

Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 9. Confirmation of the hybrid origin of *Coeligena purpurea* Gould, 1854

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Abstract.—*Coeligena purpurea* Gould, 1854 is shown to be a hybrid between *Coeligena coeligena* and *Coeligena prunellei*. The geographic distribution of the parental species suggests that the two hybrid specimens were collected in the Eastern Cordillera of the Colombian Andes. The hybrids exhibit a blended mosaic of plumage characters of the postulated parental species. External measurements of the hybrids fall within the cumulative ranges of characters of the parental species.

The taxonomic validity of *Coeligena purpurea* Gould 1854, supposedly from the vicinity of Poyayán, Colombia, was first questioned by Elliot (1876:60):

"Two specimens of this form are in Mr. Gould's collection, no others being known to exist. The characters these examples present are not sufficiently satisfactory to entitle them to an independent specific rank without giving rise to great doubts regarding the propriety of such an acknowledgment. . . . until we have further evidence that will substantiate its claim to a distinctive rank, *L. purpurea* cannot but hold a very doubtful position among the species of this group."

Elliot (1878) later opined that *C. purpurea* represented a melanistic variant of *C. wilsoni*, a species restricted to the Pacific slope of the Andes in Colombia and northwestern Ecuador. Subsequent catalogs have listed it several ways—as a valid species (Salvin 1892, Cory 1918, Simon 1921), an immature male of *C. prunellei* (Boucard 1893), or as a hybrid, *C. coeligena* × *C. prunellei* (Berlioz 1936; Peters 1945; Meyer de Schauensee 1949, 1966). Schuchmann (1999) ambiguously concluded that *C. purpurea* was either a dark variety of *C. wilsoni* or a hybrid between *C. coeligena* and *C. prunellei*. Not surprisingly, none of the aforementioned treatments provided documentation or evidence in support of taxo-

nomic conclusions. Here I confirm the hybrid origin of *Coeligena purpurea*, employing the methods and assumptions of Graves (1990) and Graves & Zusi (1990) as modified by insights on plumage color aberrations associated with hybridization (Graves 1996, 1998, 1999).

Methods

The type (BMNH 1888.7.25.165, listed as "syntype" by Warren 1966) and a second specimen (uncataloged until recently, BMNH 2000.1.9) of *Coeligena purpurea* were obtained by The Natural History Museum, Tring (formerly British Museum of Natural History) as part of the Gould Collection. I compared these specimens (Figs. 1, 2) with all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997), in that museum. Both specimens appear to be adult males in definitive plumage as judged by the absence of striations on the maxillary ramphotheca, the presence of iridescence on the crown and back, and a moderately forked tail (fork depth in type = 12.1 mm). Unless otherwise noted, subsequent descriptions in this paper refer to definitive male plumage. I discovered no evidence that *C. purpurea*

