

Taxonomic notes on hummingbirds (Aves: Trochilidae)
2. *Popelairia letitia* (Bourcier & Mulsant, 1852) is a valid species

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Abstract.—*Popelairia letitia* (Bourcier & Mulsant, 1852), known from two specimens supposedly from Bolivia, appears to be a valid species. Analysis of plumage color and morphometrics indicates that *P. letitia* does not represent an immature plumage or geographic variant of *Discosura longicauda*, although this species and *P. letitia* may be sister taxa. No credible evidence for a hybrid origin of *P. letitia* was discovered. "Letitia's Coquette" is proposed as the common English name for *P. letitia*.

Known from two specimens of vague provenance, *Popelairia letitia* (Bourcier & Mulsant, 1852), has been neither observed nor collected during the 20th century. This fact alone is reason enough to question the taxonomic validity of Letitia's Coquette, as many nominal trochiline taxa of comparable rarity have proven to be hybrids (Meyer de Schauensee 1947; Graves 1996, 1997a, 1997b, 1998a). Nonetheless, the systematic status of *P. letitia* remains unchallenged (Mulsant & Verreaux 1876, Elliot 1878, Boucard 1893, Cory 1918, Simon 1921, Peters 1945, Morony et al. 1975, Sibley & Monroe 1990), although Salvin (1892) may have been the last taxonomic authority to critically examine the type specimen. The relevance of this issue was brought to the forefront by the inclusion of *P. letitia* in a recent survey of threatened avian species (Collar et al. 1992). Here I offer an appraisal of the systematic status of *P. letitia*.

Despite its current placement in the genus *Popelairia* (Peters 1945, Morony et al. 1975, Sibley & Monroe 1990), *letitia* more closely resembles *Discosura longicauda* in plumage color (Elliot 1878). Generic limits in the Trochilidae are based primarily on male plumage traits (Taylor 1909). This has resulted in a proliferation of genera ($n = 109$), more than 1/4 of which are monospe-

cific (Sibley & Monroe 1990). Zimmer (1950) advocated merging all band-rumped coquettes and thorn-tails in a single genus, *Lophornis*. Even under a narrow interpretation of generic limits, *Popelairia* would have been merged with *Discosura* if not for the racket-tipped rectrices of the latter (Elliot 1878). In that eventuality, *Popelairia* Reichenbach 1854 would become a junior synonym of *Discosura* Bonaparte 1850. In order to avoid nomenclatural confusion, however, I use the binomial, *Popelairia letitia*, throughout this paper.

Methods

The type of *Popelairia letitia* (BMNH 1888.7.25.83 in The Natural History Museum, formerly British Museum of Natural History) was obtained from John Gould, who procured it from Bourcier (Gould 1858, Warren 1966). A second specimen in the American Museum of Natural History (AMNH 38060) was part of the Daniel Giraud Elliot collection cataloged in 1888 (fide Paul Sweet). Both specimens appear to be males in definitive plumage as judged by their brilliant gorgets, crowns, elongated rectrices, and unstriated maxillary ramphothecae (Figs. 1–3). I compared them with male specimens of all species of hum-

