

**Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 15. A new intergeneric hybrid (*Hylocharis leucotis* × *Selasphorus platycercus*) from the Huachuca Mountains, southeastern Arizona**

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*Abstract.*—A hummingbird specimen collected by W. W. Brown in 1917 in the Huachuca Mountains, southeastern Arizona, is a hybrid of *Hylocharis leucotis* (white-eared hummingbird) × *Selasphorus platycercus* (broad-tailed hummingbird). Brown's specimen, which exhibits a blended mosaic of plumage characters of the presumed parental species, represents the first known instance of hybridization between species currently placed in *Hylocharis* and *Selasphorus*.

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Ongoing analyses suggest that all sympatric species belonging to the “bee” group of hummingbirds occasionally hybridize with one another (Banks & Johnson 1961, Short & Phillips 1966, Lynch & Ames 1970, Wells et al. 1978, Stiles 1983, Graves & Newfield 1996, Graves 1997, 2003, 2006). In contrast, only a single instance of hybridization between a bee hummingbird (sensu Bleiweiss et al. 1997, Altshuler et al. 2004) and a species from another species group has been previously documented (Graves 1999a). Here, I provide a comprehensive assessment of an undescribed hybrid of *Hylocharis leucotis* (emerald group; J. McGuire, pers. com.) × *Selasphorus platycercus* (bee group), employing the methods and assumptions outlined in Graves (1990) as modified by subsequent papers (Graves & Zusi 1990, Graves 1998, 1999b).

#### Materials and Methods

The specimen in question was collected by W. W. Brown on 21 Jun 1917, in the Huachuca Mountains, Cochise County, southeastern Arizona. Originally part of

the L. C. Sanford Collection, the specimen is now cataloged in the American Museum of Natural History (AMNH 754805) as *Hylocharis leucotis*. The possibility that Brown's specimen represents a hybrid of *Hylocharis leucotis* × *Selasphorus platycercus* was noted briefly in Howell's (Howell 2002) photographic guide to hummingbirds. I subjected the specimen to an analytical procedure termed the hybrid diagnosis (Graves 1990), which focuses on the identification and characterization of apomorphic character states in putative hybrids. Complete dominance and polygenic inheritance of plumage characters may obscure the expression of parental apomorphies in hybrids. When parental apomorphies cannot be identified, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of plesiomorphic characters (Graves 1990, Graves & Zusi 1990, Graves 1998, 1999b).

Brown's specimen was sexed as ♂ on the Sanford Collection label and appears to be an adult male in definitive plumage as judged by its smooth maxillary ramphotheca, the presence of a large irides-

Table 1.—Ranges (mean  $\pm$  one standard deviation) of measurements (mm) of adult male *Hylocharis leucotis*, *Selasphorus platycercus*, and a probable hybrid (*Hylocharis leucotis*  $\times$  *Selasphorus platycercus*; AMNH No. 754805).

Character	<i>Hylocharis leucotis</i> (n = 10)	<i>Selasphorus platycercus</i> (n = 15)	Hybrid
Wing chord	55.3–58.1 (56.6 $\pm$ 0.9)	47.7–50.7 (49.4 $\pm$ 0.8)	52.5
Bill length	16.4–17.9 (17.2 $\pm$ 0.5)	15.1–18.0 (16.3 $\pm$ 0.7)	16.6
Rectrix 1 length	30.5–34.1 (32.3 $\pm$ 1.4)	30.5–32.2 (31.4 $\pm$ 0.6)	30.1
Rectrix 2 length	31.2–34.8 (33.0 $\pm$ 1.2)	31.4–33.4 (32.3 $\pm$ 0.6)	32.3
Rectrix 3 length	32.2–36.4 (33.9 $\pm$ 1.4)	32.1–34.1 (32.9 $\pm$ 0.5)	34.2
Rectrix 4 length	32.0–37.2 (34.5 $\pm$ 1.4)	31.5–34.1 (32.6 $\pm$ 0.9)	34.3
Rectrix 5 length	31.9–37.0 (34.4 $\pm$ 1.8)	29.8–33.2 (31.2 $\pm$ 1.1)	33.8

