

## GEOGRAPHIC AND AGE-RELATED VARIATION IN THE VIOLET-THROATED SUNANGEL (*HELIANGELUS VIOLA*, TROCHILIDAE): EVIDENCE FOR A NEW SPECIES AND SUBSPECIES

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**Resumen.** – Variación geográfica y relacionada con la edad en la Colibrí Violeta (*Heliangelus viola*, Trochilidae): evidencia para una nueva especie y subespecie. – El Colibrí Violeta (*Heliangelus viola* Gould, 1853) es una especie de trochilido Andina con rango de distribución desde el centro de Ecuador hasta el norte de Perú. Este artículo presenta una revisión de su variación geográfica y de grupos de edades, tras la comparación de inmaduros, subadultos y adultos de los especímenes de estudio con base en su taxonomía. Aunque *H. viola* es actualmente considerada como una especie monotípica, evidencia basada en patrones morfológicos y rangos de distribución sugiere que realmente se trata de un taxón complejo politípica. Como consecuencia taxonómica, la población de Ecuador y el noroeste de Perú es descrita como *H. splendidus* spec. nov. y comprende a *H. s. splendidus* (norte del Perú) y a *H. s. pyropus* subspec. nov. (desde Ecuador hasta el noroeste de Perú), mientras que *H. viola* está principalmente confinada a los Andes del noreste de Perú. Adicionalmente, dos especímenes de *H. splendidus* spec. nov. dan indicación de una simpatria parcial con *H. viola* al noreste de Perú. Aparte de las consideraciones referidas a la distribución y en referencia a los límites de la definición de especie para *Heliangelus*, el grupo de caracteres discriminantes califica estos taxones como especies distintas.

**Abstract.** – The Violet-throated Sunangel (*Heliangelus viola* Gould, 1853) is an Andean trochilid species ranging from central Ecuador to northern Peru. This paper reviews its geographic and age-related variation comparing immature, subadult, and adult stages of study specimens, and discusses the taxonomic status. Although *H. viola* is currently considered as monotypic, evidence from morphology and distribution suggests a polytypic taxon complex. As a taxonomical consequence, the populations from Ecuador and northwestern Peru are described as *H. splendidus* spec. nov. comprising *H. s. splendidus* (northern Peru) and *H. s. pyropus* subspec. nov. (Ecuador to northwestern Peru), while *H. viola* is mainly confined to the Andes of northeastern Peru. In addition, two specimens of *H. splendidus* spec. nov. indicate partial sympatry with *H. viola* in northeastern Peru. Apart from distributional considerations and with regard to the species limits in *Heliangelus*, the set of discriminating characters qualifies these taxa as distinct species. Accepted 2 December 2011.

**Key words:** Violet-throated Sunangel, *Heliangelus viola*, *Heliangelus splendidus* spec. nov., *Heliangelus splendidus splendidus* subspec. nov., *Heliangelus splendidus pyropus* subspec. nov., Trochilidae, Andes, Ecuador, Peru, taxonomy.

### INTRODUCTION

Owing to particular oreographical and climatological conditions, the Andes of southern Ecuador and northern Peru are major centres

of biodiversity and endemism for the South American avifauna (Chapman 1926, Parker *et al.* 1985, Johnson & Jones 2001, Ridgely & Greenfield 2001). Not surprisingly, hummingbirds (Trochilidae) are among the taxa with

the highest rate of radiation and endemism, showing a remarkable radiation throughout the South American cordilleras (Bleiweiss 1998, Schuchmann 1999, Rahbek & Graves 2000). Royal Sunangel *Helianthus regalis* (Fitzpatrick *et al.* 1979; new subspecies: Graves *et al.* 2011), Neblina Metaltail *Metallura odomae* (Graves 1980), and Pinche Puffleg *Eriocnemis isabellae* (Cortés-Diago *et al.* 2007) are prominent examples of trochilids recently described from the northern Andes.

With a total of nine currently recognized species (Schuchmann 1999, Ridgely & Greenfield 2001), the sunangels *Helianthus* form the second largest Andean trochilid genus, distributed throughout the northern and central Andes. Among the monotypic members of this taxon, the Violet-throated Sunangel (*Helianthus viola*) has been described ranging in the subtropical and temperate zone from central Ecuador to northern Peru. However, as a result of biogeographic surveys of several high-Andean trochilid clades including *Helianthus* (see Weller 2009), I became aware of previously unrecognized geographic, sexual, and age-related plumage variation in the Violet-throated Sunangel. This paper focuses on distributional data and external morphological characters derived from study specimens of different age stages, suggesting that the current taxonomy cannot be maintained in view of the distinctive morphological and biogeographic patterns found in this taxon.

## METHODS

A total of 116 specimens of the Violet-throated Sunangel housed in major ornithological collections was examined (for acronyms, see Acknowledgments) for morphology and biometrics using methods already applied in previous studies (cf. Weller 2009). Colors visible to the naked eye were described according to Smithe (1975). Mensural traits (bill length: from tip to nostril; wings in

unflattened position; rectrices 1 and 5) were measured with a digital calliper to the nearest 0.1 mm. Immature birds were generally excluded from statistical comparisons of subpopulations and from taxonomic analyses as they may show significant individual differences, i.e., in coloration, thus closely resembling the female-type plumage. However, due to significant numbers of immature specimens in collections that partly exceed those of adult ones they were included in the general comparison of biometric data (Table 1).

Localities and altitudes were either derived from specimen labels, ornithological gazetteers (Paynter 1993, Stephens & Traylor 1983), or the Alexandria Digital Library Gazetteer (formerly available under <http://fat-albert.alexandria.ucsb.edu:8827/gazetteer/>) and are listed in the Appendix.

