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BIOGEOGRAPHY AND TAXONOMY OF *LAFRESNAYA* (TROCHILIDAE), WITH A NEW SUBSPECIES FROM COLOMBIA

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Resumen. – Biogeografía y taxonomía de *Lafresnaya* (Trochilidae), con una nueva subespecie de Colombia. – Entre los colibríes alto-andinos, el género monotípico *Lafresnaya* (Bonaparte 1850) tiene su centro de distribución básicamente en el norte de Sudamérica, encontrándose desde el norte de Colombia y el oeste de Venezuela hasta el sur del Perú. La única especie, *Lafresnaya lafresnayi* (Boissonneau 1840), se divide en varias subespecies que habitan el bosque nublado y la zona del sub-páramo, a altitudes entre los 2500 y 3000 m s.n.m. Este artículo tiene como objetivo revisar los aspectos taxonómicos, la variación geográfica de los patrones de plumaje y de biometría (e.g., pico, cola), así como la biogeografía de todos los taxa del género *Lafresnaya*. Basado en diferencias en la morfología del pico, se describe una nueva subespecie, *L. l. longirostris* ssp. nov., de la Cordillera Central en Colombia, anteriormente incluida en la forma nominal. Tomando en cuenta tanto los caracteres de plumaje como los caracteres biométricos, se recomienda mantener la raza *L. l. orestes*, anteriormente cuestionada. Por otro lado, la población del suroeste de Táchira, Venezuela, conocida bajo el nombre de *L. l. tamae*, no es suficientemente diferente de *L. l. lafresnayi* y debería ser considerada como sinónimo de la última.

Abstract. – Among the high-Andean trochilid taxa, the monotypic genus *Lafresnaya* (Bonaparte 1850) has a northern focus of distribution, occurring from northern Colombia and western Venezuela to southern Peru. The only species, the Mountain Velvetbreast (*Lafresnaya lafresnayi*, Boissonneau 1840), is represented by several subspecies which commonly inhabit the cloud forest and sub-paramo zone, mostly at altitudes between 2000 and 3500 m a.s.l.. The current paper reviews taxonomic aspects, the geographic variation of plumage and biometric patterns (e.g., bill, tail), and the biogeography of all taxa of *Lafresnaya*. Based on a distinct bill morphology, a new taxon, *L. l. longirostris* subsp. nov., is described from the Cordillera Central, Colombia, a population formerly included in the nominotypical form. Taking into account both plumage and biometric characters, it is recommended the previously questioned race *L. l. orestes* be maintained. On the other hand, the population from southwestern Táchira, known as *L. l. tamae*, is insufficiently different from *L. l. lafresnayi* and should therefore be regarded as a synonym of the latter. *Accepted 22 November 2002.*

Key words: *Lafresnaya*, *Lafresnaya lafresnayi longirostris* ssp. nov., Trochilidae, Andes, biogeography, geographic variation, taxonomy.

INTRODUCTION

As a typical inhabitant of the cloud forest and sub-paramo zone, the genus *Lafresnaya* is endemic to the northern and central Andes (Figs. 1 and 2). It is currently regarded as monotypic; the only representative, *Lafresnaya lafresnayi* (Boissonneau 1840), comprises

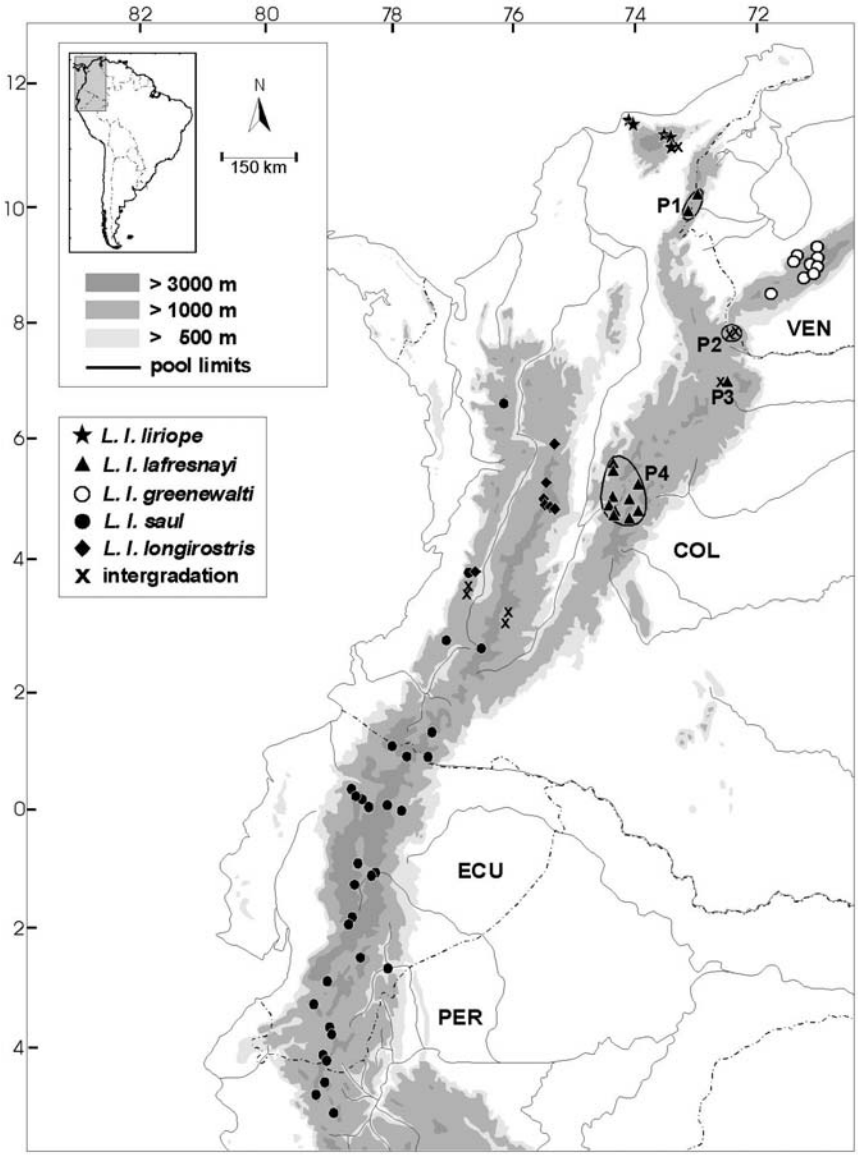

FIG. 1. Distribution of *Lafresnaya* taxa (northern range). Localities of specimens pooled for statistical comparison (cf. Fig. 3) are encircled; for coordinates and altitudes, see Appendix 1. For explanation of intergradation, see text. Abbreviations: VEN = Venezuela, COL = Colombia, ECU = Ecuador, PER = Peru.