cent gorget, and the absence of tail spots. Consequently, description and discussion in this paper refer to definitive male plumage. Given the migratory behavior of hummingbirds in western North America, Brown's specimen could have been hatched at some distant location (e.g., California or Chihuahua, Mexico). Thus, I compared the specimen with a series of all trochiline species (National Museum of Natural History, Smithsonian Institution) which regularly breed in California, Arizona, northern Chihuahua, and Sonora: *Calypte anna* (Anna's hummingbird), *C. costae* (Costa's hummingbird), *Selasphorus platycercus*, *S. rufus* (rufous hummingbird), *S. sasin* (Allen's hummingbird), *Stellula calliope* (calliope hummingbird), *Archilochus alexandri* (black-chinned hummingbird), *Calothorax lucifer* (Lucifer hummingbird), *Helimaster constantii* (plain-capped starthroat), *Eugenes fulgens* (magnificent hummingbird), *Lampornis clemenciae* (blue-throated hummingbird), *Amazilia beryllina* (berylline hummingbird), *A. violiceps* (violet-crowned hummingbird), *Hylocharis leucotis* (white-eared hummingbird), and *Cynanthus latirostris* (broad-billed hummingbird) (Friedmann et al. 1950, Howell & Webb 1995, Russell & Monson 1998).

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).

Rectrices (R1–R5) and primaries (P1–P10) are numbered from the innermost to the outermost. Scatterplots of measurements were used to illustrate size differences among specimens. General color descriptions presented in Appendix 1 were made under natural light.

#### Results and Discussion

I considered three hypotheses—the Brown specimen represents (i) a color morph or subadult plumage of *Hylocharis leucotis*, (ii) an undescribed species, or (iii) a hybrid. The first hypothesis can be rejected because the external measurements of the specimen are substantially different from those of subadult and adult males of *H. leucotis* (Table 1). The second hypothesis seems highly improbable although several putative trochiline species are known from one or two specimens (Graves & Olson 1987, Graves 1993, 1999c). Evidence presented below suggests that Brown's specimen represents an intergeneric hybrid of *Hylocharis leucotis*  $\times$  *Selasphorus platycercus*. Consequently, I refer to the specimen as a hybrid in the remainder of the paper.

Several plumage characters of the hybrid facilitated the identification of its parental species: (a) emarginated inner vane of P10; (b) brilliant gorget; (c) yellowish mandibular ramphotheca (red or orange-red in life); (d) unmarked rectrices; (e) prominent white postocular stripe; and (f) the absence of rufous



Fig. 1. Lateral views of adult males: *Selasphorus platycercus* (top), a probable hybrid (middle), *Hylocharis leucotis* × *Selasphorus platycercus* (AMNH No. 754805), and *Hylocharis leucotis* (bottom).

pigmentation on the head or flanks (Figs. 1–2; Appendix). Three of the potential parental species (*Selasphorus platycercus*, *S. rufus*, *S. sasin*) exhibit an emarginated outermost primary (P10).

This trio may be quickly reduced to a single possibility by focusing on the absence of rufous or buff pigmentation on the head, back, or flanks of the hybrid. Because brown and reddish-brown pigments appear to exhibit consistent penetrance in the body plumage of hummingbird hybrids (Banks & Johnson 1961, Graves & Newfield 1996), *Selasphorus rufus* and *S. sasin* can be eliminated from further consideration. Plumage characters thus suggest that the hybrid represents the offspring of *Selasphorus platycercus* and a second species with a red or orange-red mandibular ramphotheca.

