Ornithol. Anz. 43: 115-136

Biogeographic and taxonomic revision of the trainbearers *Lesbia* (Trochilidae), with the description of two new subspecies

André-A. Weller and Karl-L. Schuchmann

Biogeografische und taxonomische Revision der Kolibrigattung *Lesbia* (Trochilidae), mit Beschreibung von zwei neuen Subspezies.

Basierend auf Verbreitung und Gefiedermorphologie werden die Biogeografie und Taxonomie der weitverbreiteten andinen Kolibrigattung *Lesbia* LESSON, 1833 untersucht. Gegenwärtig werden zwei Arten anerkannt, die Schwarzschwanz-Lesbia *(L. victoriae)* und die Grünschwanz-Lesbia *(L. nuna)*. Aufgrund geografischer Variation in der Schwanzfärbung und den biometrischen Merkmalen bei *L. nuna* erscheint aber die taxonomische Trennung von Goulds Lesbia *(L. gouldii)* gerechtfertigt. Die Typusexemplare von »*Lesbia eucharis*«, die bisher als Unterart von *L. nuna* mit Verbreitungsgebiet in Huánuco, Zentralperu, angesehen wurden, stammen aus den Nordanden und repräsentieren wahrscheinlich Hybriden von *L. gouldii* × *L. victoriae*. Die zentralperuanische Population von Goulds Lesbia sollte daher als neue Unterart, *L. gouldii huallagae* subsp. nov., geführt werden. Sie ist durch eine stark bronzegrüne Färbung und die weißlichen Fransen im Bauchgefieder der Männchen gekennzeichnet. Als weiteres neues Taxon wird *L. gouldii aureliae* subsp. nov. von Südecuador beschrieben, charakterisiert durch eine goldbronzene Färbung des Grundgefieders. Die vorliegende Studie bestätigt zudem die taxonomische Eigenständigkeit von *L. nuna boliviana* und *L. gouldii* (früher *nuna*) *gracilis*, während die Validität von *L. victoriae aequatorialis* nicht durch morphometrische Merkmale gestützt wird. Morphologische Ähnlichkeiten (Weibchengefieder, Schwanzmuster, Körpermaße) deuten eine enge Verwandtschaft von *Lesbia* mit den Kleinschnabelkolibris *(Ramphomicron)* und dem Sapphokolibri *(Sappho sparganura)* an.

Key words: *Lesbia*, *L. gouldii*, *L. gouldii huallagae* subsp. nov., *L. gouldii aureliae* subsp. nov., Trochilidae, biogeography, taxonomy.

Dr. André-A. Weller and Prof. Dr. Karl-L. Schuchmann, Alexander Koenig Research Institute and Museum of Zoology, Leibniz Institute for Terrestrial Biodiversity, Research Group: Biology and Phylogeny of Tropical Birds, Adenauerallee 160, D-53113 Bonn, Germany;
e-mail: kl.schuchmann.zfmk@uni-bonn.de

Introduction

Current hummingbird taxonomy and systematics still dates back to the middle, or even the beginning of the 20th century (e.g., Simon 1921, Peters 1945, Zimmer 1951). Recent studies have demonstrated vigorously the need for biogeographic-systematic revisions for an appropriate classification both at the intrageneric and genus level (e.g., Graves 1986, Stiles 1996, Hinkelmann & Schuchmann 1997, Weller 1998, Peterson & Navarro 2000, Schuchmann et al. 2001). The present paper focuses on the biogeography, geographic variation, and taxonomy of the Andean taxon *Lesbia* (Lesson, 1833) and reassesses the current species limits based on the actual morphological and distributional patterns of these hummingbirds. Moreover, we present qualita-

tive and quantitative data on intraspecific variation. This includes a discussion of the affinities of the enigmatic *L. eucharis* (Bourcier & Mulsant, 1848), presently included as a subspecies in *L. nuna*. Our results indicate that *Lesbia* contains more than two species and the existence of additional subspecies, due to previously unrecognized geographic variation both in color and morphometric features. Finally, biogeographic and morphological findings point to a close affinity of *Lesbia* to the high-Andean taxa *Ramphomicron* and *Sappho*.