six generally accepted subspecies, *L. l. liriope* (Bangs 1910; Sierra Nevada de Santa Marta, N Colombia), *L. l. greenewalti* (Phelps & Phelps 1961; Sierra Nevada de Mérida, Venezuela), *L. l. lafresnayi* (Cordilleras Central and Oriental, Colombia), *L. l. saul* (Delattre &

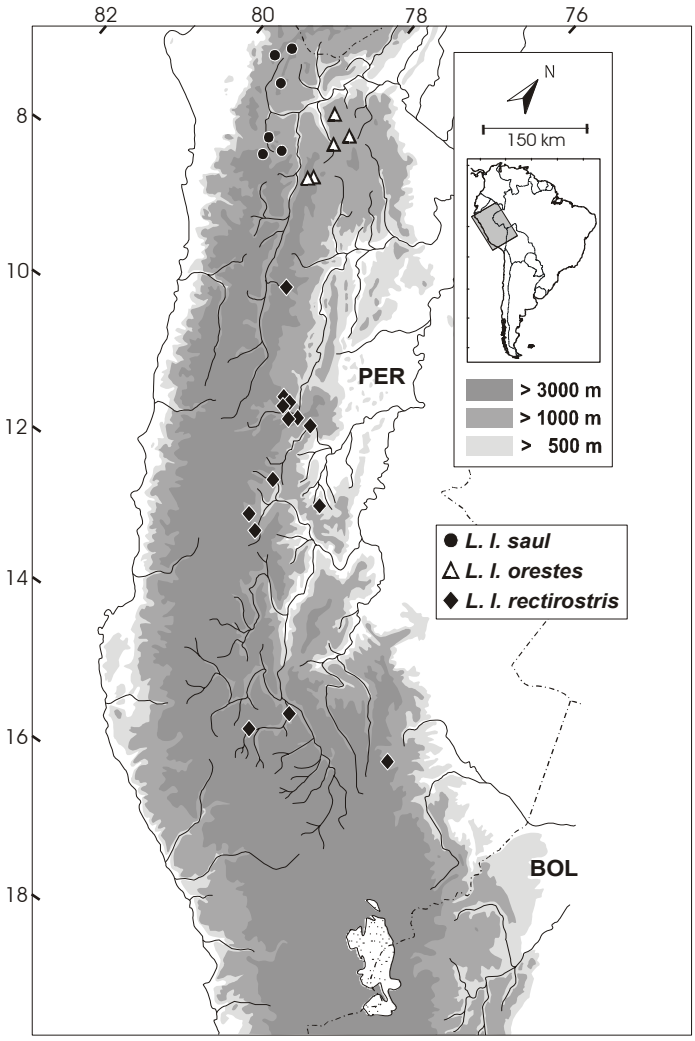

FIG. 2. Distribution of *Lafresnaya* taxa (southern range); for coordinates and altitudes, see Appendix 1. Abbreviations: PER = Peru, BOL = Bolivia.

Bourcier 1846; SW Colombia to NW Peru), and *L. l. rectirostris* (Berlepsch & Stolzmann 1902; NC Peru to upper Apurímac valley). Two further taxa, *L. l. tamae* (Phelps & Aveledo Hostos 1987; Páramo de Tamá and Cerro El Retiro, extreme SW Táchira, Venezuela, and probably adjacent Colombia) and *L. l. orestes* (Zimmer 1951; NE Peru), have not been generally considered as valid (cf. Schuchmann 1999). In most cases, taxonomic decisions on the validity of subspecies have been derived from their bill (e.g., more or less decurved) and tail morphology (outer rectrices whitish or buffish). Despite the description of two further subspecies since Zimmer (1951), no detailed subsequent study has been undertaken to evaluate the intraspecific affinities.

MATERIAL AND METHODS

Following the methods applied in previous studies on hummingbird biogeography (for details, see Schuchmann *et al.* 2001), we examined the geographic variation of a total of 243 *Lafresnaya* specimens (129 males, 114 females). Distribution analysis included mapping of collecting sites (coordinates after Paynter 1982, 1992, 1993, 1997; Stephens & Traylor 1983), while the amount of morphological variation was evaluated by biometric characters [bill length (operculum), bill width (culmen), wing chord (unflattened), rectrices 1, 5] and color characters (in brackets, capitalized) using a standardized color guide (Smithe 1975) or general terms (e.g., in case of iridescent colors). Individuals of different taxa or from pooled localities were statistically compared using ANOVA (significance level $P < 0.05$).

RESULTS

Ecologically, *L. lafresnayi* inhabits preferably wet, mossy habitats such as cloud and elfin forest within the subtropical zone of the Andes, but also partly extends into the adjacent sub-paramo. The overall altitudinal range varies usually from 1250 to nearly 3700 m (see Appendix 1), with some differences between the subspecies and regions. At the lower limits, *L. l. liriope* from the Santa Marta Andes is frequently recorded around 2000 m (but an extralimital record exists from near sea level at San Pedro; ICN # 23269, 23270), whereas all other forms are most common between 2500 and 3500 m.

Traditionally, the central Andes of Colombia have been included in the range of *L. l. lafresnayi* (Meyer de Schauensee 1949, Hilty & Brown 1986, Fjeldså & Krabbe 1990, Schuchmann 1999). However, based on a specimen series in the ZFMK ornithological collection (formerly part of the O. Kleinschmidt collection; cf. Kleinschmidt 1943), we found evidence for a previously unrecognized subspecies of *Lafresnaya*, with an unusual bill morphology, occurring in the central Andes of Colombia. We propose that this population should be named as:

Lafresnaya lafresnayi longirostris, subsp. nov.

Diagnosis. Differs from the nominate race and *L. l. liriope* by its longer, more decurved bill, and from the latter taxon by its less bronzy inner tail; additionally, from all other conspecifics by the pronounced horn-colored to buffish tinge of the tail.

Holotype. Adult male, ZFMK # 9569; collected at Madim, Paso del Quindío, Quindío, Colombia, 2500 m, on 29 September 1909 by A. H. Fassl.