Three potential parental species possess a red or reddish-orange bill (dull yellow in specimens) tipped with black: *Amazilia violiceps*; *Hylocharis leucotis*; and *Cynanthus latirostris*. A fourth species, *A. beryllina*, has reddish-orange at the base of the mandibular ramphotheca. This species can be quickly discarded from

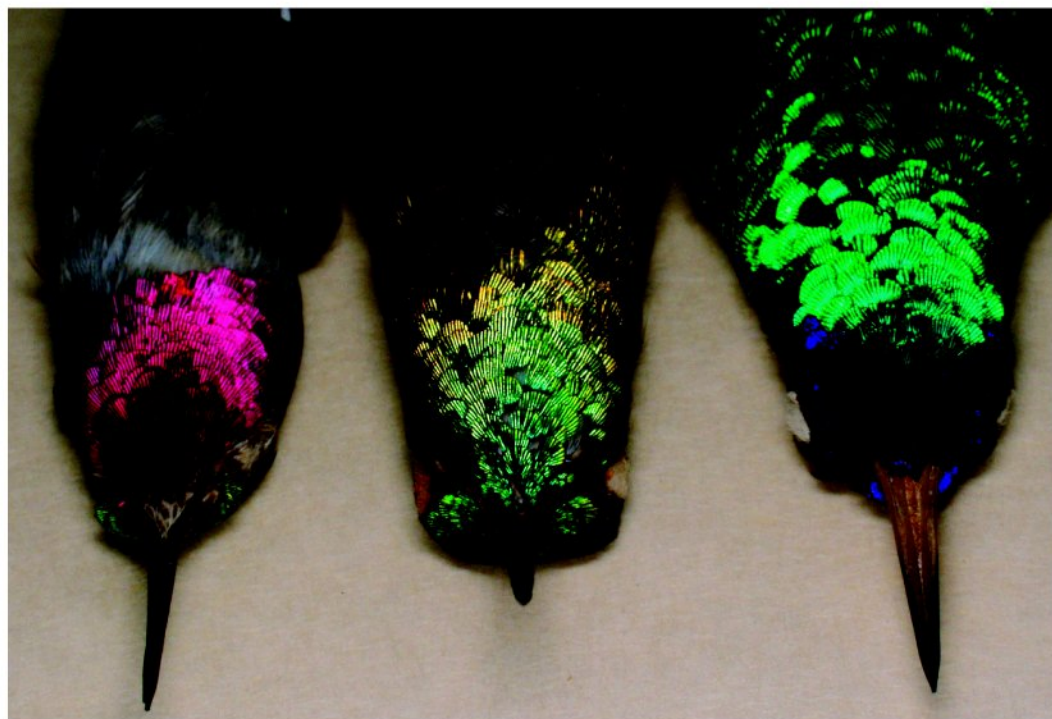


Fig. 2. Ventral iridescence of adult males: *Selasphorus platycercus* (left), a probable hybrid (middle), *Hylocharis leucotis* × *Selasphorus platycercus* (AMNH No. 754805), and *Hylocharis leucotis* (right).

consideration because it exhibits a prominent wing stripe formed by the rufous basal portions of the primaries and secondaries. No such pattern is evident in the wings of the hybrid. The hybrid also lacks tangible evidence of the violet crown and postocular region of *A. violiceps* or the gray-tipped, bluish-black retrices (P1) of *C. latirostris*. These observations and a number of other plumage details indicate that *A. beryllina*, *A. violiceps*, and *C. latirostris* were not involved in this hybridization event. On the other hand, plumage pattern and color of the hybrid are entirely consistent with the hypothesis that *H. leucotis* is the second parental species (see Appendix). In particular, the thick white postocular stripe in the hybrid resembles that of *H. leucotis*.

I tested this parental hypothesis with an examination of size and external proportions (Table 1). External measurements of trochiline hybrids invariably fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (Banks & Johnson 1961, Buckley 1982, Graves 1990, Graves & Zusi 1990, Graves 1996). Measurements of the hybrid fall within the cumulative range of parental measurements (Table 1, Fig. 3), with the exception of the innermost rectrix (R1). Because the postulated parental species are relatively similar in size, this observation provides a robust confirmation of the conclusions drawn from the emarginated primary (P10) and plumage and bill color of the hybrid. In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that Brown's specimen represents a hybrid between *Hylocharis leucotis* and *Selasphorus platycercus*. As such, it is the first intergeneric hybrid between species currently placed in *Hylocharis* and *Selasphorus*, and only the second instance of