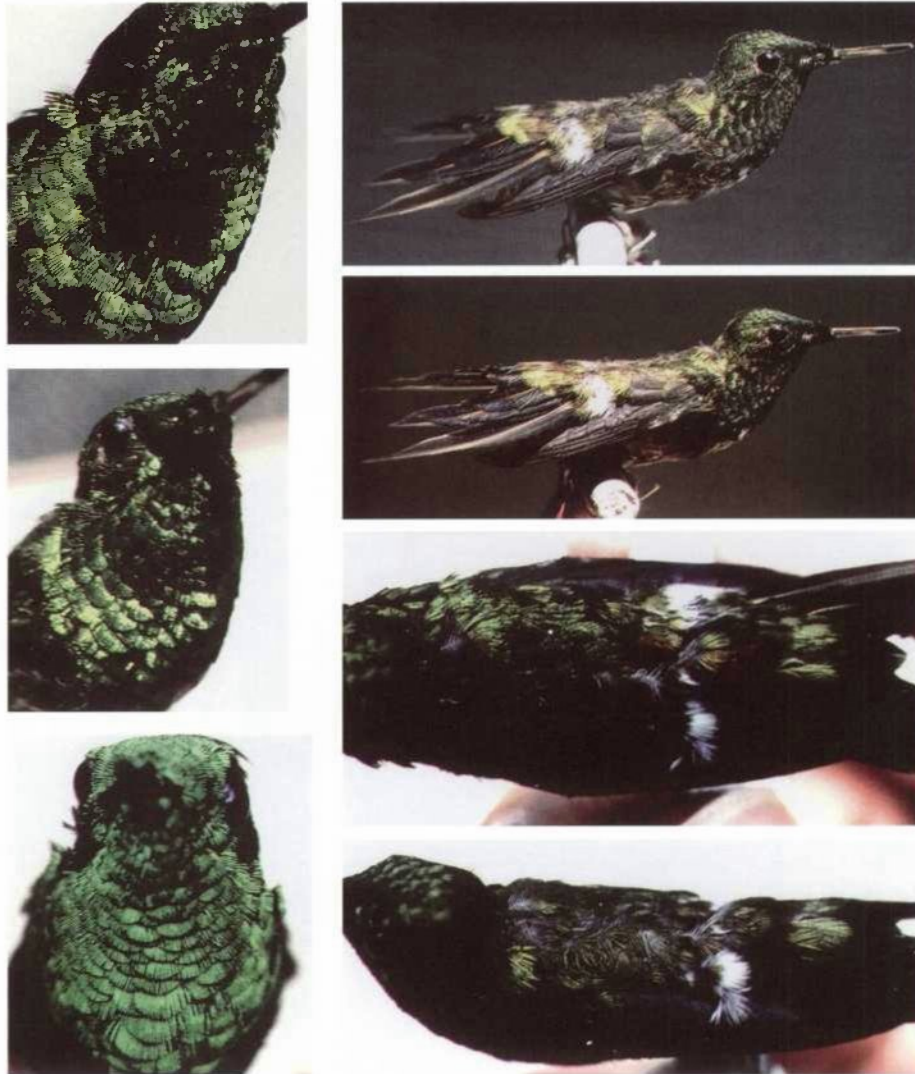


Fig. 1. Multiple exposures of the type specimen (BMNH 1888.7.25.83) of *Popelairia letitia* (Bourcier & Mulsant, 1852).

mingbirds deposited in The Natural History Museum and the American Museum of Natural History. It was not possible to compare directly the two specimens. However, I compared photographs of the AMNH specimen of *P. letitia* with the type specimen (BMNH), and vice versa. Because previous characterizations of *P. letitia* were brief and somewhat contradictory, I provide a more detailed description in Appendix 1. Measurements of wing chord, bill

length (from anterior extension of feathers), and rectrix length (from point of insertion of central rectrices to the tip of each rectrix) were made with digital calipers and rounded to the nearest 0.1 mm. Rectrices are numbered from innermost (R1) to outermost (R5) (Table 1).

I evaluated the color of the plumage (forecrown, back above white band, rump below white band, upper throat, lower side of throat, lower breast along midline) with