Description of holotype. Bill blackish, 30.4 mm (distance tip – operculum), slightly decurved; dorsal side, uppertail coverts, and flanks shining golden green, with head duller than the remaining upperparts; throat, chest, and lateral belly feathers glittering emerald-green, with belly to abdomen centrally blackish (Jet Black, 89); innermost rectrices (r1) shining golden green, the following (r2-r4) Pale Horn Color (92) with relatively narrow bronze-green tips, covering c. one fourth of the outer webs; outermost rectrices (r5) Pale Horn Color (92) with relatively broad dark purplish margins, the latter extending over the upper half of the outer webs; undertail coverts golden green, basically Pale Horn-colored (92).

Paratype. Adult female, ZFMK # 9570; collected at Río Toche, Paso del Quindío, Tolima (?), 2100 m, on 10 October 1909 by A. H. Fassl.

TABLE 1. Color variation of major plumage characters in *Lafresnaya lafresnayi* subspecies. * = including intergrading specimens (see text); ** = including *L. l. tamae*; *** = ssp. nov.

Character	Back plumage	Male throat patch	Female underparts	Inner tail	Outer rectrix bases*
liriope C, E Colombia	Emerald to bronze-green	Emerald-green	Whitish to creamish	Copper to bronze-green	Whitish to creamish
lafresnayi N Colombia	Emerald to golden green	Emerald-green	Buffish to cinnamon	Copper to golden green	Creamy buff to horn-colored
greenewalti W Venezuela	Emerald to bronze-green	Emerald-green	Whitish to creamish	Copper to bronze-green	Whitish to pale horn-colored
longirostris NC Colombia	Emerald to golden green	Emerald-green	Cinnamon	Copper to golden green	Creamy buff to horn-colored
saul SW Colombia-NW Peru	Emerald to bronze-green	Emerald-green	Creamy buff to whitish	Golden to blue-green	Whitish
orestes NE Peru	Bronze to golden green	Golden green	Creamy buff to whitish	Bronze to golden green	Whitish
rectirostris N, C Peru	Bronze to golden green	Golden green	Creamy buff to whitish	Bronze to golden green	Whitish

Description of paratype. Head above dull golden green with inconspicuous rufous fringes, the latter extending to the neck; rest of upperparts shining golden green mixed with emerald-green; rump fringed pale cinnamon; chin to throat centrally Warm Buff (118) to Buff (124), speckled with dull bronze to bronze-green spots on chin and lateral gorget, and with iridescent golden green spots on throat (iridescent on central gorget) and chest; flanks golden green; center of belly to abdomen less buffish, becoming more whitish, with a few greenish spots, particularly along sides; innermost rectrices (r1) shining golden green, the following Cream-colored (54) with relatively wide bronze-green (r2-r4) to dark purplish (r5) margins, extending across roughly the upper two-thirds of the outer webs in r5; undertail coverts golden green, basically Cream-colored (54).

Immature plumage. One immature male (ZFMK # 9572) from Volcancito, Paso de Quindío, has a general plumage pattern similar to that of the paratype but is ventrally more whitish instead of buff and more emerald-green instead of bronzish or bronze-green, exhibiting some glittering green feathers on the central gorget. In addition, some central belly and abdomen feathers are dark brown (Sepia, 219), indicating the final blackish character stage of adult males.

Body length. Males: 90, 93, 95, 95 mm; Females: 90, 91, 94 mm.

Distribution. Known mainly from the northern part of the Cordillera Central, Colombia,

between Antioquia and Tolima; one record from the Cordillera Occidental (Valle del Cauca); ranging from 2100 to 3660 m.

Etymology. This taxon is named for its distinctive, elongated bill compared with other species members.

Individual variation and remarks. Within the ZFMK series from the Quindío trail region, a slight tail variation is noticeable. A male (# 9568) from Yerbabueno has a Cream-colored (92) tail, paler than that of the paratype, whereas another female (# 9571) from Callagos shows more buffish-colored (Buff, 124) rectrices.

The collecting sites of most available specimens of *L. l. longirostris* (see Fig. 1), including those of the type series, are located along or in the vicinity of the Boquerón del Quindío (c. 04°38'N, 75°32'W) which crosses the Central Andes between Salento (04°38'N, 75°43'W) and Ibagué (04°27'N, 75°14'W; Paynter 1997). An adult male of this form, labeled as *L. l. saul* (ZFMK # 9574), was collected in the Cordillera Occidental at San Antonio (= Gamboa), Cauca, on 12 April 1909 by Fassl. This individual clearly shows the distinctive features attributable to the Central Cordilleran population of *L. l. longirostris*, i.e., a significantly longer bill (30.3 mm; cf. Table 1), slightly less decurved than in *L. l. saul*, and a cream-colored tail. The chin and upper gorget feathers have cream-colored subterminal bars and fringes, suggesting this plumage area to be in molt. A minor difference exists in the coloration of the innermost rectrices, which are more bronzish instead of golden green compared with males from the Central Andes. Interestingly, there is a specimen of *L. l. saul* (ZFMK # 9575) from the same locality but with a different collecting date (18 August 1909; Fassl). In view of no further *L. l. longirostris* specimen records from the western cordillera – despite quite extensive collecting in the Cali region – and the fact that *L. l. saul* occurs in this mountain range as far north as Páramo Frontino, Antioquia, the individual in question is more likely a straggler from the opposite Andean slope east of the Cauca valley rather than an indication of a local western *longirostris* population.

Color variation

Lafresnaya is characterized by a pronounced sexual dichromatism. Males of all subspecies share as major features the iridescent green throat patch, flanks, and upper belly, and the blackish center of lower belly and abdomen. This pattern contrasts strongly with that of females, which have a whitish to buffish basic plumage with golden to bronze-green spots across the entire ventral side.

As in most other hummingbird genera, immature males closely resemble adult females in most plumage features and can therefore barely be distinguished from the latter. Except for some biometric data (e.g., longer wings in males; see below), we found only a few discriminating characters that may hold for larger series if the male plumage is not otherwise indicated (e.g., by blackish belly feathers). First, females have a dull brownish green cap, whereas males show a dark green head with slightly iridescent feathers that may have additional cinnamon fringes (in immatures; Schuchmann 1999). Second, the chin of females is always without greenish spots. Finally, the greenish disks of the undertail coverts are narrowly fringed in subadult males but broader in females.