## RESULTS

*Historical taxonomy and implications.* Like numerous other 19<sup>th</sup> century and prior species descriptions, Gould's (1853a) first description of *Helianthus viola* lacks important details required for a sufficient taxonomic treatment. Most strikingly, obviously no holotype was designated in both contributions published on this matter (Gould 1853a, b). This omission has led to the current situation in which three specimens in the bird collection of the Natural History Museum, Tring, are considered as syntypes (Warren 1966), although the specimens involved were originally labelled as "type" (BMNH no. 1853.11.28.15), "a type" (unreg.), and "co-type" (1853.11.28.16). Further taxonomic uncertainty results from the fact that Gould did not provide detailed locality data. Instead, the collecting site was given as the "Banks of the Marañon," where the specimens were obviously taken by Warszewicz. The specimen no. 1853.11.28.16 is labelled with an additional, question-marked note "(W side Marañon?)," while another skin

TABLE 1. Mensural traits of *Heliangelus splendidus* spec. nov. and *H. viola*; given are mean  $\pm$  SD, range, and number of examined specimens (in parentheses).

Taxon/sex/age	Bill length	Wing length	Rectrix 1 length	Rectrix 5 length
<i>H. splendidus pyropus</i> ssp. nov.				
Males				
Adult	18.31 $\pm$ 0.54	66.23 $\pm$ 1.34	29.83 $\pm$ 1.14	60.68 $\pm$ 2.28
	17.2–19.5 (50)	63.0–69.4 (46)	27.8–32.5 (46)	57.0–66.3 (40)
Imm.	18.08 $\pm$ 0.35	65.87 $\pm$ 1.18	31.08 $\pm$ 2.09	56.80 $\pm$ 1.03
	17.7–18.6 (6)	63.7–67.0 (6)	27.0–32.5 (6)	55.0–57.7 (6)
Females				
Adult	17.92 $\pm$ 0.68	60.62 $\pm$ 0.97	28.16 $\pm$ 0.83	49.81 $\pm$ 1.38
	16.7–18.8 (9)	59.4–61.9 (9)	26.5–29.1 (8)	47.1–51.5 (7)
Imm.	18.45 $\pm$ 0.53	59.11 $\pm$ 1.21	29.27 $\pm$ 1.72	49.30 $\pm$ 2.61
	17.3–19.3 (18)	56.9–61.0 (18)	26.1–31.5 (16)	43.3–52.6 (15)
<i>H. s. splendidus</i> sp. nov.				
Males				
Adult	18.45 $\pm$ 0.57	66.85 $\pm$ 1.19	29.78 $\pm$ 0.86	60.15 $\pm$ 1.20
	17.6–19.6 (13)	64.7–69.1 (12)	28.5–31.6 (13)	58.3 $\pm$ 63.0 (12)
Imm.	18.30 $\pm$ 0.52	65.62 $\pm$ 2.15	30.96 $\pm$ 1.21	59.07 $\pm$ 2.48
	17.7–18.9 (5)	63.0–67.8 (5)	29.9–32.9 (5)	56.4–61.3 (3)
Females				
Adult	18.60 $\pm$ 0.67	60.51 $\pm$ 1.19	28.70 $\pm$ 1.56	49.61 $\pm$ 2.55
	18.0–19.8 (7)	59.1–62.4 (7)	27.1–31.4 (7)	44.9–52.2 (7)
Imm.	18.58 $\pm$ 0.74	60.40 $\pm$ 0.74	28.70 $\pm$ 0.89	50.04 $\pm$ 2.65
	17.7–19.4 (4)	59.1–60.9 (5)	27.6–29.7 (5)	47.7–54.4 (5)
<i>H. viola</i>				
Males				
Adult	18.42 $\pm$ 0.47	65.50 $\pm$ 1.53	29.95 $\pm$ 1.30	55.25 $\pm$ 2.28
	17.7–19.1 (13)	63.1–68.2 (12)	28.6–33.0 (13)	51.0–58.7 (13)
Imm.	18.1, 18.5 (2)	65.1, 67.2 (2)	32.2, 32.3 (2)	55.4, 56.7 (2)
Females				
Adult	18.43 $\pm$ 0.29	59.70 $\pm$ 1.14	27.60 $\pm$ 0.72	47.03 $\pm$ 1.50
	18.1–18.6 (3)	58.9–61.0 (3)	27.0–28.4 (3)	45.5–48.5 (3)
Imm.	18.68 $\pm$ 0.47	60.35 $\pm$ 1.15	28.22 $\pm$ 1.22	48.55 $\pm$ 1.40
	18.0–19.0 (4)	59.1–61.6 (4)	27.0–29.8 (4)	46.7–49.9 (4)

from the same series (1853.11.28.15) has no locality reference at all. In this context, Zimmer (1951: 30) noted that “this species nowhere reaches the actual banks of the Río Marañon,” but would be found instead around the central portion of the mountainous part of this SSE–NNW-directed valley. Based on the itinerary of the Polish collector Warszewicz, Zimmer suggested Chachapoyas, located in the eastern Andes and a known

collecting site for other specimens of the Violet-throated Sunangel (Zimmer 1951; see Appendix), as type locality.

Apart from such formal shortcomings, I found that the type series consists only of individuals in incomplete (subadult) plumage stages. Interestingly, the single male (1853.11.28.16) of this series best fits Gould’s original description, because its gorget is dull iridescent Magenta (Color 2) with some violet

reflections. However, a color plate (pl. 241) and the according text for the Violet-throated Sunangel published in “A monograph of the Trochilidae” (Gould 1853a) describe the male’s throat as deep violet (such as present in adult males, see below). The two remaining specimens of the type series are subadult females, both characterized by a less brilliant coloration than the male. According to the original description and figure, one of them (1853.11.28.15) has an entirely dark brown throat (given as dull black by the author) and thus may be the cotype rather than the other specimen, an unregistered female that exhibits additional violet-purplish spots. Despite the lack of clear evidence from the collecting data, it is nonetheless convincing to adopt Zimmer’s (1951) view that all three specimens were collected in the eastern Peruvian Andes, which is fundamentally important for further taxonomic considerations presented in the following summary.