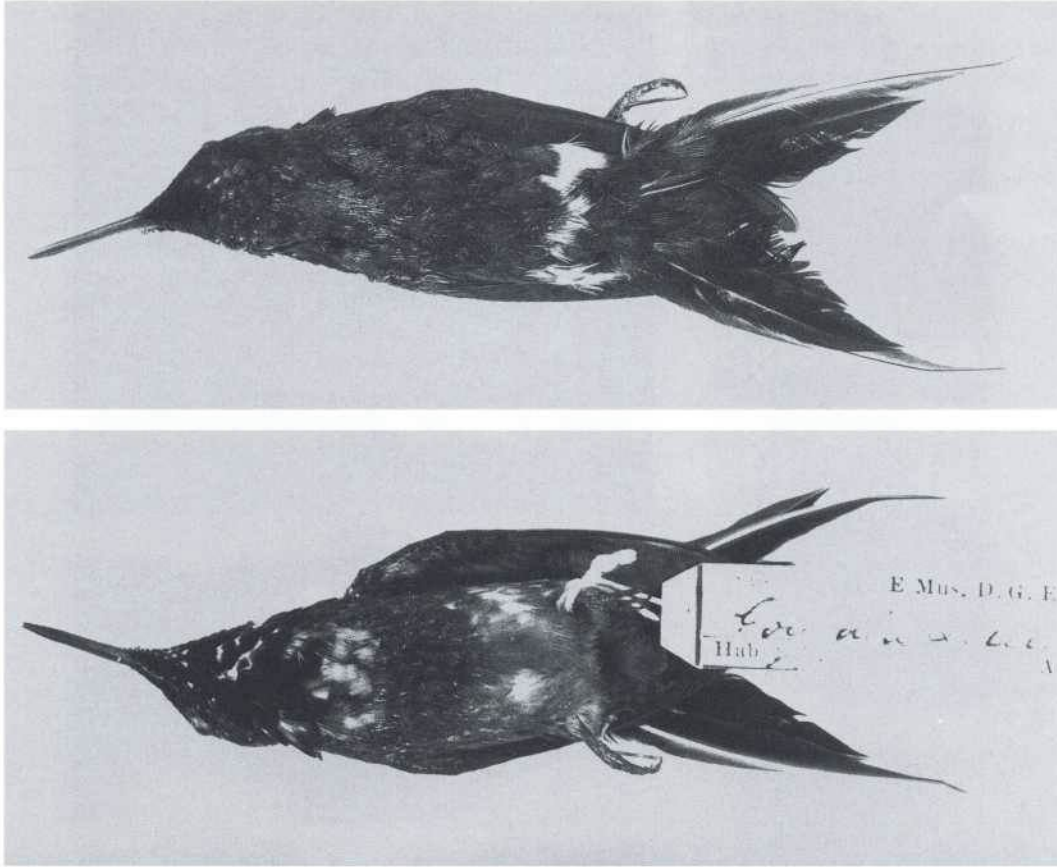


Fig. 2. Dorsal and ventral views of Elliot's specimen of *Popelairia letitia* (AMNH 38060).

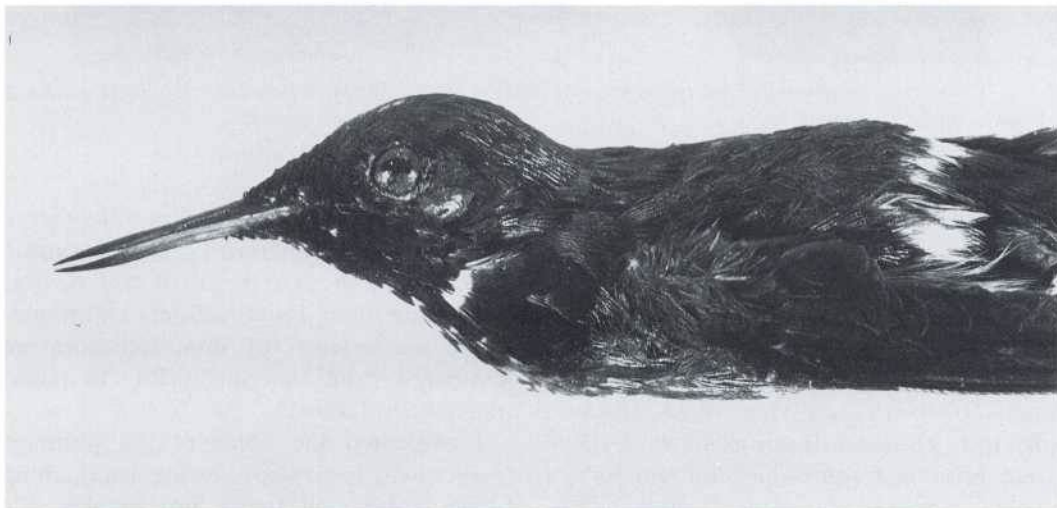


Fig. 3. Lateral view of Elliot's specimen of *Popelairia letitia* (AMNH 38060).

Table 1.—Measurements (mm) of the two known specimens of *Popelairia letitia* and male specimens of *Discosura longicauda* (range; mean \pm standard deviation) in definitive plumage.

	<i>Popelairia letitia</i>		<i>Discosura longicauda</i> <i>n</i> = 15 ^a
	BMNH 1888.7.25.83	AMNH 38060	
Wing Chord	37.8	38.0	42.1–47.5 (45.2 \pm 1.6)
Bill length	10.5	10.9	10.2–12.4 (11.4 \pm 0.6)
Rectrix 1	14.8	Missing	15.2–19.2 (16.7 \pm 0.9)
Rectrix 2	19.7	16.1	24.3–28.2 (26.0 \pm 1.1)
Rectrix 3	26.7	22.5	29.2–33.6 (32.0 \pm 1.2)
Rectrix 4	30.7	29.3	32.3–37.5 (35.0 \pm 1.4)
Rectrix 5	36.2	38.9	49.9–56.0 (52.5 \pm 2.0)

^a Bahia, Brazil (*n* = 4), Brazil (*n* = 2), "Cayenne" (*n* = 3), "British Guiana" (*n* = 1), Guyana (*n* = 4), locality unknown (*n* = 1).