Material and Methods

During our survey we examined a total of 445 skin specimens (310 males, 135 females) of *Lesbia*, using methods already employed in previous biogeographic-taxonomic studies (see Schuchmann et al. 2001). Distributional analysis included the mapping of collecting sites (after Paynter 1982, 1992, 1993, 1997, Stephens & Traylor 1983). Sight records are only mentioned when they refer to distributional limits, due to the difficulties associated with the exact determination of subspecies. Morphological analysis comprised color variation and measurement of mensural characters (bill length from operculum; wing chord; innermost and outermost rectrices: r1, r5). Descriptions of plumage colors, if not given in general terms, are derived from subjective impression (due to iridescence), refer to Smithe (1975; names in brackets, capitalized). To test for statistically significant differences in biometry between populations ($n \geq 4$ for individuals of each sex), specimens from one locality or adjacent collecting sites (not separated by topographical barriers like high mountain ranges or broad, arid valleys, and mostly within 1° latitude/longitude) were grouped in pools (Vuilleumier 1968) and compared using parametric test methods (Student's *t*-test, based on ANOVA; significance level $P < 0.05$). Immature birds, chiefly identified by their female-type plumage and shortened outer tail feathers, were therefore excluded from the statistical analysis of biometric parameters.

Taxonomic decisions are based on the Biological Species Concept (Mayr 1942, 1969), including the recognition of subspecies based on Mayr's 75 % rule and that of allospecies in the case of isolated geographic ranges.

Results and Discussion

Taxonomy and distribution. During the early taxonomic history of *Lesbia* LESSON, another synonym, *Psalidoprymna* (Cabanis & Heine, 1860), was used by various subsequent authors (e.g., Hartert 1900, Simon 1902, 1921, Chapman 1917, 1926; Table 4). Moreover, the name *Lesbia* was occasionally applied to species included currently in *Aglaiocercus* (Simon 1921).

According to the recent taxonomy (Schuchmann 1999), *Lesbia* includes two species, the Black-tailed Trainbearer *L. victoriae* (Bourcier & Mulsant, 1846) and the Green-tailed Trainbearer *L. nuna* (Lesson, 1831). In the earlier literature, Gould's Trainbearer *L. gouldii* (Loddiges, 1832; with the ssp. *gouldii, gracilis, pallidiventris*) was sometimes considered specifically distinct from *L. nuna* (e.g., Cory 1918, Meyer de Schauensee 1949). Within the present *L. nuna* complex, five to six subspecies (*gouldii, gracilis, pallidiventris, eucharis, nuna, boliviana*) are recognized, whereas *L. victoriae* comprises three to four subspecies (*victoriae, aequatorialis, juliae, berlepschi*; Hilty & Brown 1986, Fjeldså & Krabbe 1990, Schuchmann 1999, Ridgely & Greenfield 2001a, Dickinson 2003). Their distributional ranges can be summarized as follows (taxa listed from north to south):

(1) *L. victoriae*

(a) *victoriae* (Bourcier & Mulsant, 1846) – Cordillera Oriental, Colombia, and Andes of S Colombia (Nariño) to SC Ecuador;

(b) *aequatorialis* (Boucard, 1893) – Andes of NW to SC Ecuador;

(c) *juliae* (Hartert, 1899) – Andes of S Ecuador to C Peru;

(d) *berlepschi* (Hellmayr, 1915) – Andean basins of C to SE Peru.

(2) *Lesbia nuna*

(a) *gouldii* (Loddiges, 1832) – C and E Andes of Colombia; one specimen record from W Venezuela (Andes of Mérida);

(b) *gracilis* (Gould, 1846) – Andes of N to C Ecuador;

(c) *pallidiventris* (Simon, 1902) – N Peru to both sides of the upper Río Marañon;

(d) *eucharis* (Bourcier & Mulsant, 1848) – Andean basins of central depto. Huánuco, C Peru.

(e) *nuna* (Lesson, 1831) – Andean basins of S Peru;

(f) *boliviana* (Boucard, 1891) – Andean montane basins of NW to C Bolivia.

Trainbearers are fairly common to locally abundant in semi-open bushy or mesic vegetation (sub-*páramo*, *páramo* zone, edge of *puna*), *Polylepis* (Rosaceae) woodland, second growth or humid forest (Fjeldså & Krabbe 1990). They also inhabit disturbed anthropogenic habitats, such as pastures or gardens in suburban areas, e.g., in the outskirts of Bogotá and Quito (Hilty & Brown

Table 1. Biometric affinities of all currently recognized taxa of trainbearers *Lesbia*, based on examined skins (n=445); shown are means ±SD, specimen numbers (in brackets) and value ranges for males (M) and females (F). Taxon names reflect taxonomy concept as presented in this study; asterisk indicates subsp. nov. (this study). Included is "*L. eucharis*", presumably of hybrid origin *L. victoriae* × *L. gouldii*.