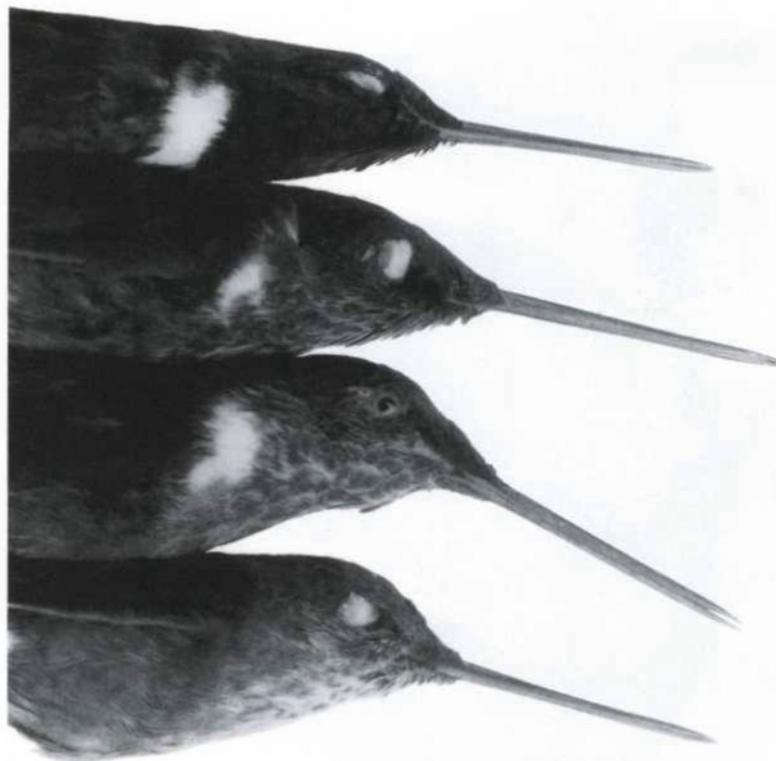


Fig. 1. Lateral views of males in definitive plumage (top to bottom): *Coeligena prunellei*; *C. coeligena colombiana* × *C. prunellei*, BMNH 2000.1.9; *C. coeligena colombiana* × *C. prunellei*, BMNH 88.7.25.165 (type of *Coeligena purpurea* Gould, 1854); and *C. coeligena colombiana*.

represented a subdefinitive plumage, aberrant color morph, or geographic variant of any known taxon (see Results and Discussion). In assessing the possibility of hybridization, I considered all species in the genus *Coeligena* (*coeligena*, *wilsoni*, *prunellei*, *torquata*, *phalerata*, *eos*, *bonapartei*, *helianthea*, *lutetiae*; taxonomy of Schuchmann 1999) that occur in Colombia and Ecuador (Hilty & Brown 1986, Fjeldså & Krabbe 1990, Krabbe et al. 1992) as potential parental species.

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). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5).

General color descriptions presented in Appendix 1 were made under natural light. I evaluated the color of the crown, center of back, and dorsal surface of rectrix 4 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

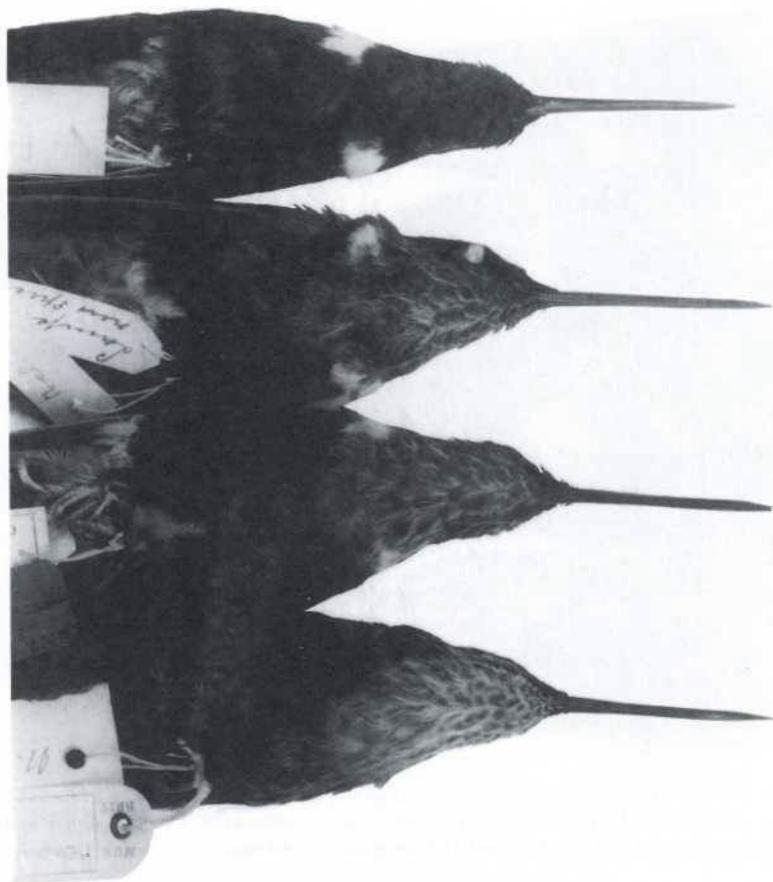


Fig. 2. Ventral views of males in definitive plumage (top to bottom): *Coeligena prunellei*; *C. coeligena colombiana* × *C. prunellei*, BMNH 2000.1.9; *C. coeligena colombiana* × *C. prunellei*, BMNH 88.7.25.165 (type of *Coeligena purpurea* Gould, 1854); and *C. coeligena colombiana*.

Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the plumage surface without depressing it. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure three times for each area of plumage, removing the aperture between trials. Each datum summarized in Table 2 thus represents the mean of three independent 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. The relevance

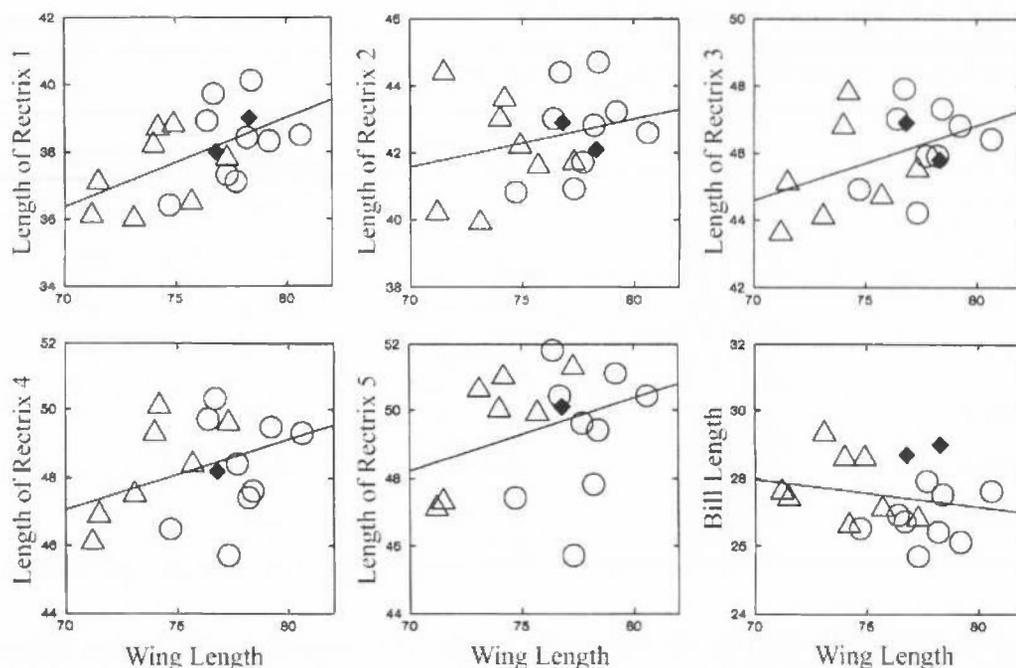


Fig. 3. Bivariate plots of measurements (see Table 1) of males in definitive plumage: *Coeligena prunellei* (○); *C. coeligena colombiana* (△); and putative hybrids (◆), *C. coeligena colombiana* × *C. prunellei* (BMNH 2000.1.9; BMNH 88.7.25.165).

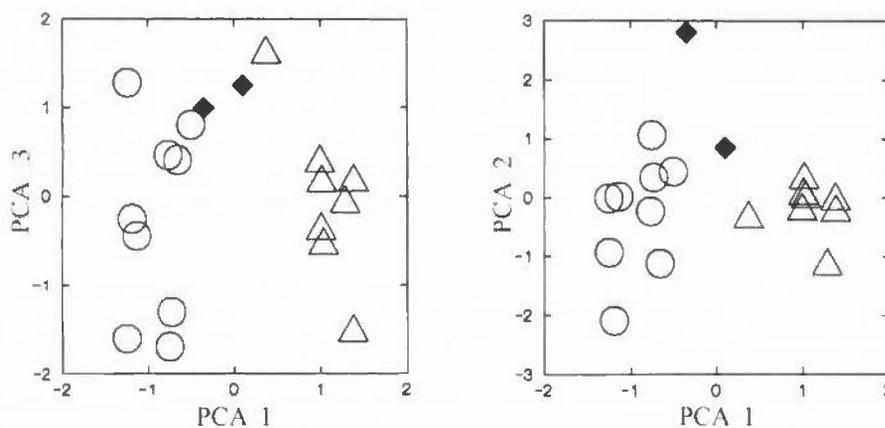


Fig. 4. Bivariate relationships of factor scores (see Table 3) from a principal components analysis of crown and breast color (L , a , b) of males in definitive plumage: *Coeligena prunellei* (○); *C. coeligena colombiana* (△); and putative hybrids (◆), *C. coeligena colombiana* × *C. prunellei* (BMNH 2000.1.9; BMNH 88.7.25.165).

of opponent color coordinates to colors perceived by hummingbirds is unknown.