Geographic variation refers to most plumage characters (Table 1; Bangs 1910, Zimmer 1930, 1951). In *orestes/rectirostris*, the dorsum and the iridescent throat patch in males are rather golden green compared with the more emerald-green sheen found in the other subspecies. Generally, females vary more strongly in the underparts than males. In the northern forms *liriope*, *greenewalti*, and

tamae, the entire ventral plumage, including the basal half of the undertail coverts, is basically whitish to cream-colored. Females of *L. l. lafresnayi* and *L. l. longirostris* differ from all other subspecies by their usually more cinnamon tone (Cinnamon, 39) of the throat, chest, and undertail coverts. In addition, some individuals have the greenish disks on the tail coverts completely reduced (e.g., ZFMK # 8712). Between the southern white-tailed races *saul*, *orestes*, and *rectirostris*, ventral differences in females are hardly detectable (Zimmer 1951). Contrary to the northern populations, the chin and the borders of the upper throat feathers are tinged creamish buff whereas the remaining underparts are basically whitish (central belly sometimes slightly cream-colored, e.g., ZFMK 8721).

Similarly to the upperparts, the coloration of the median rectrices varies from copperish or bronzish to more golden green in the southern forms, rarely mixed with some bluish tinge in *L. l. saul* (Table 1). As a diagnostic mean of major importance, the outer tail feathers are mostly whitish in *liriope/greenewalti* as well as in *saul* and the Peruvian forms *orestes/rectirostris*. This pattern differs from the usually creamy buff tail of *lafresnayi* and *longirostris* and that of *tamae*, which was described as Pale Horn-colored (92; Phelps & Aveledo Hostos 1987). Examination of the type series of *L. l. tamae*, deposited in the Phelps collection, revealed that this character seems to be more pronounced in males, since one of two females (COP # 11023) has the tail as cream-colored as nominate birds. Moreover, among five male specimens from Peña Blanca (06°33'N, 72°30'W), western slope of Cordillera Oriental Andes in Boyacá and well within the range of *L. l. lafresnayi*, only one individual (CMNH # 59640) exhibits the nominotypical tail coloration, whereas three others are pale horn-colored as in *tamae*, and another one even has an almost whitish tinge (CMNH # 59588).

Two further intergrading populations, including one previously mentioned only by Todd & Carriker (1922) and Todd (1942) but not subsequent workers (e.g., Zimmer 1951, Phelps & Phelps 1961, Fjeldså & Krabbe 1990), exist within the Colombian range. First, three female specimens of *L. l. liriope* collected on the southeastern slope of the Sierra Nevada de Santa Marta (Chendúcua; NMNH # 386995, 386997-998) have a slight creamish tinge to the rectrices, which contrasts with the regular white coloration of four other individuals (3 ad. females, 1 imm.) from the same locality. This site is located northwest of the Río César valley just opposite the Serrania de Perijá, the northernmost range limit of the cream-tailed nominotypical form (cf. Fig. 1). Second, specimens intermediate between *L. l. lafresnayi* or *L. l. longirostris* and *L. l. saul* are known from both slopes of the southern Cordillera Central (see Fig. 1, crosspoints). Similar to the preceding case, altogether five female and immature specimens from Inzá (ICN # 27355), Marquetalia (e.g., ICN # 29150), and the Cali region (PNN Farallones; e.g., ICN # 25768) exhibit the cream-colored tail characteristic of nominotypical birds and *longirostris*, while the majority of individuals (including adults of both sexes and immatures) from the same or adjacent localities (e.g., Páez) have the white rectrices of *saul*. The restriction of this character variation to the female-type plumage or, vice versa, its absence from the male plumage in both examples is striking and so far unknown for any intergrading population in trochilids (e.g., *Eriocnemis sapphiropygia*, central Peru; Schuchmann *et al.* 2001).

Other distinctive tail features include the coloration and width of the greenish margins of the outer rectrices (cf. Zimmer 1951), which extend in r5 over the upper third of the outer webs and the tips of the inner webs. They are bronze-green to golden green in all northern races (*liriope*, *lafresnayi*, *tamae*,

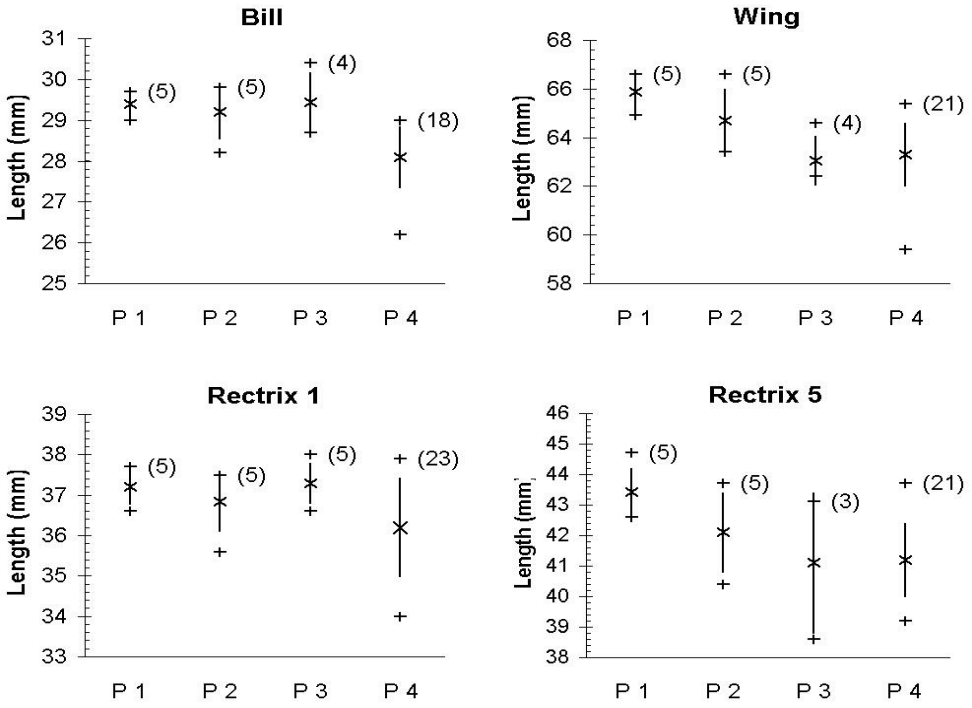

FIG. 3: Geographic variation of four morphometric characters in male pools (cf. Fig. 1) of *Lafresnaya l. lafresnayi* (P 1, 3, 4) and *L. l. tamae* (P 2), showing extreme values (crosses), means (vertical cross-points), standard deviations (columns), and numbers of study specimens (in brackets). Localities included in pools (for coordinates and altitudes, see Appendix 1), P 1: Hiroca, Camp Frontera 2, Cerro Viruela; P 2: Cerro Las Copas, Cerro El Cobre, Cerro El Retiro, Camp Páramo de Tamá; P 3: Peña Blanca; P 4: Páramo de Guasca, La Calera, Bogotá, Subían, Choachí, El Peñon.