Taxon / Range	Sex	Mensural characters (mm)			
		Bill length	Wing length	Rectrix 1 length	Rectrix 5 length
L. gouldii gouddii	M	12.8±0.38 (21)	50.9±1,67 (21)	21.5±0.87 (22)	111.9±3.50 (21)
W Venezuela, Colombia		11.8-13.6	47.2-53.8	20.1-23.3	106.6-119.0
	F	13.1±0.34 (11)	46.4±1.06 (11)	20.6±0.67 (10)	56.5±4.00 (10)
		12.4-13.6	45.0-48.9	19.7-21.8	49.7-60.4
L. g. gracilis	M	12.0±0.35 (30)	51.5±1.21 (28)	21.7±1.17 (30)	100.0±4.12 (28)
N Ecuador		11.4-12.9	49.7-53.6	19.3-24.8	95.2-110.6
	F	12.1±0.33 (15)	46.5±1.20 (15)	20.8±0.98 (15)	52.2±2.12 (15)
		11.5-12.7	44.6-49.5	18.5-22.2	46.7-54.5
*L. g. aureliae**	M	12.8±0.48 (14)	51.3±0.79 (14)	21.7±0.76 (14)	113.2±4.88 (13)
S Ecuador		12.3-13.7	50.2-56.1	20.0-23.6	103.0-120.1
	F	12.8±0.52 (10)	47.5±1.19 (10)	21.5±0.86 (10)	54.5±3.18 (7)
		12.1-14.0	44.8-49.4	20.0-23.1	50.0-59.1
L. g. pallidiventris	M	13.5±0.45 (50)	52.4±1.10 (54)	21.6±0.82 (57)	110.0±6.70 (51)
N Peru		12.8-14.6	50.2-56.1	20.0-23.6	96.8-121.9
	F	13.6±0.46 (25)	48.2±1.99 (25)	21.2±0.86 (27)	53.3±3.85 (26)
		12.5-14.6	45.4-52.6	19.8-23.0	48.8-64.3
*L. g. huallagae**	M	15.3±0.53 (7)	53.3±0.55 (6)	23.3±0.45 (7)	106.6±4.27 (6)
C Peru		14.5-16.1	52.6-53.9	23.0-24.3	100.2-110.6
	F	13.9 (1)	47.3 (1)	21.2 (1)	49.2 (1)
L. nuna nuna	M	17.6±0.68 (32)	55.9±1.40 (33)	23.9±1.08 (33)	119.7±6.56 (27)
S, SW Peru		16.4-18.8	53.5-59.0	21.2-25.9	109.7-136.7
	F	17.5±0.65 (12)	51.6±1.69 (12)	24.1±1.45 (14)	54.8±4.71 (14)
		16.5-18.6	49.3-55.1	20.5-25.8	45.5-62.9
L. n. boliviana	M	17.1±0.70 (7)	55.4±1.25 (7)	22.1±1.35 (7)	115.1±7.48 (7)
N Bolivia		16.0-18.4	54.5-58.2	20.3-23.6	105.3-125.7
	F	18.1 (1)	50.8 (1)	22.0 (1)	57.4 (1)
L. victoriae victoriae	M	19.1±0.67 (84)	59.9±1.41 (94)	24.2±1.01 (96)	172.6±7.98 (94)
Colombia, C Ecuador		17.3-20.5	57.0-64.7	22.1-28.2	126.8-170.4
	F	18.7±0.70 (45)	55.3±1.86 (46)	24.5±1.13 (45)	78.9±5.85 (43)
		17.3-19.9	51.8-60.3	22.6-27.2	67.2-91.9
L. v. juliae	M	16.1±0.67 (14)	61.2±1.56 (17)	25.9±0.59 (17)	111.6±4.19 (17)
S Ecuador, N Peru		14.6-17.0	59.9-66.6	25.0-27.1	100.5-118.1
	F	15.4±0.22 (5)	55.6±1.16 (5)	25.5±1.00 (5)	69.9±3.30 (5)
		15.1-15.7	54.5-57.4	23.9-26.5	65.7-74.2
L. v. berlepschi	M	18.7±0.84 (13)	62.3±1.01 (14)	26.6±1.02 (14)	124.2±4.18 (14)
C, SW Peru		17.2-20.0	60.2-63.8	25.0-28.3	116.6-130.0
	F	16.9-19.0 (2)	57.8-60.1 (2)	26.4 (1)	73.5-82.9 (2)
"L. eucharis"	M	15.2 (1)	56.2-59.9 (2)	23.2-24.2 (2)	141.7-146.5 (2)