*Plumage and geographic variation.* Variation in morphological characters of the Violet-throated Sunangel has been mostly overlooked by previous taxonomic researchers. In his studies on Peruvian birds, Zimmer (1951) gave no indication of variation between the Ecuadorian and Peruvian specimens of the AMNH series. Nevertheless, he later mentioned in reference to Bond (*in litt.*) that individual variation may occur in the southern distribution range, since Bond (1954) noted the increased violet iridescence of the throat in two males from Chira (Peru) at the ANSP collection. However, individual or geographic variation in this taxon remained unmentioned by later workers, e.g., in the more recent taxonomic treatments by Fjelds  & Krabbe (1990), Schuchmann (1999), or Ridgely & Greenfield (2001).

In contrast to the historical and modern literature, my analysis indicates that the plumage of specimens determined as the Violet-

throated Sunangel varies not only in relation to sex and age but also along a distributional gradient. First, the detection of sex-related variation is important since I found several females mislabeled as immature/subadult males. Adult males differ from females and subadults by the brilliant purplish to violet gorget and the greenish to blue-green glittering frontlet and breast (the latter duller in the gorget and breast). In addition, typical marks of subadults individuals of both sexes are cinnamon fringes in the ventral parts (i.e., belly) and broad cinnamon margins in the undertail coverts, which have narrow brownish centres instead of broad greenish ones of adults. Immatures of both sexes exhibit mostly a brownish gorget, occasionally spotted with violet feathers. Biometrically, immature and subadult males have on average shorter outer rectrices ( $r_5$ ) than adult males (Table 1). No age-related differences in mensural data were found in females. For these reasons, subadult and immature birds throughout the range were excluded both from statistical and color comparison of subpopulations.

I examined 121 specimens (79 males, 42 females) from the major international bird collections (see Acknowledgments), and was able to include specimens from nearly all parts of the range of the Violet-throated Sunangel (Fig. 1). Taking into account age- and sex-related color morphs, this study revealed geographical variation in the plumage patterns of three different populations. Given the amount of variation and the distributional ranges, there is strong evidence that these differences refer both to the subspecies and species level. Most discriminating characters are present both in males and females, but particularly females of northern representatives differ strikingly from those of *H. viola* in their throat pattern. Therefore, the populations from Ecuador and northwestern Peru should be recognized as a new taxon,

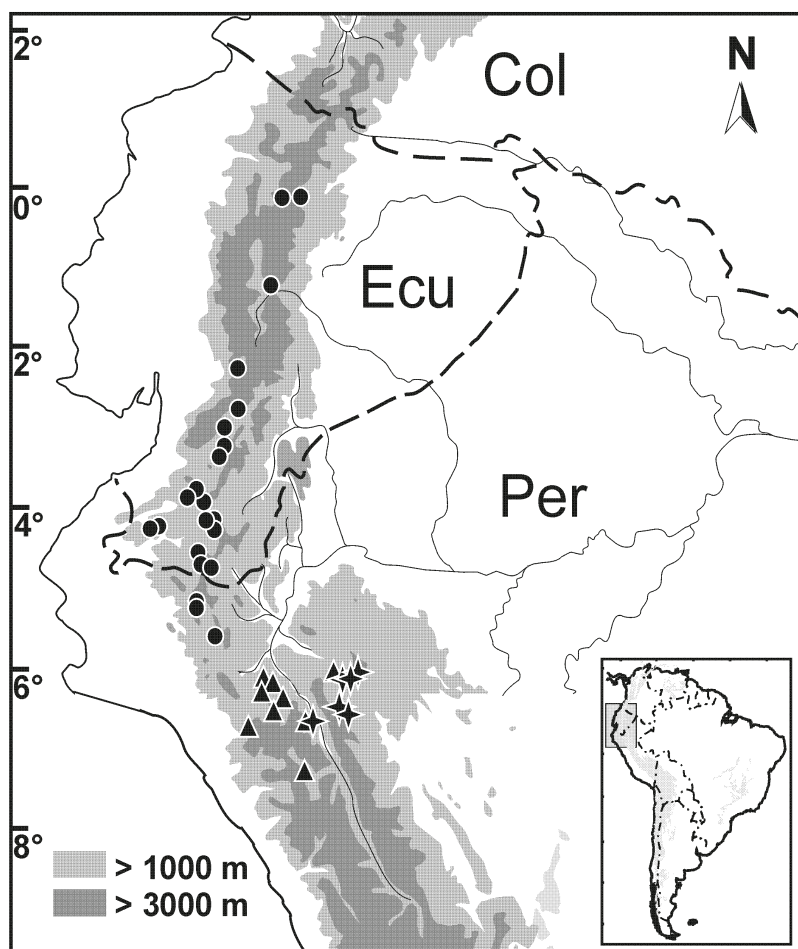


FIG. 1. Geographical distribution of *Heliangelus viola* (stars) and *H. splendidus* spec. nov. (triangles: *H. s. splendidus*; circles: *H. s. pyropus*).

***Heliangelus splendidus* spec. nov.,**

with the nominotypical form characterized (for capitalized names of colors and numbers, cf. Smithe 1975) as follows:

*Diagnosis.* Basic plumage (e.g., belly) less deep bronzish than in *H. viola* (cf. Fig. 2A); frontlet and breast more bluish-green, with the latter on average more extended to the

belly (males); gorget patch rather purplish, in females enlarged and broadened towards the breast; fringes of undertail coverts darker, more cinnamon instead of cinnamon-buffish; outer rectrices (i.e., r5) in males longer.