greenewalti, *tamae*, *longirostris*) but more dark purplish in the southern ones (*saul*, *orestes*, *rectirostris*). Based on a small skin series of *orestes* (n = 9), Zimmer also diagnosed narrower inner web borders in this taxon (2–3 mm, but this only refers to males) in comparison with *rectirostris* and *saul*. However, this feature is rather a matter of strong individual variation, and the width of the margins may even differ between the left and right outermost rectrices of the same individual (e.g., *L. l. saul*, ZFMK # 1982/38: 7.6 vs 9.4 mm). Further, there is an almost complete overlap between these three forms (all males, *orestes*: 1.8–13.8 mm; *rectirostris*: 1.0–13.8 mm; *saul*: 1.3–12.0 mm), hence we failed to detect stable significant differences with respect to geographic ranges.

Morphometric variation and body size

Body length data were obtained directly from specimen labels. The total length (including bill) varied between 117 mm (*L. l. greenewalti*, male) and 136 mm (*L. l. saul*, male). For *L. l. lafresnayi*, males had means of 124 mm (112–133 mm; n = 13) and females of 120 mm (n = 3). For males of *L. l. saul*, we noted lengths of 119–136 mm (mean = 125.2 mm, n = 10), whereas two females were both 126 mm. Males (mean = 127.6 mm, n = 9) and females (mean = 129.6 mm, n = 8) of *L. l. liriope* are

TABLE 2. Biometric affinities of all recently recognized taxa of *Lafresnaya* based on examined skins (n = 243); given are means ± s.d., specimen numbers (in brackets), and value ranges. Asterisk indicates ssp. nov.

Taxon/Sex	Mensural characters (mm)				
	Bill length	Bill width	Wings	Rectrix 1	Rectrix 2
L. l. liriope					
Male	29.4 ± 0.7 (11)	2.0-2.0 (2)	63.9 ± 1.6 (10)	37.1 ± 1.4 (11)	41.1 ± 1.2 (9)
	28.2-30.0		62.0-66.2	34.6-39.0	39.4-43.3
Female	29.4 ± 1.0 (15)	1.6 ± 0.1 (6)	62.4 ± 1.9 (14)	37.6 ± 1.3 (13)	39.7 ± 2.2 (12)
	27.7-31.7	1.4-1.7	58.3-65.0	34.1-39.2	35.8-42.2
L. l. lafresnayi					
Male	28.5 ± 0.9 (27)	1.9 ± 0.2 (17)	63.7 ± 1.5 (30)	36.5 ± 1.0 (29)	41.6 ± 1.5 (29)
	26.2-30.4	1.6-2.2	59.4-66.6	34.0-38.0	38.6-44.7
Female	29.1 ± 0.8 (17)	2.0 ± 0.1 (7)	59.7 ± 1.7 (19)	36.4 ± 1.0 (17)	38.2 ± 1.3 (17)
	27.9-30.3	1.9-2.2	56.7-62.7	34.9-38.7	36.3-41.8
L. l. greenewalti					
Male	29.9 ± 0.6 (11)	2.0 ± 0.2 (13)	64.2 ± 0.9 (11)	36.5 ± 1.2 (14)	40.6 ± 1.0 (13)
	28.8-31.0	1.7-2.2	63.0-65.6	34.8-38.9	39.4-42.8
Female	30.5 ± 0.8 (4)	1.9 ± 0.1 (3)	60.9 ± 0.8 (4)	36.6 ± 0.3 (4)	37.7 ± 0.4 (4)
	29.4-31.2	1.8-2.0	60.4-62.0	36.3-37.0	37.3-38.2
L. l. tamae					
Male	29.2 ± 0.7 (5)	1.9 ± 0.2 (5)	64.7 ± 1.3 (5)	36.8 ± 0.7 (5)	42.1 ± 1.3 (5)
	28.2-29.8	1.7-2.1	63.4-66.6	35.6-37.5	40.4-43.7
Female	30.1-30.7 (2)	1.9-2.1 (2)	60.5-60.7 (2)	37.5-38.9 (2)	38.4 (1)
*L. l. longirostris**					
Male	30.8 ± 0.6 (11)	1.9 ± 0.3 (11)	62.8 ± 1.4 (13)	37.2 ± 1.1 (13)	41.2 ± 0.9 (13)
	30.2-31.8	1.5-2.4	59.6-65.2	34.6-38.8	39.4-42.7
Female	31.3-32.6 (2)	1.9 ± 0.2 (4)	60.1 ± 1.0 (5)	37.2 ± 0.9 (5)	38.8 ± 0.8 (5)
		1.6-2.0	59.0-61.3	36.2-38.6	37.9-40.0
L. l. saul					
Male	29.0 ± 0.8 (59)	1.8 ± 0.3 (44)	62.2 ± 1.5 (65)	36.7 ± 1.1 (66)	40.6 ± 1.4 (61)
	27.0-30.9	1.2-2.3	59.1-65.1	34.2-39.0	35.5-43.7
Female	29.8 ± 1.1 (39)	1.9 ± 0.2 (39)	59.6 ± 1.8 (41)	36.6 ± 1.3 (39)	38.1 ± 1.5 (39)
	26.7-31.9	1.4-2.4	54.6-64.6	33.4-39.1	35.2-41.9
L. l. orestes					
Male	28.5 ± 0.6 (8)	1.6 ± 0.3 (9)	61.3 ± 0.8 (10)	36.9 ± 1.3 (10)	40.4 ± 1.1 (9)
	27.4-29.3	1.2-2.1	60.1-62.4	34.8-39.0	38.9-41.7
Female	29.0 ± 1.0 (5)	1.8 ± 0.2 (4)	59.5 ± 1.7 (5)	37.2 ± 1.4 (4)	38.0 ± 1.0 (5)
	27.7-30.0	1.6-2.0	57.8-61.8	35.2-38.2	36.6-39.2
L. l. rectirostris					
Male	27.7 ± 0.7 (20)	1.7 ± 0.3 (17)	63.7 ± 1.1 (21)	37.7 ± 1.6 (22)	42.4 ± 1.9 (21)
	26.7-29.0	1.2-2.2	62.0-65.8	33.5-40.6	37.4-45.9
Female	29.0 ± 0.7 (22)	1.7 ± 0.3 (16)	61.1 ± 1.9 (23)	37.5 ± 1.1 (22)	39.1 ± 1.8 (21)
	27.8-30.0	1.3-2	56.0-64.6	35.5 ± 39.2	33.5-42.1

slightly larger than the preceding taxa, in contrast to individuals of *L. l. tamae* (males: mean = 122.5 mm, n = 5). The measurements provided for *L. l. longirostris* (ANSP collection) are clearly smaller than in all other conspecifics (e.g., for males: 90–95 mm, n = 4; see descrip-

tion) but may exclude bill length (see Table 2).