I used principal components analysis (PCA) on untransformed colorimetric variables to reduce the dimensionality of data. Unrotated principal components were ex-

tracted from correlation matrices (Wilkinson 1989). Factor scores were projected on bivariate plots to illustrate the relationship of plumage color variables in postulated hybrids and parental species. Scatter plots of mensural characters and least squares re-

Table 1.—Ranges (mean \pm standard deviation) of measurements (mm) of adult males of *Coeligena prunellei*, *C. coeligena colombiana*, and two specimens of a probable hybrid, *C. c. colombiana* \times *C. prunellei* (= *Coeligena purpurea* Gould; type, BMNH 1888.7.25.165 and BMNH 2000.1.9).

	<i>Coeligena prunellei</i> (n = 9)	<i>Coeligena coeligena colombiana</i> (n = 8)	BMNH 1888.7.25.165	BMNH 2000.1.9
Wing chord	74.7–80.6 (77.7 \pm 1.7)	71.2–77.3 (74.0 \pm 2.1)	76.8	78.3
Bill length	25.8–28.0 (26.9 \pm 0.7)	26.6–29.3 (27.8 \pm 1.0)	28.7	29.0
Rectrix 1	36.5–40.2 (38.4 \pm 1.2)	36.0–38.8 (37.4 \pm 1.1)	38.0	39.0
Rectrix 2	40.9–44.8 (42.8 \pm 1.4)	39.9–44.4 (42.1 \pm 1.6)	42.9	42.1
Rectrix 3	44.3–48.0 (46.4 \pm 1.8)	43.6–47.8 (45.4 \pm 1.5)	46.9	45.8
Rectrix 4	45.8–50.4 (48.4 \pm 1.6)	46.1–50.1 (48.3 \pm 1.5)	48.2	—
Rectrix 5	45.8–51.9 (49.4 \pm 2.0)	47.1–51.3 (49.6 \pm 1.7)	50.1	—

gression lines were used to illustrate size differences among specimens.

Results and Discussion

I considered four hypotheses proposed by previous authors: *Coeligena purpurea* represents (a) a melanistic plumage of *C. wilsoni*; (b) a subdefinitive plumage of *C. prunellei*; (c) an intrageneric hybrid; or (d) a valid species. For brevity I use the epithet, *purpurea*, in the remainder of the paper.

Melanistic plumage of Coeligena wil-

soni?—The hypothesis of melanism (Elliot 1878) is contradicted by the fact that *C. wilsoni* and *purpurea* differ in external measurements (unpublished data). Both sexes of *C. wilsoni* have significantly shorter wings but marginally longer bills than *purpurea*. Additionally, the length of rectrix 5 of the type of *purpurea* exceeds the maximal values observed in *C. wilsoni*.

Subdefinitive plumage of Coeligena prunellei?—As previously noted, both specimens of *purpurea* appear to be in definitive

Table 2.—Maxima, minima, and means (\pm standard deviation) of opponent color coordinates (*L*, *a*, *b*) of crown, breast and rectrix of adult males of *Coeligena prunellei*, *C. coeligena colombiana*, and two specimens of a probable hybrid, *C. c. colombiana* \times *C. prunellei* (= *Coeligena purpurea* Gould; type, BMNH 1888.7.25.165 and BMNH 2000.1.9).

Variables	<i>Coeligena prunellei</i> (n = 9)			<i>Coeligena coeligena colombiana</i> (n = 8)			BMNH 88.7.25.165	BMNH 2000.1.9	
	Min.	Max.	Mean (\pm SD)	Min.	Max.	Mean (\pm SD)			
Crown	<i>L</i>	13.1	18.9	16.4 (\pm 1.7)	20.1	25.6	23.4 (\pm 1.6)	19.0	15.4
	<i>a</i>	-1.1	2.6	0.7 (\pm 1.5)	3.5	5.9	4.7 (\pm 0.8)	3.3	4.6
	<i>b</i>	2.1	5.2	4.0 (\pm 1.0)	5.0	16.7	12.1 (\pm 3.8)	3.3	3.5
Breast	<i>L</i>	11.7	20.3	15.4 (\pm 3.4)	37.0	46.9	41.7 (\pm 3.6)	31.9	23.8
	<i>a</i>	1.6	4.2	3.0 (\pm 0.8)	2.4	3.4	3.0 (\pm 0.3)	3.6	4.3
	<i>b</i>	2.0	6.4	3.7 (\pm 1.7)	9.2	12.7	10.8 (\pm 1.0)	3.3	7.8
Rectrix	<i>L</i>	7.2	11.6	9.6 (\pm 1.5)	18.4	24.0	21.2 (\pm 1.8)	13.1	12.9
	<i>a</i>	3.3	3.8	3.6 (\pm 0.2)	5.4	5.9	5.7 (\pm 0.2)	5.0	5.1
	<i>b</i>	2.1	3.8	3.1 (\pm 0.5)	12.6	18.3	16.0 (\pm 1.8)	3.6	9.3