*Holotype.* Adult male, ZFMK reg. no. 9152 (Fig. 2B), from Cutervo, Cajamarca, Peru, collected in November 1910 by Bautista.

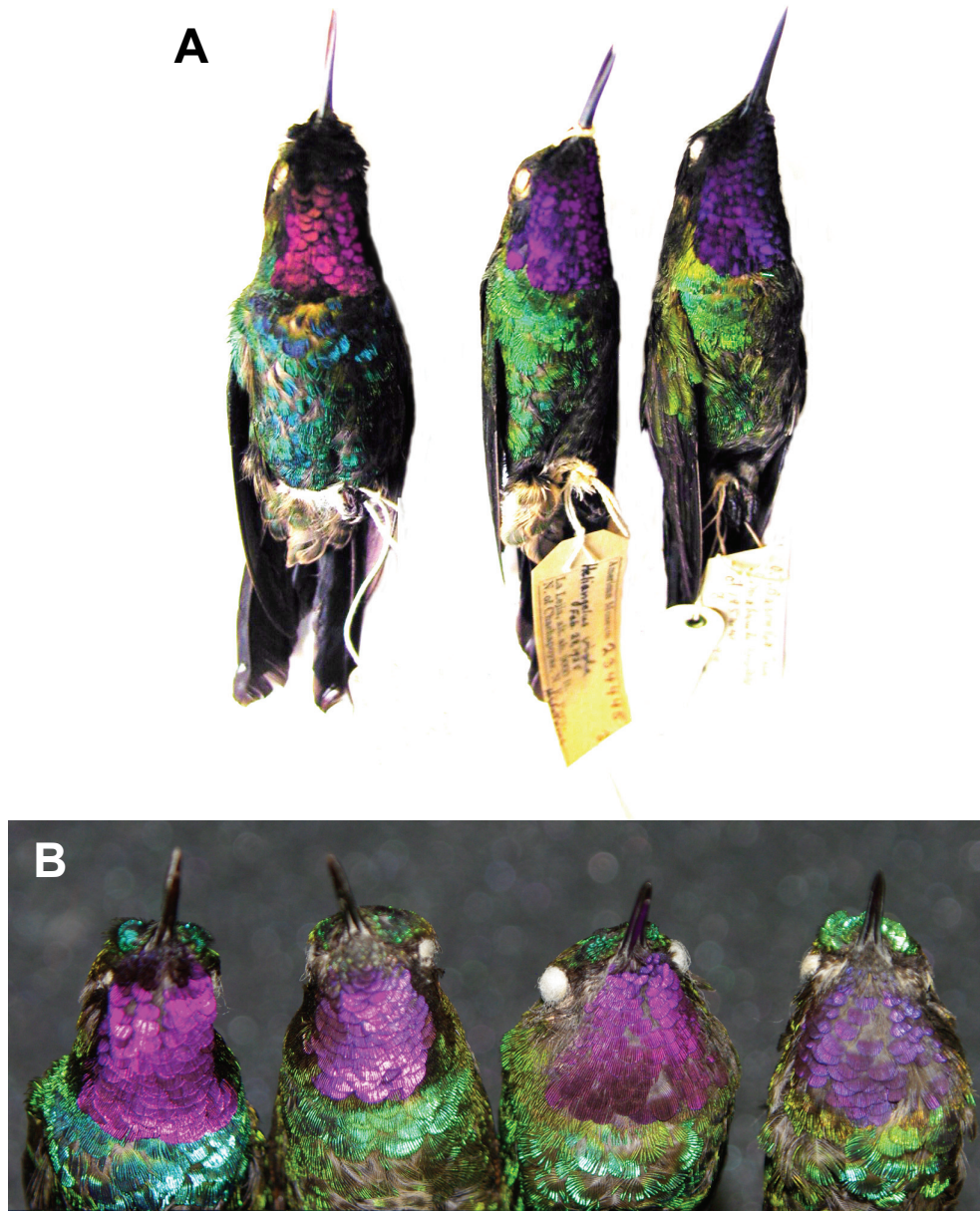


FIG. 2. Geographic variation among Violet-throated and Brilliant Sunangel. A) Comparison of males of *Helianthus splendidus* spec. nov. (holotype – ZFMK 9152, Cutervo, left) and *H. viola* (AMNH 234445, La Lejía, centre; AMNH 483732, Leimebamba, right). B) Geographic variation within *Helianthus splendidus*, spec. nov. (from left to right): *Helianthus s. splendidus*, male (holotype, ZFMK 9152); *Helianthus s. splendidus*, spec. nov., female (cotype, ZFMK 9154); *Helianthus s. pyropus*, male (holotype, ZMH 58.2806); *Helianthus s. pyropus*, female (cotype, ZMH 58.2810).

*Description of holotype.* Bill blackish, straight, medium-long (from tip to nasal operculum: 17.6 mm); frontlet basically glittering turquoise-blue (most similar to Cyan, 164), towards ramphoteca more golden green; eyebrow, lores dark bronzish, with whitish postocular spot; rest of crown, hindneck, upper back, wing coverts and uppertail shining golden green (viewed from above), centre of back and inner rectrix pairs shining bluish-green; tail strongly bifurcated, with outer rectrices more blackish-golden green, lighter on outer webs; chin darker purplish-violet (*c.* Royal Purple, 172A; gorget glittering rosy purple (*c.* Magenta, 2 × Rose, 9); breast glittering Cyan (164); belly shining blue-green to weak golden green; discs of undertail coverts shining bronze-green, narrowly fringed Cinnamon (39).

*Cotype.* Adult female, ZFMK reg. no. 9154 (Fig. 2B), from Cutervo, Cajamarca, Peru, collected in August 1901 by Bautista.

