown color of adult males of *Calliphlox mitchellii*, *Chaetocercus mulsant*, and a probable hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

	L darkness			a/a red/green			b/b yellow/blue		
	Min.	Max.	Mean \pm SD	Min.	Max.	Mean \pm SD	Min.	Max.	Mean \pm SD
<i>Calliphlox mitchellii</i>	29.9	32.2	31.3 \pm 0.8	0.5	2.7	1.1 \pm 0.8	8.8	12.1	9.8 \pm 1.3
<i>Chaetocercus mulsant</i>	13.6	20.2	16.9 \pm 1.7	-0.3	4.4	1.9 \pm 1.4	-4.3	1.6	-1.6 \pm 1.8
Hybrid			22.2			-1.6			7.7

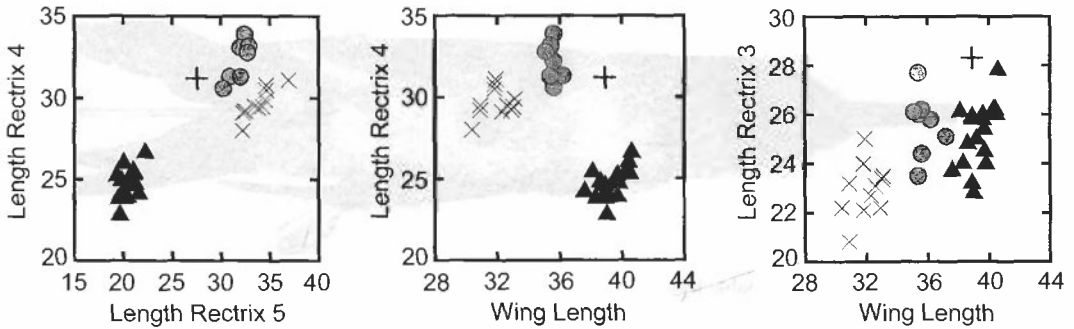


Fig. 3. Bivariate plots of selected measurements (see Table 1) of males in definitive plumage: *Calliphlox mitchellii* (●), *Calliphlox amethystina* (×), *Chaetocercus mulsant* (▲), and a probable hybrid (+), *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

liphlox amethystina × *Chaetocercus mulsant* was not excluded as a parental combination by mensural measurements (Table 1). However, inspection of bivariate plots of the wing and rectrix measurements suggest that *Calliphlox mitchellii* was the most likely *Calliphlox* parent (Fig. 3). In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that Kleinschmidt's specimen represents a hybrid between *Calliphlox mitchellii* and *Chaetocercus mulsant*.

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Literature Cited

- Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—*Condor* 63:3–28.
- Bleiweiss, R., J. A. W. Kirsch, & J. C. Matheus. 1997. DNA hybridization evidence for the principal lineages of hummingbirds (Aves: Trochilidae).—*Molecular Biology and Evolution* 14: 325–343.
- Goldsmith, T. H., & K. M. Goldsmith. 1979. Discrimination of colors by the black-chinned hummingbird, *Archilochus alexandri*.—*Journal of Comparative Physiology A* 130:209–220. Colombia.—*Condor* 92:754–760.
- Graves, G. R. 1986. Systematics of the Gorgeted Woodstars (Trochilidae: *Acestrura*). *Proceedings of the Biological Society of Washington* 99:218–224.
- . 1990. Systematics of the “green-throated sun-angels” (Aves: Trochilidae): valid taxa or hybrids?—*Proceedings of the Biological Society of Washington* 103:6–25.
- . 1996. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes.—*Proceedings of the Biological Society of Washington* 109:373–390.
- . 1997. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 4. Hybrid origin of *Calothorax decoratus* Gould. *Proceedings of the Biological Society of Washington* 110:320–325.
- . 1998. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 6. An intergeneric hybrid, *Agelaiocercus kingi* × *Metallura tyrianthina*, from Venezuela.—*Proceedings of the Biological Society of Washington* 111:511–520.
- . 1999. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 8. A provisional hypothesis for the hybrid origin of *Zodalia glyceria* (Gould, 1858).—*Proceedings of the Biological Society of Washington* 112:491–502.
- , & N. L. Newfield. 1996. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 1. Characterization of *Calypte anna* × *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* × *Helian-gelus amethysticollis*) from northern Colombia.—*Condor* 92:754–760.
- Gray, A. P. 1958. *Bird hybrids*. Commonwealth Agricultural Bureaux, Bucks, England, 390 pp.
- Hilty, S. L., and W. L. Brown. 1986. *A guide to the birds of Colombia*. Princeton University Press, Princeton, New Jersey, 836 pp.
- Hunter, R. S., & R. W. Harold. 1987. *The measurement of appearance*, 2nd edition. Wiley, New York, 411 pp.
- Kleinschmidt, O. 1943. *Katalog meiner ornithologischen Sammlung*. Gebauer-Schwetschke, Halle, Germany. I–XII + 236 + A–H pages.
- Meyer de Schauensee, R. M. 1949. *Birds of the Republic of Colombia*, part 2.—*Caldasia* 5:381–644.
- Panov, E. N. 1989. *Natural hybridisation and ethological isolation in birds (in Russian)*. Nauka, Moscow, 510 pp.
- Schuchmann, K. L. 1999. Family Trochilidae. Pp. 468–680 in J. del Hoyo, A. Elliott, & J. Sargatal, eds., *Handbook of the birds of the world*, vol. 5. *Barn-owls to hummingbirds*. Lynx Edicions, Barcelona, 759 pp.
- Sibley, C. G., & B. L. Monroe, Jr. 1990. *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, Connecticut, 1111 pp.
- Zusi, R. L., & G. D. Bentz. 1982. Variation of a muscle in hummingbirds and swifts and its systematic implications.—*Proceedings of the Biological Society of Washington* 95:412–420.