Table 3.—Factor loadings from a principal components analysis (PCA) of crown and breast color (*L*, *a*, *b*) of *Coeligena prunellei*, *C. coeligena colombiana*, and hybrids, *C. coeligena colombiana* × *C. prunellei* (BMNH 2000.1.9; BMNH 88.7.25.165).

Variables		PCA 1	PCA 2	PCA 3
Crown	<i>L</i> (dark/light)	0.96	-0.14	-0.15
	<i>a</i> (red/green)	0.88	0.13	0.35
	<i>b</i> (yellow/blue)	0.89	-0.23	-0.32
Breast	<i>L</i> (dark/light)	0.95	-0.08	0.03
	<i>a</i> (red/green)	0.01	0.98	-0.17
	<i>b</i> (yellow/blue)	0.91	0.31	0.09
Percent variance explained		70.4%	19.2%	4.7%

plumage. Specimens of *C. prunellei* in definitive and subdefinitive plumages differ in numerous ways from *purpurea* (see Appendix 1).

Hybrid?—Because hybrids lack formal standing in zoological nomenclature, hybridity must be ruled out before species status is conferred. In this instance, the evidence is consistent with the hypothesis that *purpurea* represents an intrageneric hybrid, *Coeligena coeligena* × *C. prunellei* (Berlioz 1936). Several characters of *purpurea* facilitate the identification of its parental species: (a) throat feathers conspicuously margined with pale buffy-white; (b) elliptical white spots on both sides of the upper breast; (c) unmarked rectrices; (d) absence of rufous or buff pigmentation on the secondaries; (e) absence of a brilliant frontlet or coronal patch; and (f) the absence of strong iridescence on the lower breast and belly (see Appendix I).

Here I present a synopsis of the critical steps of the hybrid diagnosis. The pool of potential parental species may be quickly narrowed by focusing on the scalloped pattern of chin and throat feathers of *purpurea*. Among the potential parental species, this character is shared only by *C. coeligena*. The white breast spots of *purpurea* were inherited from the other parental species. Three species in the source pool either have white breast spots (*C. wilsoni*, *C. prunellei*) or a white pectoral band (*C. torquata*). *Coeligena torquata* can be eliminated from further consideration because its rectrices (1–

4) are predominately white (rectrices are dark and unmarked in *purpurea*). Only one of the two remaining pairs of species (*C. coeligena* × *C. prunellei*) could have contributed the unique combination of characters exhibited by *purpurea* (Appendix).

The hybrid diagnosis focuses on the identification of apomorphic character states in putative hybrids (Graves 1990). Complete dominance and polygenic inheritance of plumage characters, however, may preclude or obscure the expression of parental apomorphies in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of a suite of plesiomorphic characters. In this case, rejection of taxa whose prominent plesiomorphic characters were not identified (even as traces) in *purpurea* reduces the species pool to the same couplet of species that share apomorphic characters with *purpurea*. For example, hybridization of *C. wilsoni* and *C. coeligena* would likely produce offspring with plumage that is significantly less melanized than that of *purpurea*. In a similar fashion, *Coeligena eos* (brilliant frontlet, cinnamon secondaries and rectrices, brilliant iridescence on lower breast), *C. bonapartei* (brilliant frontlet, brilliant iridescence on lower breast), *C. helianthea* (brilliant frontlet, brilliant iridescence on lower breast), *C. phalerata* (brilliant frontlet, completely white rectrices), and *C. lutetiae* (brilliant frontlet, buff secondaries) are exceedingly unlikely to be pa-

rental species because they possess a combination of characters not observed in *purpurea*.