*Description of female.* Similar to male, but generally smaller except for bill (18.8 mm); frontlet glittering turquoise (*c.* Turquoise Blue (65); chin dark bronze-green; gorget duller, slightly more violet-purple (*c.* Purple, 1 × Magenta, 2), towards breast narrowly margined dark bronze-green; breast weakly glittering turquoise (*c.* Turquoise Green, 64); undertail coverts broadly fringed Cinnamon (39); tail less bifurcated than in male; outer three rectrix pairs with small buffy-whitish margins or spots on tips of inner webs.

*Immature/subadult plumage.* Generally, less brilliant-colored than adults, e.g., on frontlet and breast; gorget chiefly dark bronzish to bronze-green with broad cinnamon-buff subterminal bars and lateral fringes, in advanced subadult stages either with scattered violet blue spots (Bluish Violet, 172B) or with solid but incompletely developed patch, the latter

in males most similar in coloration to that of adult females (Purple, 1 × Magenta, 2) or rather violet blue in females; breast strike narrower in size; outer rectrices significantly shorter in males; longer undertail coverts with either greyish-brown (Light Drab, 119C) or reduced greenish centres and cinnamon fringes.

*Body length and mass.* Adult males: 132, 133 mm; 5.3, 5.4, 5.4 g; ad. female: 123 mm; 4.4 g. Immature male: 125 mm; imm. females: 4.6, 4.6 g.

*Range.* Northern Peru, in central Andes of Cajamarca and locally along the eastern slope of Amazonas in the Utcubamba valley (Fig. 1); extent of migration unknown.

*Habitat.* As provided by annotations on specimen tags and literature information (e.g., Ridgely & Greenfield 2001), the taxon prefers humid and cloud forest of the temperate zone, forest borders, and second growth at altitudes from 2200–3050 m a.s.l.

*Etymology.* The scientific name refers to the strong iridescence of the frontlet, throat, and chest, also present in female birds and being more prominent than in other genus members; as vernacular names are proposed Brilliant Sunangel for English, Colibrí Brillante for Spanish, and Glänzender Sonnenengel for German.

*Color variation.* An adult male from “Abra Celendín, Amazonas” (FMNH 395953), has a more violet-colored throat (*c.* Purple, 1 × Bluish Violet, 172B) and a coppery-tinged crown than typical nominate birds, but resembles them in all other plumage aspects.

*Specimens examined.* AMNH 37639, 235826–235831; ANSP 115650, 118363, 118364, 118370; BMNH 87.3.14.323; FMNH 256654,

395953; LSUMZ 84474, 84475, 84477, 84481–84483; SMF 6.12.1878; WFVZ 21734; ZFMK 9152–9158; 541374.

Since the northern population of *H. splendidus* spec. nov., inhabiting Ecuador and extreme northwestern Peru, differs slightly but noticeable in coloration from nominate birds, it is suggested as a distinct subspecies,

***H. splendidus pyropus* subspec. nov.**

*Diagnosis.* Differs from the nominotypical form in both sexes by an average more golden to bronze-green tinge of plumage, a golden- to turquoise-green, less bluish-green glittering frontlet and breast strike, the latter often slightly narrower in males (therein similar to *H. viola*); in females by the duller, more violet shine of the throat.

*Holotype.* Adult male, ZMH reg. no. 58.2806 (Fig. 2B), Baños, Azuay, Ecuador, 2800 m a.s.l., 02°58'S, 79°04'W, collected on 26 August 1939 by L. Gomez.

*Description of holotype.* Bill blackish, straight, medium-long (from tip to nasal operculum: 16.5 mm); frontlet basically glittering turquoise (*c.* Turquoise Green, 64), towards the ramphoteca more golden green; eyebrow, lores dark bronze-green; upperparts, wing coverts, and uppertail viewed from above shining golden to emerald green, inner rectrix pairs shining bluish-green with golden-bronze tips; tail strongly bifurcated, with outer rectrices becoming more blackish-golden green, lighter on outer webs; lores bronzy; chin, gorget glittering purplish (*c.* Purple, 1 × Magenta, 2), surrounded by a narrow bronze-green ring; breast glittering Turquoise Green (64); belly shining bluish to golden green; undertail coverts golden-green to brownish, narrowly fringed cinnamon-rufous (*c.* Cinnamon, 39 × Cinnamon Rufous, 40).

*Cotype.* Adult female, ZMH reg. no. 58.2810 (Fig. 2B), Baños, Azuay, Ecuador, 2750 m a.s.l., 02°58'S, 79°04'W, collected on 5 June 1939 by L. Gomez.

*Description of female.* Similar to male, but generally smaller in all mensural traits; frontlet glittering golden to turquoise green (Cyan, 164); chin dark bronze-green; gorget duller, with more prominent bronze-green feather bases, slightly more violet-purple (*c.* Purple, 1 × Magenta, 2), towards breast with narrow dark bronze-green margin; breast weakly iridescent turquoise green (164); undertail coverts centrally bronze-green to grey-brown, broadly fringed pale cinnamon (*c.* Cinnamon, 39) to grayish (Smoky Gray, 45); tail less bifurcated than in male; outer rectrices terminally with pale buffy margins or spots.

*Immature/subadult plumage.* With the exception of the subspecific affinities, most similar to that already described for nominate birds.

*Body length and mass.* Adult males: 120, 122, 126 mm; 3.0–7.0 g, mean = 5.4 g (n = 11); ad. females: 5.3, 5.4 g. Immature male: 5.7 g.

*Range.* Subtropical to temperate zone from northern central Ecuador to northwestern Peru (Piura) (Fig. 1); regularly recorded at altitudes from 1650–3350 m a.s.l., but occasionally lower than 1500 m a.s.l. (e.g., Salvias, El Oro, 1050 m; AMNH 166972). Ridgely & Greenfield (2001) questioned the occurrence of the Violet-throated Sunangel “as far north as Pichincha,” giving the distributional limits with southern Chimborazo (p. 373). However, there is sufficient evidence both from collecting and sight records that the range of *pyropus* extends farther north. First, recent field observations were made by K.-L. Schuchmann (pers. com.) in a cloud forest near Papallacta, Napo, representing the currently known northernmost species' locality.