^b Tip (–0.2–0.4 mm) missing.

a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CP-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 gorget feathers are acutely dependent on the angle of measurement, the curvature of the gorget surface 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 plumage surface without depressing the plumage surface. 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. Thus, each datum summarized in Table 2 represents the mean of three independent measurements, each of which represents the average of three sequential default 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 of opponent color coordinates to colors perceived by hummingbirds is unknown.

I considered four hypotheses: *Popelairia letitia* represents (1) an immature plumage of *Discosura longicauda*; (2) a geographic variant of *D. longicauda*; (3) a hybrid; or (4) a valid species. In investigating the possibility of hybridization, I considered the band-rumped coquettes and thorntails that occur in South America (i.e., *Lophornis ornatus*, *L. gouldii*, *L. magnificus*, *L. delattrei*, *L. stictolophus*, *L. chalybeus*, *L. pavoninus*, *Popelairia popelairii*, *P. langsdorfii*, *P.*

Table 2.—*L a b* opponent color coordinates for plumage characters of the two known specimens of *Popelairia letitia*: L = lightness; a/-a = red/green; b/-b = yellow/blue.

Plumage character	Color ^a	BMNH BMNH 1888.7.25.83			AMNH 38060		
		L	a	b	L	a	b
Forecrown	golden-green	19.9	-5.7	12.0	23.1	-4.0	13.3
Lower back above band	coppery-bronze	24.5	4.3	15.0	21.4	5.0	10.5
Rump below band	coppery-bronze	25.1	9.2	20.1	19.6	8.5	11.4
Upper throat	golden-green	11.6	-0.2	4.5	16.8	-3.4	8.9
Lower throat (side)	golden-green	13.9	-1.3	9.0	13.4	-0.5	6.7
Lower breast (midline)	bronze-green	25.6	2.1	15.8	22.9	3.9	10.7

^a General color observed when specimen is held in a position that yields the greatest apparent brilliance.

conversii, *Discosura longicauda*) as potential parental species (taxonomy of Sibley & Monroe 1990). Fewer than half (23 of 55) of the possible pairwise combinations of the aforementioned species actually occur in nature (i.e., species sympatric at the resolution of 1° × 1° latitude-longitude blocks). Unless otherwise noted, assessments of plumage characters refer to those of males in definitive plumage. Assumptions and methods of hybrid diagnosis follow Graves (1990) and Graves & Zusi (1990).

Results

Immature plumage or geographic variant of Discosura longicauda?—A review of plumage and mensural characters demonstrates that *Popelairia letitia* is not an immature of *Discosura longicauda*. Immature males of *D. longicauda* possess rounded rectrices (USNM 328627, AMNH 46737) that are replaced in subsequent molts by sharply attenuated (R2–R4) and racket-tipped (R5) rectrices. The outer rectrices (R4–R5) of *Popelairia letitia* are sharply attenuated and lack rackets. *P. letitia* also differs from *D. longicauda* in lacking a black chin spot, in possessing a yellowish-brown mandibular ramphotheca (black in *D. longicauda*), coppery-bronze back plumage (green in *D. longicauda*), white rump band (buff in sub-definitive plumages of *Discosura longicauda*), coppery-bronze rump (green in definitive plumages, pur-

plish-black in sub-definitive plumages of *D. longicauda*), and dull bronze-green lower breast and abdomen (spangled with iridescent golden-bronze disks in both definitive and sub-definitive plumages of *D. longicauda*). Finally, bill length is similar in *P. letitia* and *D. longicauda*, but the wing and rectrices are substantially shorter in *P. letitia* (Table 1). The qualitative differences between *P. letitia* and *D. longicauda* far exceed the magnitude of geographic variation exhibited within species of *Popelairia* and *Lophornis*, and approximate the level of morphological divergence observed among the largely allopatric rufous-crested species of *Lophornis* (Zimmer 1950).