External measurements.—As a second step, the restrictive hypothesis was tested with an analysis of size and external proportions (Table 1, Fig. 3). 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 *Coeligena coeligena* and *C. prunellei* overlap and the percent difference in character means is small (larger species divided by smaller): wing chord (5.0%), bill length (3.3%), rectrix 1 (2.7%); rectrix 2 (1.7%), rectrix 3 (2.2%), rectrix 4 (0.2%), and rectrix 5 (0.4%). Nevertheless, measurements of *purpurea* fall within the cumulative ranges of measurements of the postulated parental species, and, in many cases, approximate the values predicted by least squares regression (Fig. 3).

Colorimetric measurement.—Colorimetric values of *purpurea* fall within the range of values exhibited by the postulated parental species. The intermediate appearance of *purpurea* is neatly summarized by bivariate plots of factor scores from a principal components analysis (Fig. 4, Table 3) of crown and breast color. In particular, factor scores for *purpurea* are bracketed by those of *Coeligena coeligena* and *C. prunellei* along PCA 1, which explains 70.4% of the variance in color among specimens.

In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that *Coeligena purpurea* is an intrageneric hybrid between *Coeligena coeligena* and *Coeligena prunellei*. *Coeligena purpurea* Gould, 1854 is thus available in taxonomy only for the purposes of homonymy.

Geographic origin.—As noted by Gould (1854; opposite plate 256), the geographic origin of *Coeligena purpurea* is indeterminate: "I have lately received from M. Par-

zudaki, of Paris, a fine specimen of this bird, which I believe to be from the neighbourhood of Popayan; a second example forms part of the collection of Edward Wilson, Esq., and is said to have been killed in Peru." I suspect both specimens were collected in the Eastern Cordillera of the Colombian Andes for the simple reason that one of its parental species, *Coeligena prunellei*, is restricted to this region (Hilty & Brown 1986, Collar et al. 1992). Collar et al.'s (1990) report of a single specimen of *C. prunellei* from the Central Cordillera at Salento, Department of Quindío, is unconfirmed. *Coeligena prunellei* (~1400–2600 m elevation) and *Coeligena coeligena colombiana* (1500–2600 m) overlap geographically in humid montane forest in the Department of Cundinamarca (Snow & Snow 1980, Hilty & Brown 1986, Fjeldså & Krabbe 1990, Collar et al. 1992).

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Appendix 1

Comparative description of selected characters of adult male *Coeligena prunellei*, *C. coeligena colombiana*, and two specimens of a probable hybrid, *C. coeligena colombiana* × *C. prunellei* (= *Coeligena purpurea* Gould; type, BMNH 1888.7.25.165; BMNH 2000.1.9). Unless noted otherwise, descriptions of *purpurea* refer to the type (BMNH 1888.7.25.165).

Viewed "head-on," the dorsum of *prunellei* is matte black. When viewed from a "tail-on" position, the dorsum exhibits weak iridescence, which varies in color from silvery-green on the forecrown and crown, to dark purple on the hindneck and mantle, to coppery-purple on the upper back, and bronze-green on the lower back and rump. The lesser wing coverts are iridescent steel blue. The median wing coverts and pri-

mary coverts are tipped with dark purple. Upper tail coverts are black faintly tinted with purple iridescence.

The dorsum of *coeligena*, which generally can be characterized as dark olive-bronze, exhibits weak bronze to coppery-bronze iridescence when viewed head-on. Exposed portions of dorsal feathers, all of which are narrowly or broadly tipped with rufous barbs, vary in color from bronze on the forecrown to coppery-bronze on the wing coverts, scapulars, and mantle, to olive-bronze or green on the back and rump. The imbrication of rufous-tipped feathers produces a subtly banded appearance on the back and rump. When viewed tail-on, the anterior dorsal plumage emits a dull golden-bronze iridescence which shifts to brighter bluish-green on the back and rump. The upper tail coverts are dark olive-bronze, narrowly edged with rufous.