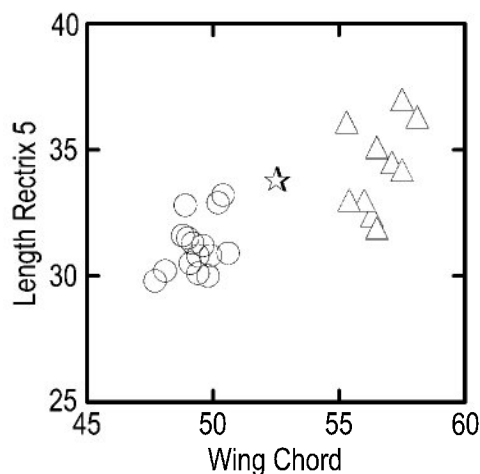


Fig. 3. Bivariate relationships of measurements (mm) of *Hylocharis leucotis* ( $\Delta$ ); *Selasphorus platycercus* ( $\circ$ ), and probable hybrid (star), *Hylocharis leucotis*  $\times$  *Selasphorus platycercus* (AMNH No. 754805).

hybridization between species in the "bee" group of hummingbirds and those belonging to the "emerald" group.

Both *Hylocharis leucotis* and *Selasphorus platycercus* are known to occur during the breeding season at higher elevations in the Huachuca Mountains and neighboring ranges in southeastern Arizona (Swarth 1904, Phillips et al. 1964) and throughout the Cordillera Occidental of Mexico (Friedmann et al. 1950, Howell & Webb 1995, Russell & Monson 1998). Little is known about Brown's field itinerary, and he failed to indicate exactly where, or at what elevation, he collected the hybrid in the Huachuca Mountains. Besides the hybrid, the list of specimens collected by Brown on 21 June 1917 included *Hylocharis leucotis* (AMNH 754804), *Selasphorus platycercus*, *Pyrocephalus rubinus* (vermillion flycatcher), and *Eremophila alpestris* (horned lark). This eclectic combination of species indicates that Brown collected not only in one of the mesic montane canyons where hummingbirds occur but also in arid grasslands where he would have obtained the larks.

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## Literature Cited

- Altshuler, D. L., R. Dudley, & J. A. McGuire. 2004. Resolution of a paradox: Hummingbird flight at high elevation does not come without a cost.—*Proceedings of the National Academy of Sciences U.S.A.* 101:17731–17736.
- 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.
- Buckley, P. A. 1982. Avian genetics. Pp. 21–110 in M. Petrak, ed., *Diseases of cage and aviary birds*. 2nd ed. Lea and Febiger, Philadelphia.
- Friedmann, H., L. Griscom, & R. T. Moore. 1950. Distributional check-list of the birds of Mexico. Part 1.—*Pacific Coast Avifauna* 29:1–202.
- Graves, G. R. 1990. Systematics of the “green-throated sunangels” (Aves: Trochilidae): valid taxa or hybrids?—*Proceedings of the Biological Society of Washington* 103:6–25.
- . 1993. Relic of a lost world: a new species of sunangel (Trochilidae: *Heliangelus*) from “Bogota.”—*Auk* 110:1–8.
- . 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, *Aglaiocercus kingi* × *Metallura tyrrianthina*, from Venezuela.—*Proceedings of the Biological Society of Washington* 111:511–520.
- . 1999a. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 7. Probable parentage of *Calliphlox iridescens* Gould 1860.—*Proceedings of the Biological Society of Washington* 112:443–450.
- . 1999b. 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.
- . 1999c. Taxonomic notes on hummingbirds (Aves: Trochilidae). 2. *Popelairia letitia* (Bourcier & Mulsant, 1852) is a valid species.—*Proceedings of the Biological Society of Washington* 112:804–812.
- . 2003. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 11. Documentation of an intergeneric woodstar hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant*.—*Proceedings of the Biological Society of Washington* 116:820–826.
- . 2006. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 14. New perspectives on Sefton's specimen (*Calypte costae* × *Selasphorus platycercus*) from the Rincon Mountains, southeastern Arizona.—*Proceedings of the Biological Society of Washington* 119:516–521.
- , & N. L. Newfield. 1996. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 1. Characterization of *Calypte ama* × *Stellula calliope* and the possible effects of egg volume on hybridization potential.—*Proceedings of the Biological Society of Washington* 109:755–763.
- , & S. L. Olson. 1987. *Chlorostilbon bracei* Lawrence, an extinct species of hummingbird from New Providence Island, Bahamas.—*Auk* 104:296–302.
- , & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.—*Condor* 92:754–760.
- Howell, S. N. G. 2002. *Hummingbirds of North America: The Photographic Guide*. Academic Press, San Diego, 219 pp.
- , & S. Webb. 1995. *The Birds of Mexico and Northern Central America*. Oxford University Press, Oxford, UK, 851 pp.
- Lynch, J. F., & P. L. Ames. 1970. A new hybrid hummingbird, *Archilochus alexandri* × *Selasphorus sasin*.—*Condor* 72:209–212.