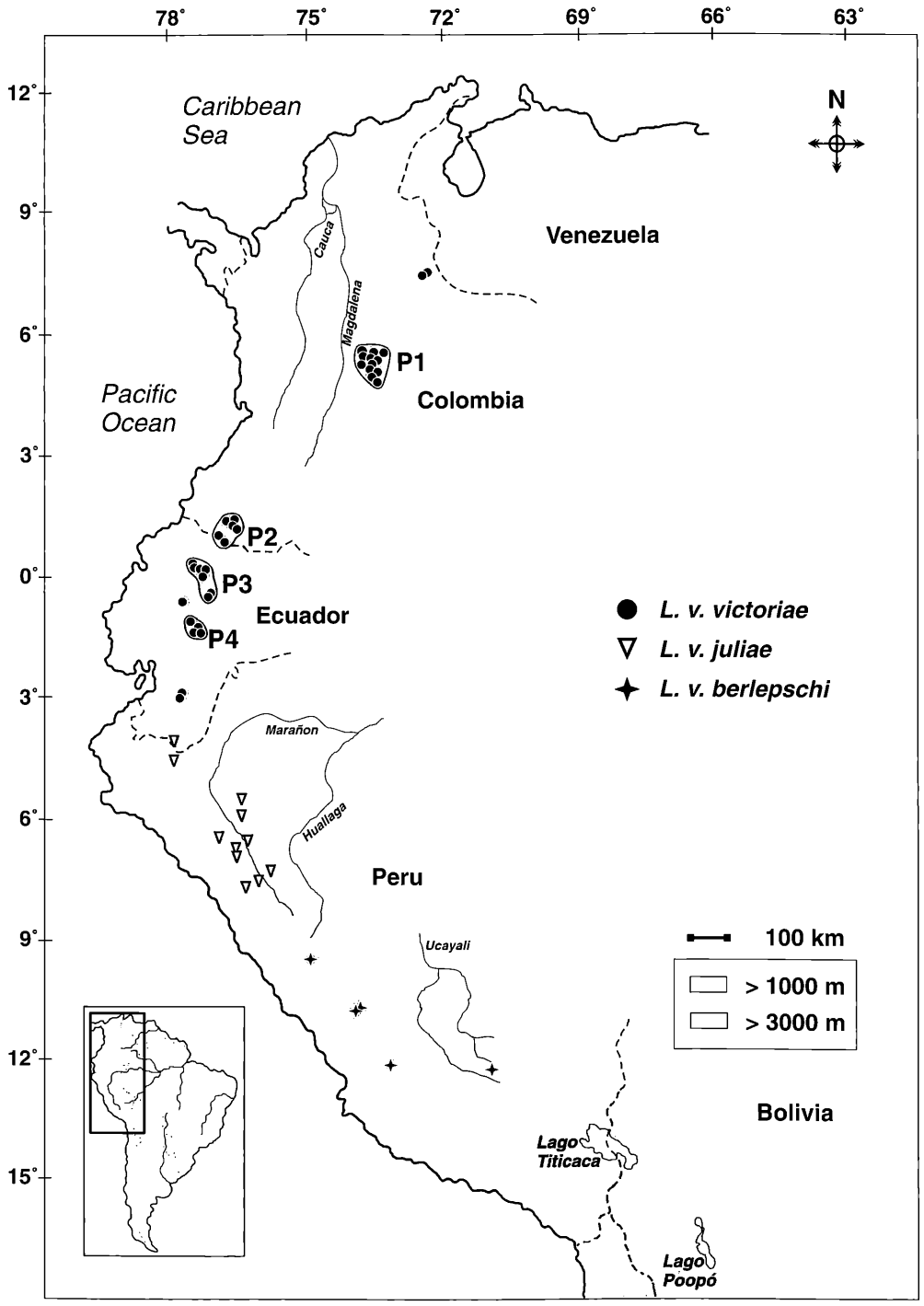

Fig. 1. Distribution and subspecies of *Lesbia victoriae*, based on study specimens and literature data (see Appendix). Localities of specimens pooled for statistical comparison are encircled, with numbers referring to pools as in Fig. 4; for coordinates and altitudes, see Appendix.