Hybrid?—I failed to discover convincing evidence for a hybrid origin of *Popelairia letitia*. Among the pool of potential parental species, the pale mandibular ramphotheca (possibly orange in life) of *P. letitia* is shared with the rufous-crested species of *Lophornis* (*ornatus*, *gouldii*, *magnificus*, *delattrei*, *stictolophus*). These same species also exhibit varying amounts of rufous in the gorget. Because rufous pigmentation appears to be inherited in a codominant fashion in hummingbird hybrids (see Banks & Johnson 1961, Graves & Newfield 1996), I would expect *Lophornis* hybrids in definitive plumage to exhibit traces of ochraceous or rufous pigments in crown and gorget feathers. However, none were found in *P. letitia* (10× magnification). This forcefully suggests that *P. letitia* shares no im-

mediate genealogical relationship with the rufous-crested species of *Lophornis*. Likewise, I could see no manifestation of a coronal apterium (blue in life) present in *L. chalybeus* (Ruschi 1962) or the elongated and spectacularly spotted auriculars of *L. pavoninus* in either specimen of *P. letitiae*. Further, none of the pairwise species combinations drawn from the subset consisting of *Discosura longicauda* and *Popelairia* (*popelairii*, *langsдорffii*, *conversii*) could have produced the suite of characters exhibited by *P. letitiae* (e.g., pale mandibular ramphotheca, coppery-bronze rump).

Additional evidence arguing against the hybrid hypothesis is provided by feather length and shape, both of which appear to be controlled polygenically in hummingbird hybrids (Banks & Johnson 1961, Graves 1990). *Lophornis ornatus*, *L. gouldii*, *L. magnificus*, *L. delattrei*, and *L. stictolophus* possess elongated crests (>11 mm), and *L. chalybeus* and *L. gouldii* have lateral gorget feathers that exceed 15 mm in length. Crown (4.3–5.5 mm) and lateral gorget feathers (6.8–7.0 mm) of *P. letitiae* are rounded, similar in size and shape to those of *Discosura longicauda*. These data provide further grounds for excluding *Lophornis* species from the pool of potential parental species. All combinations of species drawn from the subset of thorn-tails (*Popelairia popelairii*, *P. langsдорffii*, *P. conversii*) and *Discosura longicauda* can again be eliminated from consideration because their outer rectrices are substantially longer than those of *P. letitiae*.

The two specimens of *Popelairia letitiae* are similar in size and shape (Table 1). Wing length differs by 0.5%, whereas the difference in rectrix lengths vary from 4.7% (R4) to 22.4% (R2). These values fall within the normal range of variation found among museum samples of trochiline hummingbirds (e.g., Graves 1996, 1997a, 1998c). Plumage pattern and color are nearly identical, agreeing in such minor characters as tibial feathering and undertail coverts (Table 2, Appendix 1). These obser-

vations are consistent with the hypothesis that *P. letitiae* is a valid species.

In conclusion, analysis of plumage and size characters indicates that *Popelairia letitiae* does not represent an immature plumage or geographic variant of *Discosura longicauda*, although the close resemblance of the two suggests a sister species relationship. As noted in the introduction, the very rarity of *P. letitiae* in museum collections raises the specter of hybridization. However, based on known patterns of phenotypic inheritance in trochiline hybrids (Banks & Johnson 1961; Graves 1990, 1998c, 1999; Graves & Zusi 1990) and the characteristics of phenotypic variants (e.g., Graves 1998b), the possibility that *P. letitiae* represents a hybrid seems remote. Barring discovery of contradictory data, *P. letitiae* should be regarded a valid species.

Geographic origin.—Both specimens of *Popelairia letitiae* were thought to have been collected in "Bolivia" (Bourcier & Mulsant 1852, Elliot 1878), and Remsen & T aylor (1989) suggested "northeastern Bolivia" as a possible site. The purveyor of the type specimen is unknown (Bourcier & Mulsant 1852), whereas "Verreaux" was listed as the collector of the AMNH specimen. Both are relaxed taxidermy mounts prepared in a similar style, perhaps by the Verreaux brothers, who operated a thriving import/export business in natural history specimens in Paris during the middle decades of the 19th century.

Collecting localities inscribed on labels of 19th century hummingbird specimens are frequently unreliable (Berlioz & Jouanin 1944). For example, in the same paper in which *Popelairia letitiae* was described, Bourcier & Mulsant (1852) reported the type locality of *Ramphodon dohrnii* as "la République de l'Équateur," although this species is apparently restricted to the Atlantic coastal forest of Brazil. Consequently, it would be unwise to confine a contemporary search for *P. letitiae* to Bolivia.