- Phillips, A., J. Marshall, & G. Monson. 1964. *The Birds of Arizona*. University of Arizona Press, Tucson, 212 pp.
- Russell, S. M., & G. Monson. 1998. *The Birds of Sonora*. University of Arizona, Tucson, 360 pp.
- Short, L. L. J., & A. R. Phillips. 1966. More hybrid hummingbirds from the United States.—*Auk* 83:253–265.
- Stiles, F. G. 1983. Systematics of the southern forms of *Selasphorus* (Trochilidae).—*Auk* 100:311–325.
- Swarth, H. S. 1904. Birds of the Huachuca Mountains, Arizona.—*Pacific Coast Avifauna* 4:1–70.
- Wells, S., R. A. Bradley, & L. F. Baptista. 1978. Hybridization in *Calypte* hummingbirds.—*Auk* 95:537–549.

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#### Appendix 1

Comparative description of male *Hylocharis leucotis*, *Selasphorus platycercus*, and a probable hybrid, *Hylocharis leucotis* × *Selasphorus platycercus* (AMNH No. 754805). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

The forecrown, loreal region, and crown of *leucotis* are black or bluish-black in diffuse light, becoming dark bronze on the hindneck, and then dark bronzy-green on the back and scapulars. The uppertail coverts are bronzy-green narrowly margined with rufous. When viewed head-on under direct light, the frontlet, forecrown, loreal region, and upper throat exhibit a glowing deep purple iridescence. A thick white stripe extends from the posterior margin of the eye down the side of the neck around the black auriculars.

The forecrown, crown, hindneck, back, and rump of *platycercus* are green to golden-green with turquoise highlights, depending on the angle of inspection. When viewed head-on under direct light, crown feathers, and to a lesser extent, back feathers, exhibit glittering golden-green iridescence. The loreal streak is pale grayish-white flecked with green or brownish feather barbules.

The dorsal plumage of the hybrid combines features of *leucotis* and *platycercus*. The coronal region is dark dusky green and only faintly iridescent when viewed in diffuse light; crown feathers are margined with grayish-buff. The frontlet and forecrown, however, exhibit brilliant golden-green iridescence when viewed head-on under direct

light. Under diffuse light the remainder of the dorsal plumage is brighter than the crown, ranging from dark bluish-green on the hindneck to golden-green or bronzy-green on the back and uppertail coverts. Several of the uppertail coverts are narrowly margined with buff. Overall, the dorsal iridescence of the hybrid is brighter green, less bronzy than in *leucotis*, but duller than in *platycercus*. Although the hybrid lacks a faint loreal or supraocular stripe as in *platycercus*, it does possess a conspicuous white postocular stripe similar to that of *leucotis*.

The chin and upper throat of *leucotis*, when viewed head-on, emit a glowing deep purple iridescence that is bordered posteriorly by a contrasting band of brilliant iridescent green extending across the lower throat. The brilliant green of the lower throat blends smoothly into a less intense golden-green iridescence on the upper breast. Strongly iridescent terminal discs, however, are restricted to the throat. The lower breast, sides, flanks, and abdomen are green. Feathers from the sides and flanks are narrowly margined with pale grayish-buff whereas abdominal feathers, particularly those along the midline, are broadly margined with grayish-buff. Vent feathers are white. The undertail coverts of *leucotis* are pale bronzy-green to grayish-green broadly margined with pale buff or grayish-white.