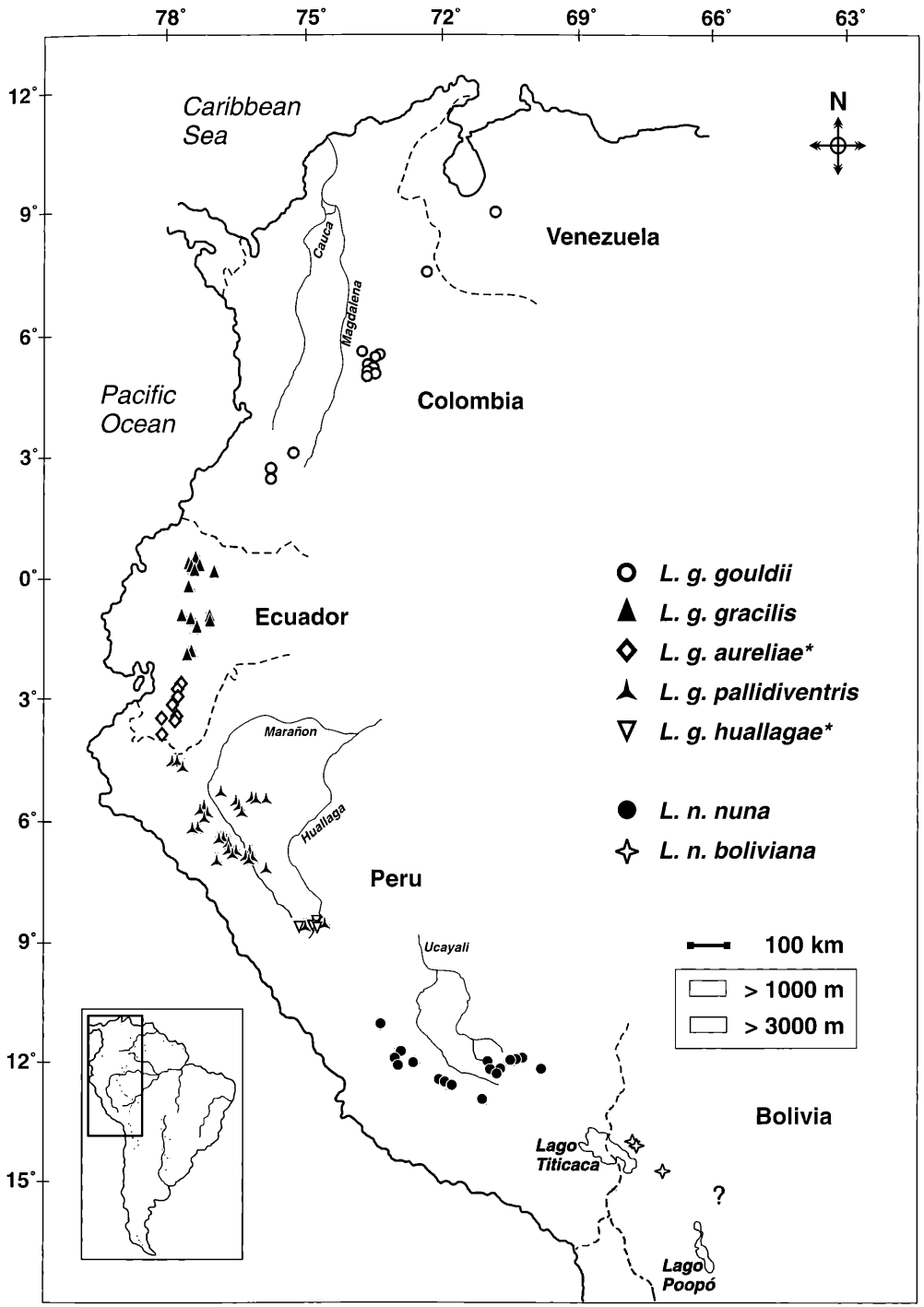

Fig. 2. Distribution and subspecies of Gould's Trainbearer *Lesbia gouldii* and Green-tailed Trainbearer *L. nuna*, based on study specimens. Taxon names reflect taxonomy concept as presented in this study; asterisk indicates subsp. nov., question mark possible range of *L. nuna boliviana* (see Fjeldså & Krabbe 1990). For coordinates and altitudes of localities, see Appendix.

Plate 1. Geographic and sexual variation in *Lesbia*. From left: *L. victoriae victoriae*, male and female; *L. gouldii gracilis*, male; *L. nuna nuna*, male and female. Plate by David Alker, UK.

1986, Ridgely & Greenfield 2001a). *L. victoriae* and *L. nuna* represent valid species under any species concept due to their sympatric occurrences in large parts of the northern and central range of the genus (Figs. 1, 2), where they are ecologically fully compatible (Fjeldså & Krabbe 1990). This may be partly explained by their different niches (i.e., *L. victoriae* in more arid habitats; Ridgely & Greenfield 2001b; but see Fjeldså & Krabbe 1990) or vertical segregation, especially in the northern Andes (Hilty & Brown 1986, Fjeldså & Krabbe 1990). Accordingly, *L. victoriae* has been mostly recorded from above 2500 m, whereas the remaining taxa are usually found at elevations between 2000 and 3000 m (Fig. 3).