The measurements of five biometric characters determined for the recently recognized taxa of *Lafresnaya* are summarized in Table 2. All conspecifics are relatively similar, as indicated by the strong overlap within most characters. Thus the only slight geographical variation is often masked by individual variation or sexual differences. As is typical for most trochilids, males have on average shorter bills but longer wings and rectrices than females.

The shape and length of the bill provide major diagnostic means for the separation of *Lafresnaya* subspecies. Its decurvature varies clinally and is minor in the northern forms *liriope*, *greenewalti*, *lafresnayi*, *longirostris*, and also in the southernmost subspecies *rectirostris*, but more pronounced in *saul* and particularly *orestes* (this being the only character in which the latter can be sufficiently distinguished from *rectirostris*; see also Zimmer 1951). *L. l. longirostris* clearly exhibits the longest bill of all species members, averaging 30.8 mm in males (e.g., $P < 0.001$ vs nominate birds). Though the number of female *longirostris* specimens, due to numerous individuals with broken bills, was insufficient for statistical comparison (n = 2; cf. Table 2), the bill length of the two available specimens exceeds those of the other races (except for one individual of *L. l. liriope*). Both length and width of the bill decrease slightly from north to south in males, the latter character averaging in males between 2.0 mm (*liriope*, *greenewalti*) and 1.6 mm (*orestes*). Males of race *saul* have the bill longer than those of *rectrirostris* ($P < 0.001$) and slightly wider than *orestes* males ($P < 0.05$).

Wing length differences between subspecies are restricted to females of the northern taxa (see Table 2). Individuals of *liriope* possess prolonged remiges compared with females of *lafresnayi* ($P < 0.001$), *longirostris* ($P < 0.01$), and *greenewalti* ($P < 0.05$). Within *L. l. lafresnayi*, males from the Serrania Périja (pool 1, Fig. 3) are largest, differing both in wings ($P < 0.01$ vs pool 3; $P < 0.001$ vs pool 4) and rectrices (r5: $P < 0.001$ vs pool 4) from more southerly populations. Based on all mensural data (Table 2, Fig. 3), the population from the Páramo de Tamá ("*tamae*", pool 3) proves to be inseparable from adjacent populations of the nominotypical form.

DISCUSSION

Taxonomy

The early taxonomic history of *Lafresnaya* is rather obscure, both in terms of the generic and species nomenclature. Previously placed in the 19th-century assemblage *Trochilus* and subsequently in *Calothorax* (Gray 1844–49), Bonaparte (1850) introduced the currently valid genus name *Lafresnaya*. For uncertain reasons the latter was later substituted by *Entima* (Cabanis & Heyne 1860) and *Euclosia* (Mulsant *et al.* 1866). Nevertheless, the emendation *Lafresnayea* (after the French ornithologist Lafresnaye) was predominant until the early 20th century (e.g., Hartert 1900, Chapman 1917, Simon 1921).

At the lower taxonomic level, *L. l. saul* (Delattre & Bourcier 1846) has not been spared from similar nomenclatural confusion since the form *gayi* (Bourcier & Mulsant 1846), apparently described a few weeks before the publication of the former, was subsequently often used instead of the name *saul* (e.g., Simon 1921). Since Bourcier was involved in both descriptions, it seems unlikely that these forms, both characterized by a whitish tail, refer to the same taxon; but the fact that the *gayi* holotype appears to be lost leaves this question, as well as that of its true origin, unanswered (for details, see Zimmer 1930). Consequently, the name *saul* has been applied by all more recent taxonomists.

L. l. liriope was initially considered to be specifically distinct from *L. lafresnayi* (Bangs

1910). Prior to the description of *L. l. greenewalti* (Phelps & Phelps 1961), most major reviewers allocated the population from the Andes of Venezuela either to *liriope* or to *saul* on the basis of a changing taxonomic concept (see above; e.g., Hartert 1900, Simon 1921, Todd 1942, Peters 1945, Zimmer 1951). The population from southwestern Táchira, more recently described as *L. l. tamae* (Phelps & Aveledo Hostos 1987), was hitherto included in the taxa *liriope* or *greenewalti* (Phelps & Phelps 1961, Hilty & Brown 1986). This study reveals that *tamae* should be disgarded as a valid species member since the pale horn tail coloration is matched by several more southerly representatives of the nominotypical form (pool 3, Colombia), suggesting clinal variation in this character with *L. l. greenewalti*.

Biogeographic and phylogenetic aspects

Unlike other high Andean trochilid clades of similar geographic distribution, *Lafresnaya* shows a relatively homogeneous pattern of morphological differentiation which renders the evaluation of its biogeographic origin more difficult. Consequently, this question may be answered from a more phylogenetic point of view. Based on various characteristics, it has been postulated that the genus might be closely related to two other taxa, the sunbeams *Aglaeactis* and the hillstars *Oreotrochilus* (e.g., Fjeldså & Krabbe 1990, Schuchmann 1999), that occur partly in sympatry with members of *Lafresnaya*. *Aglaeactis* spp. share some ethological features with *Lafresnaya*, e.g., a prominent monosyllabic flight call absent from the bioacoustic repertoire of all other Andean trochilids (KLS, pers. obs.). Moreover, both groups build similar cup-shaped nests, usually located in the forks of branches (unlike the saddle-nest type of most trochilines). However, as can be judged from external morphological features, e.g., the dorsal and tail coloration (strongly pigmented, mostly rufous tails), *Aglaeactis* appears to be more closely related to *Boissonneaua* (Fjeldså 1992). In this respect, *Lafresnaya* more resembles *Oreotrochilus*, chiefly in having a blackish belly in males and a similar tail pattern (whitish with green inner rectrices or rectrix tips in *Oreotrochilus* and most members of *Lafresnaya*) in common. Given a close phylogenetic relationship of these groups, one can postulate a whitish-tailed ancestral population. This would suggest that *Lafresnaya* more likely originated in the central than in the northern Andes, e.g., in the range of the present subspecies *saul* or *rectirostris*. If *Aglaeactis* is considered as the nearest relative of *Lafresnaya*, the common precursor of both taxa would have been characterized by more pigmented rectrices, thus pointing to an evolutionary center located in the northern Andes (present range of nominotypical form and *L. l. longirostris*).