Secondly, various study specimens apparently originate from northern and northern central Ecuador, among them four from Papallacta (all in NHNM collection). Further skins were collected at Tambillo, Pichincha (NMNH 88465), and at Baños, Tungurahua (BMNH 1953.68.208, NMNH 388872). A 19<sup>th</sup> century specimen, which was not included in this study, is tagged “northern side of Pichincha” (Fjeldså & Krabbe 1990). Additionally, some Whitely specimens (BMNH collection), although more imprecisely labeled “Rio Napo,” could refer somewhere to the region (south-)east of Volcan Cotopaxi, Napo.

*Habitat.* Similar to nominate form, but more frequently found in open habitats, such as lighter woodland, brush forest, shrubby areas, and gardens (*cf.* Ridgely & Greenfield 2001).

*Color variation.* Although individuals of *H. splendidus pyropus* may vary to a minor extent in most plumage aspects, color variation is mainly restricted to the dorsal side and the throat patch. Representatives from the central southern Ecuadorian range are on average above more bronzy to copperish than those from southern Loja and northern Peru. Further, some males show a slight violet-blue tinge of the gorget (e.g., ANSP 181572), similar to that of some lighter-coloured *H. viola* males. The frontlet is rarely more turquoise-blue as in nominate birds (e.g., one male from Yoyaxi, SMF unreg., 22.9.1883). In general, I found no indication that colour variation in iridescent plumage parts among specimens of *H. splendidus* spec. nov. - and likewise of *H. viola* - is the result of unfavourable storing of specimens, e.g., due to chemical contamination or light exposure that may have altered colors artificially (*cf.* Graves 1986, 1991). This is supported by the facts that specimens exhibiting similar colors (e.g., on throat) (1) are housed under different conditions in various bird collections and (2) were collected at

different times (with partly several decades of temporal distance).

*Specimens examined.* AMNH 129494, 129496, 129498, 129501, 166959–166965, 166967, 166970–166975, 166977–166982, 171118–171120, 171122, 175172–175178; ANSP 59148–59149, 59163–59165, 59251, 181572, 182327, 184608, 185241; BMNH (18)87.3.22.870, 1953.68.208, 1969.37.95; LSUMZ 35145, 78105, 14.7.1998, 17.7.1998, 24.7.1998; MCZ 137957, 288533–298537; NHMB 19695–19696, 20999–21001; NMNH 88465, 174009–174012, 388872; SMF 22.9.1883; WFVZ 43025–42029, ZMH 58.2805–58.2807, 58.2810, 58.2812, 58.2816, 58.2820–58.2825.

*Morphometric variation.* The biometric data of Brilliant and Violet-throated Sunangel are summarized in Table 1. Generally, males of all taxa are larger than females in most mensural characters except for bill length. Age-related variation occurs in *H. splendidus pyropus* where immature males of exhibit slightly shorter tails ( $r_5$ ) than adult ones ( $p < 0.01$ ).

All taxa are very similar in their biometric characteristics (Table 1). However, males of the new species differ strikingly in having the outermost rectrix ( $r_5$ ) significantly longer ( $p < 0.001$ ) than those of *H. viola*. Owing to the low specimen number ( $n = 3$ ) in female *H. viola* available, it was impossible to compare females of both species with statistical means; nevertheless, the difference in tail length seems to be less prominent. Two individuals (one male, one female) of *H. s. splendidus* sub-spec. nov. from the eastern Andes have similar biometric data (i.e.,  $r_5$  length) than birds of the western main population.

*Etymology.* The scientific name reflects the more golden to bronzy plumage of the new subspecies when compared with the nominotypical form.

*Behavior.* Rather territorial and dominant, i.e., at feeding places superior on smaller trochilids (K.-L. Schuchmann pers. com.). Partially migratory, but extent of seasonal movements poorly known (cf. Ridgely & Greenfield 2001).

## DISCUSSION

Despite the fact that more than 150 years have passed since its discovery, astonishingly few numbers of the Violet-throated Sunangel have been compiled in the international bird collections (only 20 skins were included in this study), with the overwhelming majority of specimens collected between the second half of the 19<sup>th</sup> and the first half of the 20<sup>th</sup> century. Under the new taxonomic arrangement, this species remains restricted mainly to the completely unprotected mountains of the Utcubamba drainage and the Cerros Calla Calla. Further northeast, collecting activities by recent LSUMZ field parties in appropriate habitats of the Cordillera de Colan near La Peca, Amazonas, failed to secure any specimen of either *H. viola* or *H. splendidus* spec. nov., indicating that these species may be outnumbered or even replaced there by a slightly larger congener, the Amethyst-throated Sunangel (*H. amethysticollis decolor*), with numerous specimen records from this region (e.g., in LSUMZ; cf. Weller 2009). However, a more recent observation and photographic record from the Rio Chido valley, Amazonas (J. Ferdinand pers. com., 2002), indicates that this species may have remained undetected in adjacent regions, and may still be locally common.

Unlike to the Violet-throated Sunangel, the Brilliant Sunangel inhabits both Andean slopes, ranging from northern Ecuador to northern Peru (Fig. 1). Interestingly, parapatric contact between both taxa is indicated in the Marañon valley (Celendín) as well as along the upper Utcubamba valley (Levanto; cf.