Morphology and species limits. All members of the genus are sexually dichromatic, exhibiting (1) in males a greenish ventral plumage (except for abdomen) with an iridescent throat patch, and greenish disks on the under tail coverts, and (2) in females and immatures a basically whitish to buffish ventral plumage (i.e., under tail coverts) with shining greenish throat spots (Plate 1). As in many other trochilids, they are sexually dimorphic in most mensural characters (Table 1). Males are characterized by their deeply forked tail, which results from the extreme elongation of the (parallel) outer rectrices, a feature shared also by some other Neotropical trochilids, such as the sylphs *Aglaiocercus* spp., the Scissor-tailed Hum-

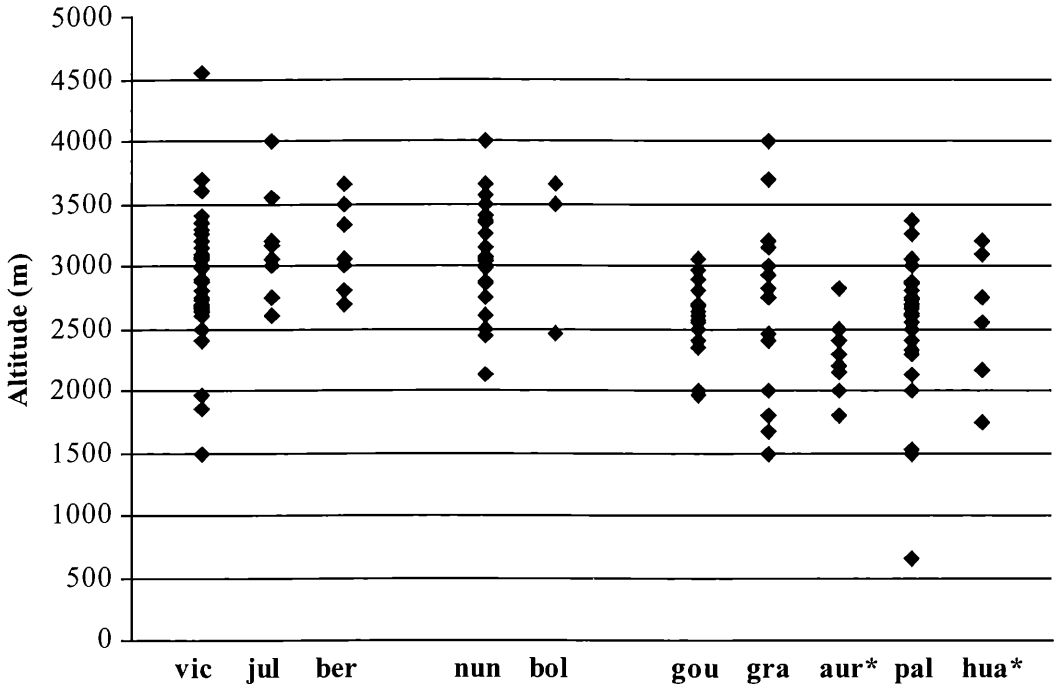

Fig. 3. Altitudinal range of *Lesbia*, based on localities of study specimens and literature data (see Appendix). Abbrevations: **vic**, *L. victoriae victoriae*; **jul**, *L. v. juliae*; **ber**, *L. v. berlepschi*; **nun**, *L. nuna nuna*; **bol**, *L. n. boliviana*; **gou**, *L. gouldii gouldii*; **gra**, *L. g. gracilis*; **aur***, *L. g. aureliae*; **pal**, *L. g. pallidiventris*; **hua***, *L. g. huallagae*. Taxon names reflect taxonomy concept as presented in this study; asterisk indicates subsp. nov.

Table 2. Color variation in males of subspecies of Gould's Trainbearer *Lesbia gouldii*. Shaded characters indicate main diagnostic features. Taxon names reflect taxonomy concept as presented in this study; asterisk indicates subsp. nov.