The disjunct occurrence of whitish rectrices in *Lafresnaya* represents a good example of a leap-frog pattern (Remsen 1984). Together with the intergradation phenomena in tail coloration observed in some subpopulations, this can be best explained by rapid adaptive radiations across the Andean range. Subsequently, mutation-sensitive characters (e.g., bill length and shape) were moderately modified depending on local conditions. For example, the latter is expressed by the bill elongation of *L. l. longirostris*, a feature similarly pronounced in two *Eriocnemis* taxa (*E. derbyi longirostris*, *E. mosquera bogotensis*; Schuchmann *et al.* 2001) endemic to the same region of the Cordillera Central in Colombia. Nevertheless, clarifying the actual phylogenetic relationships and evolutionary traits of *Lafresnaya*, as well as of other montane hummingbird clades, will require further analyses, including ethological and molecular biological aspects.

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APPENDIX 1. Localities and altitudes (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 (Meyer de Schauensee 1949), listed from N to S (coordinates after Paynter 1982, 1992, 1993, 1997; Stephens & Traylor 1983; n. loc. = not located).

L. lafresnayi liriope. COLOMBIA: Sierra Nevada de Santa Marta: San Pedro, Magdalena, altitude ?, 11°14'N/74°11'W; Cuchilla San Lorenzo, Magdalena, 2000 m, c. 11°10'N/74°07'W; San Miguel, La Guajira, 1700 m, 10°58'N/73°29'W; Macotama, La Guajira, 2500 m, 10°55'N/73°30'W; Chendúcua, Cesar, 1775–1900 m, 10°47'N/73°25'W; San José, Cesar, 2150 m, 10°45'N/73°24'W.

L. l. lafresnayi (including *L. l. tamae**). VENEZUELA: Camp Frontera 2, Zulia, 3000 m, c. 09°59'N/72°58'W; Cerro Viruela, Zulia, 3100 m, n. loc.; Cumbres Cerro El Retiro, La Rebancha, Táchira, 2800 m, 07°30'N/72°20'W; Cerro Las Copas*, La Rebancha, Táchira, 2200–2700 m, 07°27'N/72°22'W; Páramo de Tama*, Camp, Táchira, 2400–2500 m, 07°25'N/72°26'W;

Cerro El Cobre*, Táchira, 2800 m, 07°25'N/72°21'W. COLOMBIA: above Hiroca, Serranía de Perijá, Cesar, 2900–3050 m, c. 09°42'N/73°05'W; Peña Blanca, Boyacá (?), 2800 m, c. 06°33'N/72°30'W; Pacho, Las Palmas, Cundinamarca, 1859 m, 05°08'N/74°10'W; La Vega, Hacienda El Roble, Cundinamarca, altitude ?, c. 05°00'N/74°21'W; Páramo de Guasca, 3000–3300 m, c. 04°55'N/73°52'W; Laguna de Pedropalo, Cundinamarca, 2010 m, 04°45'N/74°24'W; La Calera, Cundinamarca, 2718 m, 04°43'N/73°58'W; Hacienda de Fute, km 27 between Mosquera/La Mesa, Cundinamarca, altitude ?, c. 04°38'N/74°28'W; Bogotá, Cundinamarca, altitude ?, 04°36'N/74°05'W; Subía, Cundinamarca, 1900 m, 04°34'N/74°27'W; Choachí, Cundinamarca, 2000–2700 m, 04°32'N/73°56'W; Chipaque, Cundinamarca, 2470 m, 04°27'N/74°03'W; El Peñón, Cundinamarca, 2880 m, 04°26'N/74°18'W; El Roble, Cundinamarca, 2440 m, c. 04°23'N/74°19'W.

L. l. greenewalti. VENEZUELA: Mérida: Llano Rucio, 2500 m, 09°00'N/71°05'W; Páramo Conejos, 2000 m, 08°50'N/71°15'W; La Culata, 4000 m, 08°45'N/71°05'W; Valle, 2500 m, 08°40'N/71°06'W; Páramo Escorial, 2500 m, 08°38'N/71°05'W; Páramo Tambor, 3000 m, 08°36'N/71°24'W; Sierra Moñtanas, 3000 m, c. 08°36'N/71°00'W; Páramo de Mérida, 3000 m, 08°36'N/71°00'W; Sierra Nevada, 2300 m, 08°33'N/71°03'W; Los Nevados, 3000 m, 08°28'N/71°04'W; Páramo de Aricagua, El Muerto, 3000 m, 08°20'N/71°11'W; Boca de Monte, Pregonero, 2400 m, 08°01'N/71°46'W.

L. l. longirostris, ssp. nov. COLOMBIA: Páramo Sonsón, Antioquia, 3000 m, 05°43'N/75°15'W; El Zancudo, Caldas, 2400 m, 05°05'N/75°30'W; Santa Isabel, Quindío, 3650 m, 04°47'N/75°28'W; Boquerón del Quindío, Quindío, c. 04°38'N/75°32'W: Madim, 2500 m, Callagos, 3000 m, Yerbabueno, 3000 m, Volcancito, 3500 m, all n. loc.; Laguneta, Quindío, 2150–3050 m, 04°35'N/75°30'W; Toche, Tolima, 2100–2250 m, 04°32'N/75°25'W; El Edén, Tolima, 2530 m, 04°30'N/75°20'W; Río Toche, Tolima, 2100 m, 04°26'N/75°22'W; San Antonio (= Tocotá), Valle del Cauca, 2100 m, 03°30'N/76°38'W.