Common English name.—Bourcier & Mulsant (1852:144) dedicated *Popelairia*

letitiae to the "jeune enfant de M^{me} la marquise Delgallo, fille de l'un des ornithologistes les plus célèbres de l'Europe, M. Le prince Charles Bonaparte." The authors offered no common name and Gould (1858) referred to the taxon simply as "Letitia" in his Monograph of the Trochilidae. Sixty years later, Cory (1918) proposed "Letitia's Thorn-bill." The group name "thornbill" is now restricted to short-billed species in two related Andean genera, *Chalcostigma* and *Ramphomicron* (Sibley & Monroe 1990). No other common English name was used in taxonomic literature until Meyer de Schauensee (1966) coined a new name, "Coppery Thorn-tail," which has been used sporadically since then (e.g., Collar et al. 1992). Meyer de Schauensee's name was inappropriate because other species in the complex possess "coppery" plumage, and because *Popelairia letitiae* does not possess a "thorntail" on par with those of the so-called thorn-tails (*Popelairia popelairii*, *P. langsdorffii*, *P. conversii*). I recommend "coquette" as a group name for the small band-rumped species currently placed in the genera, *Lophornis*, *Popelairia*, and *Discosura* (Sibley & Monroe 1990), and the common English name, "Letitia's Coquette," for *Popelairia letitiae*.

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Appendix 1

Description of male *Popelairia leittiae* in definitive plumage based on the two known specimens (type, BMNH 1888.7.25.83; AMNH 38060). Characterization of structural colors is unusually subjective as color seen by the observer varies according to the angle of inspection and direction of light. Color descriptions were made under natural light.

Forecrown and crown (to a line drawn behind the eyes) are brilliant golden-green. The crown color blends smoothly into dark bronze-green on the hind-neck and back. Crown feathers are of moderate length (4.3-5.5 mm long) and rounded. The mantle emits a coppery-bronze iridescence when viewed in direct light. Wing coverts are the same color as back plumage. A narrow white band crosses the lower back. Band feathers are gray, broadly tipped with silky white barbs (especially apparent at the sides). The white band is bordered posteriorly by a coppery-bronze (coppery-purple or coppery-red at some angles) rump, which in turn is bordered by bronze-green uppertail coverts.

The chin to upper breast is brilliant golden-green (about the same as crown; see Table 2), with coppery-gold reflections at the sides of the throat (when viewed head-on). Iridescent terminal disks are bordered proximally by a narrow subterminal bronze-green zone, a broader band of dull white (obscured by imbricated feather tips), and finally by gray basal barbs. Obscured portions of gorget feathers become progressively gray-

er toward the sides of the throat; the outer vane of lateral gorget feathers is gray below the iridescent disk. Lateral gorget feathers are of moderate length (6.8–7.0 mm), the iridescent disks are slightly wider (~2.8–3.1 mm) than long (~2.3–2.4 mm). Green terminal disks are reduced or absent along the posterior border of the gorget, producing a mottled green and white pectoral band. The breast below the pectoral band is bronze-green along the midline. This area is burnished with coppery-gold (AMNH specimen) and a few spangles of coppery-red immediately below the pectoral band. Feathers of the lower belly and sides are broadly tipped with buffy-white and grayish-white barbs. Vent feathers are dark gray, tipped with white. The undertail coverts are dark green with gray bases and rufous tips. Tibial feathers are of moderate length (reaching about half way to the base of the hallux), dark gray, tipped with a mixture of white and cinnamonaceous barbs.

The outermost rectrix (R5) is brownish-black with a bluish sheen on the medial vane. A pale stripe bordering the rachis becomes wider and buffier near the base of the shaft. Dorsal rachis color is pale cinnamonaceous, becoming browner distally. The inner rec-

trices (R2–R4) are similar in color and pattern. The outer vanes of R4 & R3 in the AMNH specimen are faintly glossed with bronzy-green. Both vanes of R2 in the AMNH specimen are glossed with bronze-green (less pronounced in the type). There is a small V-shaped buffy spot at the tip of R2 in both specimens. The innermost pair of rectrices is absent in the AMNH specimen. Those of the BMNH specimen are bronze-green, broadly tipped with black, and faintly marked with terminal V-shaped cinnamonaceous spot. From below, the medial vanes are bluish-black (R3–R5); the rachises are white, becoming very pale buffy-white proximally. The remiges, which lack emarginations or markedly thickened rachises, are black with faint purple and bronze glossing under strong light.

The maxillary ramphotheca is black becoming dark brown at the nares. The nares are completely obscured by adpressed feathers. The mandibular ramphotheca is brownish-yellow (slightly darker in the type) becoming dark brown about half way to the bill tip. Scutes of toes and tarsometatarsus are medium brown—less heavily melanized than in *Popelairia langsdorffi* or *Discosura longicauda*.