Character	*gouldii*	*gracilis*	*aureliae**	*pallidiventris*	*huallagae**
basic plumage	emerald to golden green	emerald to golden green	**strongly golden bronze**	emerald to golden green	**bronze-green**
throat patch	emerald green	emerald green	strongly golden green	golden to emerald green	strongly golden green
ventral fringes	grayish buff, reduced to belly	grayish to , cinnamon-buff reduced to belly	creamy buff	creamy buff	**chest pale grayish, belly creamish**
abdomen – under tail	grayish buff	**cinnamon-buff**	creamy buff	creamish to grayish buff	creamish
tail above (r1-r4, exposed)	emerald to bluish green	emerald green	emerald to golden green	emerald green	**strongly golden green**
tail above (r5, exposed), except for tip	blackish golden to bluish green	blackish emerald to golden green	blackish emerald to bronze-green	blackish golden to bluish green	dark golden green to bronze
outer web base (r5)	pale creamish	pale creamish	pale creamish	pale creamish	**grayish white**
extent of pale outer web (r5)	**three-fifths to two-thirds**	**two-thirds to three-fourths**	two-thirds	two-thirds	two-thirds

mingbird *Eugenes macrocerca* (Renner & Schuchmann 2004, this issue), the Jamaican streamertails *Trochilus* spp. and the Red-tailed Comet *Sappho sparganura* of the southern Andes. In contrast, the outermost rectrices of females and immatures reach only about one half (female) or two-thirds (immature) of the male r5 length.

The species limits of *L. victoriae* and *L. nuna* have been defined by a number of plumage characters, such as the intensity of the brilliance in body plumage, the shape of the bill and the throat patch, the tail pattern, and biometric characteristics (Schuchmann 1999, Ridgely & Greenfield 2001b; Table 1).

Diagnosis of *L. victoriae*. This species is the largest member of the genus and especially marked by a longer bill and longer wings (Table 1). There is a strong variation in the tail length of males, whereas the mean of females exceeds that of female individuals of *L. nuna*. Both sexes differ in the color pattern from other congeners. Males are marked by an elongated, rather v-shaped throat patch and under tail coverts with reduced greenish centers. The rectrices of both sexes are mostly blackish, except for the narrow greenish tips (smallest in r5) with contrasting blue-black subterminal areas. Most adult females show a reduced gorget patch or exhibit at least some strongly glittering, golden-copper-colored throat feathers. In accordance with Zimmer (1951), we found that immature males are distinguished from females by their emerald green gorget patch.

Diagnosis of *L. nuna*. Males of this taxon exhibit an oval instead of v-shaped, glittering patch on the gorget. The golden greenish areas of the male median rectrix pairs, particularly of r3-r4, are reduced and replaced basally by bluish-black to green-black subterminal areas, whereas r5 is mostly blackish, except for the bronze tips. The extension of the pale outer webs in r5 varies geographically (see Table 2). Females show dull bronze-green throat spots and buff to cinnamon abdominal parts. As in *L. victoriae*, the throat plumage of immatures closely resembles that of adult females but is marked by more prominent, irregularly distributed greenish spots (Schuchmann 1983).

However, there is further evidence for geographic variation among the populations of *L. nuna*. Males of the northern populations from Colombia to central Peru – including *gouldii*, *gracilis*, and *pallidiventris* and the form presently known as *eucharis* – are separable from the southern forms *nuna* and *boliviana* by the extended greenish sheen on the central and outer rectrices (r3-r5) that covers at least their upper half, the more bronze instead of blackish bases of these feathers, and the broader, less sharply defined bronze tips of r5. The pale outer webs of r5 in northern males are more extended than those in southern males, contrary to the latter reaching more than half of the rectrix length (Table 2). In addition, females of *nuna* and *boliviana* show bluish-green central parts of the inner rectrices (r1-r3). Northern representatives average smaller than southern ones in all morphometric characteristics, but most strikingly in bill length (Table 1).

Altogether, the southern forms *nuna* and *boliviana* occupy an intermediate morphological position (especially in tail) between the northern populations from Colombia to central Peru *(gouldii, gracilis, pallidiventris, "eucharis")* and the *L. victoriae* complex, being similar to forms of the latter in one or more morphometric traits (bill length: *L. v. juliae*; r1 length: *L. v. victoriae*; r5 length: *L. v. berlepschi*, *L. v. juliae*; Table 1). Thus we recommend to separate the northern *"L. nuna"* populations *(gouldii, gracilis, pallidiventris, "eucharis")* as an allospecies from the southern ones *(nuna, boliviana)* as *L. gouldii* (Loddiges, 1832), using the previously adopted vernacular name Gould's Trainbearer (Cory 1918, Meyer de Schauensee 1949).