Appendix). If these records are not regarded as vagrants (at least questionable in the case of Levanto, with two specimens of *H. s. splendidus* subsp. nov. collected within the peripheral range of *H. viola*), this overlap may be only of recent origin, being founded in the species' biogeographic history. The main range patterns suggest that *H. viola* rised in the Andes east of the Marañon while *H. splendidus* spec. nov. originated west of it, with the valley likely representing an important barrier and speciation factor during dry glacial phases. It is possible that a precursor population of the *H. viola-splendidus* complex could have had a range that extended across the current total range of all three taxa but became split during less favourable climatic conditions (cf. "refuge theory", Haffer 1967). Such a scenario is likewise reflected in the distribution of other congeners (*H. micraster* vs *H. amethysticollis*; e.g., Fjeldså & Krabbe 1990, AAW unpubl. data) or high Andean hummingbird taxa, respectively, e.g., *Metallura* (*M. odomae* vs *M. eupogon*; Heindl & Schuchmann 1998) and *Eriocnemis* (*E. luciani* vs *E. sapphirinopygia*; Schuchmann *et al.* 2001). Subsequently, *H. viola* and *H. splendidus* spec. nov. might have come in parapatric contact in the Andes east of the Marañon that seems to be no longer a biogeographic barrier in recent times for some hummingbirds with similar geographical and altitudinal distribution patterns (e.g., *Ramphomicron*, cf. Weller & Schuchmann 2002).

*Biogeography, systematics, and species limits in Heliangelus.* The genus' range comprises the Andes from Colombia and western Venezuela southward to northern Bolivia. Recently, up to nine species have been recognized in *Heliangelus*, of which five are considered restricted-in-range (e.g., Schuchmann 1999, Ridgely & Greenfield 2001, Hilty 2003).

In coloration, all genus members are characterized by a more or less iridescent frontlet,

a brilliant gorget in males (except for *H. regalis*), and a distinctive chest patch. The frontlet is mostly (dark-)bluish to bluish-green (*H. mavors*: orange-red), while the throat coloration varies from purplish-violet (e.g., *H. amethysticollis*, *H. clarisse*, *H. strophianus*) to roseate (*H. exortis*), flame-orange (*H. micraster*), or orange-red (*H. mavors*). Other ventral characteristics refer to the chest, that is either iridescent (*H. viola*, *H. splendidus* spec. nov.) or whitish (e.g., *H. clarisse*, *H. strophianus*) to buffish (e.g., *H. amethysticollis*, *H. mavors*), and the undertail coverts (pure whitish or with green-brown centres). The morphologically outstanding taxa *H. zuzii* (known only from a single 19<sup>th</sup> century “Bogota” trade skin; Graves 1993) and *H. regalis* are characterized by an extremely dark, blackish-blue (*regalis*) to blackish-green (*zuzii*) basic plumage and differ biometrically from other genus members by their deeply furcated tail.

Since *H. viola* and *H. splendidus* spec. nov. exhibit a broad mix of unique characters (e.g., female throat pattern) and those shared by other congeners (e.g., iridescent frontlet, greenish tail), their intrageneric placement in terms of morphology is currently poorly understood (Schuchmann 1999). Nevertheless, the combination of characters, including the metallic shine of the chest, the glittering greenish frontlet, and the undertail pattern suggest a close relationship with genus members of the northern Andes, particularly *H. clarisse*, rather than with representatives from the southern range of the genus (e.g., *H. amethysticollis*). Given the well-pronounced sexual dichromatism in most taxa of *Helianthus*, similarities observed in the male’s and female’s throat and ventral plumage of *H. viola* and *H. splendidus* spec. nov. and - less pronounced - in the *H. [exortis]* superspecies (including *H. micraster*), indicate that this common pattern may represent a secondary, advanced stage within the genus’ evolution. Hence, it is likely that a proto-*Helianthus* was sexually dichro-

matic, a characteristic found in most of the recent Andean hummingbird clades (Schuchmann 1999, pers. observ.).

*Conclusions and validity of species concepts.* Recent systematic studies using the concepts of the biological species (BSC, Mayr 1942) or phylogenetic species (PSC, Cracraft 1983) have pointed to the conditions under which such models can be used as appropriate tools for taxonomic decisions (for details, see Haffer 1997). A main point of criticism of the BSC, the lack of knowledge on species limits under allopatric conditions, may be excluded for the present case due to indication of overlapping ranges of *H. splendidus* spec. nov. and *H. viola* in northeastern Peru.

The Brilliant Sunangel qualifies as a good species under both BSC and PSC. While the amount of geographic variation is minor (but constant) among *H. s. splendidus* spec. nov. and *H. s. pyropus* subspec. nov., being restricted to iridescent plumage parts, phenotypical differences are much more pronounced in various independent characters, such as female-type plumage, throat coloration, and tail length. Particularly, the plumage differences in adult females of *H. viola* and *H. splendidus* spec. nov. are striking and, as this morphological feature is generally considered a conservative character, supportive of the validity of the new taxon. Moreover, distinctness at species level is justified when comparing the current species limits in *Helianthus* (e.g., *H. exortis* vs *H. micraster*, cf. discussion below; variation in female patterns) and other Andean clades, such as the metaltails *Metallura* (Heindl & Schuchmann 1998), pufflegs *Eriocnemis* (Schuchmann *et al.* 2001, Cortés-Diago *et al.* 2007), and wood-nymphs *Thalurania* (Valdés-Velásquez & Schuchmann 2009). Although there is indication for parapatric occurrence (Fig. 1, Appendix), it is suggested to consider *H. viola* and *H. splendidus* spec. nov. as

members of the same first order superspecies (*sensu* Haffer 1986).