The dorsum of *purpurea* is nearly intermediate in appearance between that of *prunellei* and *coeligena*. Crown, nape, and mantle are black, faintly tinted with brownish-purple; feathers are narrowly fringed with rufescent barbs. Purplish and coppery iridescence appears on the upper back. Viewed head-on, the forecrown of the type of *purpurea* exhibits a very faint purple iridescence, much less pronounced than in *prunellei*. The second specimen of *purpurea* (BMNH 2000.1.9) differs from the type in exhibiting a more intense iridescence (purple) on the crown and hindneck. Feathers on the rump are subtly banded, but significantly darker, than in *coeligena*: dark neutral grayish-brown basally, bordered distally by an iridescent band which changes spectrally toward the tip from dull coppery red through gold to green. The terminal barbs are tipped with rufescent barbs. The extent of green iridescence increases posteriorly from the lower back to the rump. Viewed tail-on, the mantle and hack emits weak coppery-purple iridescence, shifting to golden-bronze on the lower back and rump. The upper tail coverts are dark purplish-brown (same color as crown), narrowly tipped with rufous.

Wing coverts and flight feathers of *purpurea* are intermediate in color and degree of melanism to those of *coeligena* and *prunellei*. The lesser wing coverts of *purpurea* are dark iridescent purple, whereas the margins of the adjacent upper scapulars are dark coppery-purple. Posterior scapulars are banded as in the middle back. Margins of the median wing coverts, primary coverts, and coverts at the bend of the wing are dark purple (darker than lesser wing coverts). Tiny coverts at the edge of the wing (best seen by raising the wing slightly) are tipped with chestnut. Greater wing coverts are dark bronzy purplish-brown. Flight feathers are dull black, tinted with purplish-brown. Outer vane of outermost primary is buff proximally, gradually darkening toward the tip to dark brown (similar to *prunellei* and *coeligena*). Underwing coverts dark brownish-black, intermediate between *prunellei* and *coeligena*.

Auriculars of *coeligena* are brown with some buffy-

white barbs. Feathers of the chin, throat, malar region, and upper breast are scalloped; feathers are brownish-black with wide pale margins, either white or white faintly tinted with grayish-buff. Feathers of the lower breast, flanks, and abdomen are bronze to dark brown, paler and grayer toward the midline. Undertail coverts are dark brown, broadly edged with buff.

Auriculars, throat and upper breast of *prunellei* are black. Feathers of the central throat are tipped with brilliant steel blue to light purple disks, forming a gorget. An elliptical white patch occurs at the side of breast anterior to the bend of the wing in museum skins. The lower breast, flanks, and belly are black, less lustrous near the midline. The undertail coverts are black, broadly margined with white.

The ventral plumage of *purpurea* is nearly intermediate to that of *coeligena* and *prunellei*. Feathers of the chin, auricular margins, and throat are dark brownish-black (margined on the lower chin, throat, and malar area with pale buffy-white). When viewed head-on, the dark subterminal disks of the central throat emit a dull purple iridescence—iridescence was not observed at other angles of inspection. In *prunellei*, the exposed portions of the longest feathers that compose the white shoulder patch are silky white throughout their length. The shoulder patch of *purpurea* is similar to that of *prunellei*, but the margins are less well defined, the feathers less lustrous, narrowly to broadly fringed with dark brownish-black (same color as rest of ventral plumage). The breast, flanks, and abdomen of *purpurea* are dark brownish-black, with scattered buff or brown barb tips, especially along the midline. The undertail coverts are almost perfectly intermediate in color between those of *prunellei* and *coeligena*. The density of melanin in the central lanceolate spot increases with covert size. A couple of very short coverts are mostly buff (with dark brownish-black bases). Feather margins become progressively paler with increasing feather size, buffy to rufous in short feathers, very pale buffy-white in the longest feather. The second specimen of *purpurea* differs from the type in having the smaller undertail coverts more extensively fringed with buff and rufescent. The tibial plumes are dark brownish-black, tipped with brown barbs.

The unmarked rectrices of *purpurea* are intermediate in color and intensity of iridescence between those of *prunellei* (black, faintly tinted with purple) and *coeligena* (bronze or olive-bronze).

Feet and tarsi of *prunellei* are pale brownish-yellow (rose red in life, Hilty & Brown 1986), the claws are dark brown, but, on occasion, may be yellow. The feet and tarsi of *coeligena* are light brown with dark brown scutes, whereas the claws are dark brown. The feet and tarsi of *purpurea* are yellowish brown with medium brown scutes (claws brown). The maxillary ramphotheca is black in *prunellei*, *coeligena*, and *purpurea*. The mandibular ramphotheca is black in *prunellei*, medium brown in *coeligena*, and brownish-black in *purpurea*.