Appendix

Comparative description of selected characters of adult male *Calliphlox mitchellii*, *Chaetocercus mulsant*, and a probable hybrid, *C. mitchellii* × *C. mulsant* (Museum Alexander Koenig 9837). 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 dorsal plumage in *mitchellii*, from forecrown to uppertail coverts, is weakly iridescent and dark green in coloration. When viewed head-on, the dorsum is sooty green. The dorsal plumage of *mulsant* is significantly more iridescent than in *mitchellii*, appearing bluish-green, particularly on the rump and uppertail coverts. When viewed head-on, the dorsum of *mulsant* exhibits a moderate degree of green iridescence which becomes progressively bluer from crown to uppertail

coverts. The color and intensity of dorsal iridescence in the hybrid were intermediate in appearance to that of the parental species. Both parental species and the hybrid possess silky white tufts of flank feathers.

In *mitchellii* the central rectrices (R1) are black, toned with dull bronze, the outer vanes glossed with dark green. The remainder of the rectrices (R2–R5) are black, toned with bronze or purplish-bronze at certain angles of inspection under intense light. In *mulsant*, the central rectrices are black, glossed with dull green on the proximal two-thirds of the inner and outer vanes; the outer rectrices (R2–R5) are black. Rectrices of the hybrid are intermediate in color and shape (width of R4 = ~1.3 mm, width of R5 = ~1.1 mm; both measured 5 mm from the feather tip).

In *mulsant*, dark green wing coverts contrast with dull black secondaries and primaries. The contrast between wing coverts and flight feathers in *mitchellii* is negligible. Wing coverts and flight feathers in the hybrid are intermediate in color between those of *mulsant* and *mitchellii*.

In *mitchellii*, a white post-ocular spot elongates to form a tenuous connection to the side of the white pectoral band. The postocular facial stripe (obscured by lateral gorget feathers in Fig. 2) in *mulsant* and in the hybrid is more pronounced.

The purplish-rose gorget of *mitchellii* extends laterally to the lower edge of the eyering and posteriorly to the lower throat. Gorget feathers are pale gray basally (with a few dark gray lateral barbs near the base of the feather), banded distally by a narrow transitional band of dark gray, and tipped with a purplish-rose disk. The gorget is bordered posteriorly by a creamy-white pectoral band. The abdomen and sides are dull green. Feather tips along the midline are tipped with gray. Feathers of the lower flanks are tipped with cinnamon or rufus. Vent feathers are white, whereas undertail coverts are dull green narrowly fringed with gray or buff.

The purplish-rose gorget of *mulsant* does not extend laterally to the eyering. A small white chin spot speckled with iridescent disks is found in most specimens. The gorget is bordered posteriorly by a white pectoral band (whiter than in *mitchellii*). Gorget feathers are pale gray, grayish-white or creamy white, banded distally by a narrow transitional band of dull bronzy-green, and tipped with a purplish-rose disk. A broad white stripe extends along the midline from the pectoral band to the vent (also white). The flanks and sides of the breast below the pectoral band are bluish-green. Undertail coverts are white with an indistinct grayish or bluish-gray lanceolate subterminal spot. Lower flank feathers lack cinnamon or rufus tips.

The ventral plumage of the hybrid is intermediate in appearance between that of *mitchellii* and *mulsant*. A few feathers on the chin have scattered white barbs.

The gorget extends laterally to the lower margin of the eyering as in *mitchellii*. The gray basal portions of gorget feathers are intermediate in darkness between those of *mitchellii* and *mulsant*; the narrow subterminal band of gorget feathers exhibits dull bronze reflections. The remainder of the underparts are nearly intermediate in appearance between that of the parental species although the elongated preparation of the skin makes it difficult to compare homologous parts efficiently. The

hybrid possesses a distinctive pectoral band (darker than in *mulsant*) and a white midline stripe extending to the vent area (Fig. 2). Feathers on the lower flanks are tipped with cinnamon or rufus. The undertail coverts are creamy white or buff with a subterminal grayish-green spot. Longer coverts are narrowly tipped with gray whereas shorter ones are tipped with buff or rufus. The maxillary and mandibular ramphotheca of *mitchellii*, *mulsant*, and the hybrid are black.