*Status and conservation.* The Violet-throated Sunangel has been classified as restricted-in-range and not globally threatened (Schuchmann 1999), a designation that should also be applied to the Brilliant Sunangel. Locally common in appropriate habitat, the latter seems to be more tolerant to habitat disturbance than its congener and frequents cultivated areas, such as shrubby fields and gardens (e.g., Ridgely & Greenfield 2001). Considering the occurrence in protected areas, specimen records of *H. splendidus pyropus* ssp. nov. are from Parque Nacional Podocarpus, at the border Loja/Zamora-Chinchipec, southern Ecuador. The taxon may be also present in Santuario Nacional Tabaconas Namballe, northwestern Amazonas, Peru (nearest records from the adjacent Huancabamba region). The nominotypical population is likely to be found in Parque Nacional Cutervo, located just a short distance northeast of the type locality. Altogether, future surveys of *H. splendidus* spec. nov. and *H. viola* are recommended not only to estimate the range extension and potential threats (i.e., habitat sensitivity) but also to indicate the amount of parapatry or even sympatry. As a biogeographical consequence, the Violet-throated Sunangel is now considered endemic to Peru.

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## APPENDIX

Localities and altitudes (a.s.l.) either obtained from specimen labels, ornithological gazetteers, or the Alexandria Digital Library Gazetteer (<http://fat-albert.alexandria.ucsb.edu:8827/gazetteer>) of study skins and additional records from literature (coordinates after Paynter 1993, Stephens & Traylor 1983; n. loc. = not located):

*H. splendidus splendidus* spec. nov.: PERU, western Andes: Tambillo, Cajamarca, 2200 m, 06°10'S, 78°45'W; Chira, Cajamarca, 2290 m, 06°16'S, 78°42'W; Cutervo, Cajamarca, 2410–3050 m, 06°22'S, 78°51'W; 7 km N, 3 km E Chota, Cajamarca, 2600 m, ca. 06°33'S, 78°39'W; Chugur, Cajamarca, 2745 m, 06°40'S, 78°45'W; Taulis, Cajamarca, 2500 m, 06°54'S, 79°03'W; Hacienda Sunchubamba, Cajamarca, 2650 m, 07°29'S, 78°24'W; Abra Celendín, Cajamarca, n. loc.; eastern Andes: Levanto, Amazonas, 2745 m, 06°16'S, 78°42'W.

*H. splendidus pyropus* spec. nov., subspec. nov.: ECUADOR: Papallacta, Napo, 3150 m, 00°22'S, 78°08'W; Tambillo, Pichincha, 2785 m, 00°25'S, 78°32'W; Baños, Tungurahua, 1850 m, 01°24'S, 78°24'W; Pagma, Chimborazo, 1900–2000 m, n. loc., near Chunchi (02°17'S, 78°55'W); Hacienda Jalancay, Chimborazo, 1750–1950 m, n. loc., near Chunchi (02°17'S, 78°55'W); Huigra, Chimborazo, 1200–1500 m, 02°17'S, 78°59'W; Yoyaxi, Chimborazo (?), 2750 m, n. loc.; Biblián, Cañar, 2500 m, 02°42'S, 78°52'W; Cuenca, Azuay, 3000 m, 02°53'S, 78°59'W; Yanaurcu, Azuay, 3100 m, 02°55'S, 79°10'W; Chilla Range, Azuay, 2200 m, c. 03°32', 79°37'W; Baños, Azuay, 2750–2900 m, 02°58'S, 79°04'W; San Martin Lake, Azuay, 2500 m, 03°11'S, 79°123'W; Gima, Azuay, 2950 m, 03°12'S, 78°57'W; Hacienda El Paso, R'ó Charcay, Azuay, 2760 m, 03°22'S, 79°05'W; Zaruma-Saraguro trail, Loja/El Oro, 2900–3350 m, between 03°36'S, 79°13'W–03°41'S, 79°37'W; El Chiral, El Oro, 1650 m, 03°38'S, 79°41'W; Taraguacocha, El Oro, 2950 m, 03°40'S, 79°40'W; Salvias, El Oro, 1050 m, 03°47'S, 79°21'W; Loja, Loja, 2200 m, 04°00'S, 79°13'W; Cerro Villanaco, 7 km W Loja, Loja, altitude ?, n. loc.; Guanchanamá, Loja, 2775 m, 04°02'S, 79°53'W; San Bartolo, Loja, 2300 m, 04°02'S, 79°55'W; Nudo de Cajanuma, Loja, 2400–2500 m, 04°05'S, 79°12'W; 5, 6.6 km W Celica, Loja, 1900–2100 m, 04°07'S, 79°59'W; 5 km SE Gonzanamá, Loja, 2300 m, 04°15'S, 79°27'W; Jimbura to Zumba, near pass S of Amaluzza (= Cordillera del Potachuelo), Zamora-Chinchi, 3000 m, 04°37'S, 79°20'W; 9 km SSE Jimbura, Loja, 2650 m, ca. 04°37'S, 79°26'W; PERU: El Tambo, Piura, 2865 m, 05°20'S, 79°30'W; Huancabamba to Canchaque, Piura, 1830–3000 m, between 05°20'S, 79°32'W–05°24'S, 79°36'W; Tambo to Canchaque, 3200 m, Piura, between 05°21'S, 79°33'W–05°24'S, 79°36'W; Huando to Canchaque, Piura, 2550 m, n. loc.; Quebrada Lanchal, Piura, 8 km ESE Sallique, 2430–2750 m, 05°41'S, 79°15'W.

*H. viola*, PERU, eastern Andes: La Lejía, Amazonas, 2745 m, 06°10'S, 77°31'W; Chachapoyas, Amazonas, 2250–2350 m, 06°13'S, 77°51'W; Levanto, Amazonas, 2745 m, 06°16'S, 77°49'W; Leimebamba, Amazonas, 2745 m, 06°41'S, 77°47'W; San Pedro, SE of Leimebamba, Amazonas, 2625–2865 m, n. loc.; western Andes: Celendín, Cajamarca, 2625 m, 06°52'S, 78°09'W.