L. l. saul. COLOMBIA: Hacienda La Ilusión, Rio Urrao, base of Páramo Frontino, Antioquia, 2725 m, 06°25'N/76°05'W; San Antonio (= Tocotá), Valle del Cauca, 2100 m, 03°30'N/76°38'W; Cali, Alto Pato, PNN Farrallones de Cali, Valle del Cauca, 3600 m, c. 03°22'N/76°45'W; Corea, PNN Farallones de Cali, Valle del Cauca, 2650 m, n. loc.; Est. Terminales, Páez, Nevado del Huila, Cauca, 2800–2970 m, 02°48'N/75°57'W; Inzá, Finca Santo Tómas, Cauca, 2630 m, 02°33'N/76°03'W; Marquetalia, Cauca, 2000 m, n. loc.; Páramo de Puracé, Cauca/Huila, 3300 m, c. 02°24'N/76°23'W; Cordillera de Guamués, Nariño, 3400 m, 00°50'N/77°20'W; Cerro Pax, Nariño, 3350 m, 00°23'N/77°26'W. ECUADOR: San Francisco, Carchi, altitude ?, 00°50'N/77°41'W; S of road Maldonado-Tulcán, Río de la Plata, Carchi, 2225 m, 00°40'N/78°02'W; El Pun, Carchi, 2600–2800 m, 00°40'N/77°37'W; W slope Cerro Mongus, 3 km SE Impueran, Carchi, 3300 m, 00°27'N/77°52'W; Mindo, Pichincha, altitude ?, 00°02'S/78°48'W; Verdecocha, Pichincha, 2850 m, 00°06'S/78°36'W; Quito, Pichincha, c. 2820 m, 00°13'S/73°30'W; Lloa, Pichincha, 3577 m, 00°15'S/78°35'W; Chillo Valley, Pichincha, 3050 m, 00°20'S/78°27'W; Papallacta, Napo, 3150 m, 00°22'S/78°08'W; Cuyujúa, Napo, 2400 m, 00°24'S/78°02'W; Baeza, Napo, 1250 m, 00°27'S/77°53'W; Ambato, Tungurahua, 2600 m, 01°15'S/78°37'W; Baños, Tungurahua, 2200 m, 01°24'S/78°24'W; Runtún, Tungurahua, 1850 m, 01°26'S/78°24'W; Volcan Tungurahua, Tungurahua, 2300 m, 01°27'S/78°26'W; Riobamba-

Guaillabamba, Chimborazo, 3500 m, 01°40'S/78°38'W; Chaguarpata, Chimborazo, 1775 m, c. 02°07'S/78°59'W; Hacienda Jalancay, near Chunchi, Chimborazo, 2000 m, c. 02°17'S/78°55'W; San Vicente, Morona-Santiago, 3100 m, c. 02°58'S/78°33'W; San Martin, Azuay, 2800 m, 03°11'S/79°13'W; Taraguacocha, El Oro, 2950 m, 03°40'S/79°40'W; Loja, Loja, 2200 m, 04°00'S/79°13'W; Nudo de Cajanuma (= Cajanuma Divide), Loja, 2400–2600 m, 04°05'S/79°12'W; 9 km E Jimbura, Zamora-Chinchipe, 2700 m, 04°38'S/79°26'W; E slope Cordillera Lagunillas, 25 km SSE Jimbura, Zamora-Chinchipe, 3050 m, c. 04°47'S/79°24'W. PERU: Cerro Chinguela, Piura, 2900 m, 05°07'S/79°23'W; Cruz Blanca, 33 km SW Huancabamba, Piura, 2900–3050 m, 05°20'S/79°32'W; Canchaque Tambo, Piura, 3300 m, 05°21'S/79°33'W; Palambla, Piura, 1250 m, 05°23'S/79°37'W; Quebrada Las Palmas, 13 km WSW Chontalí, Cajamarca, 2220–2250 m, 05°40'S/79°12'W; Quebrada Lanchal, 8 km ESE Sallique, Cajamarca, 2900–2925 m, 05°41'S/79°15'W; Chira, Cajamarca, 2290 m, 06°16'S/78°42'W; Cutervo, Cajamarca, 2650 m, 06°22'S/78°51'W; 7 km N, 3 km E Chota, Cajamarca, 2650 m, 06°33'S/78°39'W; Chugur, Cajamarca, 2745 m, 06°40'S/78°45'W.

L. lafresnayi orestes. PERU: Amazonas: Cordillera de Colán, E of La Peca Nueva, 2440 m, 05°34'S/78°17'W; 33 km NE Ingenio, on road to Laguna Pomacochas, c. 2200 m, 05°50'S/77°55'W; La Lejia, 2745 m, 06°10'S/77°31'W; Leimebamba, 2135 m, 06°41'S/77°27'W; San Pedro, SE of Leimebamba, 2625–2865 m, n. loc.; Lluy, 3200 m, 06°45'S/77°49'W.

L. lafresnayi rectirostris. PERU: Mashua, La Libertad, 3050 m, 08°12'S/77°14'W; Hacienda Paty, 11 km NW Cordillera Carpish, Huánuco, 2450 m, 09°38'S/76°08'W; above Carpish Tunnel, Huánuco, 2760 m, c. 09°40'S/76°05'W; Bosque Zapatogocha, Huánuco, 2530–2660 m, 09°40'S/76°03'W; Hacienda Huarapa, 26 km NE of Huánuco (09°55'S/76°14'W), Huánuco, 2745 m, n. loc.; Millpo, E of Tambo de Vacas, Huánuco, 3600 m, c. 09°42'S/75°47'W; Panao Mountains, Huánuco, 3140 m, 09°50'S/76°02'W; Huancapata, Huánuco, 2750 m, 09°50'S/76°00'W; Pachachupan, Huánuco, 2800 m, n. loc.; Pampa Playa, 8 km NW Cushi, Pasco, 2100 m, c. 09°51'S/75°37'W; Pagancho (= Huánuco Mountains), Huánuco, 3600–3720 m, c. 09°54'S/76°09'W; San Pablo, Pasco, 2290 m, 10°27'S/74°52'W; Rumicruz, Pasco, 2960 m, 10°44'S/75°55'W; Huacapistana, Junín, 2745-3050 m, 11°14'S/75°29'W; Quebrada Tranca, near Palca, Junín, 2900 m, c. 11°19'S/75°33'W; Maraynioc, Junín, 3660 m, 11°22'S/75°24'W; Cachupata, Cuzco, 3555 m, 13°17'S/71°22'W; Pomayaco, near Ahuayro (13°22'S/73°52'W), Apurímac, 2745 m, n. loc.; Bosque Ampay, Apurímac, 2800 m, 13°38'S/72°57'W; Cerro Turronmocco, Apurímac, 3500 m, 14°03'S/73°21'W.