In *platycercus*, gorget feathers are broadly tipped with brilliant rose-red discs. Lateral gorget feathers are more elongated (~8–9 mm) than in *leucotis*. Plumage immediately posterior to the gorget is grayish-white. The lower breast, sides, flanks, and abdomen are grayish-green with scattered gray and buff barb tips, particularly along the flanks. The undertail coverts are pale bronzy-green or grayish-green broadly margined with white or pale gray.

The ventral plumage of the hybrid combines elements of both parental species. The hybrid's gorget (similar in shape to that of *platycercus*) exhibits a brilliant golden-green iridescence when viewed head-on under direct light. Iridescent turquoise highlights become progressively less intense and coppery highlights more intense toward the posterior margin of the gorget. Some white feather barbules are visible on the chin, similar to the typical condition in *platycercus*. The longest lateral gorget feathers are ~7.0 mm whereas the brilliant terminal discs average ~2.9 × 2.9 mm. The basal two-thirds of the chin and upper throat feathers are white or grayish-white; a narrow transitional band of gray occurs between the white feather base and terminal iridescent disc. The concealed feather bases along the lateral and posterior margins of the gorget are darker. Overall, the degree of melanization of the basal portions of the hybrid's gorget feathers is intermediate between that observed in *leucotis* (darker) and *platycercus* (paler). The remainder of the hybrid's under parts is similar to that of *leucotis*,

but paler, particularly along the posterior margin of the gorget and along the midline.

The rectrices of *leucotis* and *platycercus* differ significantly in shape and are fairly dissimilar in color. In *leucotis*, the central rectrix (R1) is bronze to greenish-bronze whereas the other rectrices (R2–R5) are dark purplish-brown, nearly black, with bronzy or coppery iridescence on the outer vane (especially on R2). All rectrices are relatively broad with rounded tips.

In *platycercus*, the innermost rectrix (R1) is iridescent bluish-green. The remaining rectrices (R2–R5) are dark purplish-brown, nearly black. The outer vane of R2 is narrowly margined with rufous, with lesser amounts of rufous or buff along the margins of the outer vanes of R1 and R3. The inner vanes of all rectrices are narrowly margined with rufous or buff. The tip of R1, and to a lesser extent of R2 and R3, is emarginated.

The shape and pigmentation of the hybrid's rectrices are intermediate between those of *leucotis* and *platycercus*. The innermost rectrix (R1) is green whereas the outermost rectrices (R2–R5) are dark purplish-brown, nearly black. The outer vane of R2 is flushed with bronzy-green iridescence whereas the

outer vane of R3 exhibits faint bronzy-green iridescence and the tips of R4 and R5 emit faint bronzy-green iridescence. However, I detected no evidence of rufous or buff pigmentation on the inner or outer margins of any of the rectrices that might be expected if *platycercus* was the parent (Banks & Johnson 1961, Graves 2006). Rectrix shape in the hybrid is roughly intermediate between that of *leucotis* and *platycercus* but none of the rectrices exhibit emarginated tips as in *platycercus*.

Wing color in *leucotis*, *platycercus*, and the hybrid is similar. The two outer primaries in *platycercus* (P9 and P10) have emarginated inner vanes whereas the primaries of *leucotis* are unmodified. The outermost primary (P10) of the hybrid has a distinctly emarginated inner vane. The maxillary and mandibular ramphothecas of *leucotis* are red or reddish-orange (dull yellow in specimens) tipped with blackish-brown. The nasal operculum in *leucotis* is bare. The bill is black in *platycercus* and feathers extend anteriorly to cover the nasal operculum. The pattern of pigmentation and feathering at the base of the bill in the hybrid is intermediate to that observed in adult male specimens of *leucotis* and *platycercus*.