Lesbia victoriae Bourcier & Mulsant, 1846

Distribution and taxonomy. The Black-tailed Trainbearer inhabits the northern and central Andes, usually occurring at higher elevations than the smaller Gould's Trainbearer (Zimmer 1930, Hilty & Brown 1986; Fig. 3). Three to four subspecies have been recognized, depending on the treatment of *L. victoriae aequatorialis* (Boucard, 1892). Two allopatric populations (see Fig. 1) are found in the northern part of range, a northeastern one, *L. v. victoriae* (eastern Andes of Colombia, chiefly in the Bogotá region) and a more southern one, either regarded as *L. v. victoriae* or *L. v. aequatorialis* (upper Cauca valley to southern central Ecuador in Shingata valley, Azuay; Hilty & Brown 1986, Fjeldså & Krabbe 1990, Ridgely & Greenfield 2001a). The latter form was initially separated from the nominate form by a distinct

bill morphology, but is presently usually synonymized with the latter (e.g., Greenway 1978, Ridgely & Greenfield 2001a). A synonym for the nominate form provided by Bourcier & Mulsant (1848) is "*Lesbia amaryllis*," because these authors apparently overlooked their earlier description of *L. victoriae* (Bourcier & Mulsant 1846; see Simon 1921).

The species' central range is occupied by *L. v. juliae*, which northward just reaches Ecuador in Loja and Zamora-Chinchipe (ANSP 185255 from SSE Jimbura, and additional sightings mentioned by Ridgely & Greenfield 2001a). *L. v. juliae* consists of allopatric subpopulations, separated by the Marañon valley. In central and southern Peru, from deptos. Huánuco to Cuzco, this subspecies is replaced by *L. v. berlepschi.*

Color variation. Males of *L. v. juliae* differ from those of other subspecies in having strong golden green, rather than emerald green, gorgets. Other differences refer to the tail and ventral parts. Males of *L. v. victoriae* have cinnamon-buff belly centers, whereas those of *L. v. juliae* and *L. v. berlepschi* are more buff or cream-colored. The pale bases of the outer webs hardly reach the middle of r5 in nominate males, but extend to two-thirds to three-fourths in the other races, and are grayish white instead of creamish in *L. v. berlepschi.*

An aberrant morph of *L. v. victoriae* is represented by a male specimen probably originating from Ecuador (AMNH 59747). The upper parts are grayish golden green, whereas the ventral plumage is golden green mixed with Grayish Olive (43), towards the belly exhibiting weakly purplish-shining disks. The gorget patch reflects silky grayish to golden green (depending on light angle). Tail and upper tail coverts show purplish to dark purplish traces, the latter being partly tinged copperish, whereas the under tail is Tawny Olive (223D). The rectrices are tipped bluish- instead of bronze-green. Another aberrant skin from "Colombia" (AMNH 38108), likely a subadult male (r5 = 144 mm), is deeply copperish in body plumage and rectrix tips and ventrally marked by a dark cinnamon-fringed belly. Finally, an immature male (AMNH 484215, "Bogotá collections") is partly leucistic, having the left outermost rectrix entirely white.

Morphometric variation. *L. v. victoriae* is the largest form in the genus, with an average wing length of 59.9 mm and r5 length of 172.6 mm in males (Table 1). For both sexes, the bill length is similar to that of *L. v. berlepschi* but differs significantly from *L. v. juliae* ($P < 0.001$). Moreover, the latter has the shortest outer rectrices within this species, whereas *berlepschi* is intermediate in this character between *juliae* and nominate birds. Females differ from males of all ages mainly in wing and r5 length (Table 1, Fig. 4; only adults shown).

Owing to the relatively scarce specimen numbers (particularly females) in *juliae* and *berlepschi*, we were able to examine only the intraspecific variation of the nominotypical form, grouping the individuals of both sexes to four different, statistically comparable pools. Using this approach, we tested the variance of all four standard mensural characters to re-evaluate the status of *aequatorialis*, initially separated by its longer bill and tail (e.g., Hartert 1900). Based on an extensive specimen series (males, $n = 94$; females, $n = 46$), we found a strong clinal north-south increase in the male bill length from the eastern Andes of Colombia to northern Ecuador (pools 1-3, Fig. 4), but only a slight decrease in central Ecuador (pool 4). In females, the character change is more pronounced (pool 2 *vs.* pool 3: $P < 0.001$). A minor but insignificant increase throughout the range is noticeable in the length of r5 of males (Fig. 4). In accordance with Zimmer (1951), these results indicate considerable overlap in both characters between adjacent populations. Consequently, *aequatorialis* is not diagnosable and thus should be synonymized with the nominotypical form.

Lesbia nuna Lesson, 1831

Distribution and taxonomy. Under the taxonomy concept used in this study, *L. nuna* consists of two allopatric populations, restricted to the Andes of southern Peru and northern Bolivia (sometimes regarded as *L. n. boliviana*; Fig. 2). Contrary to the supposition of Fjeldså & Krabbe (1990), the northernmost distributional limit of *L. nuna* is not in depto. Huancavelica but at least in southern depto. Junín; a specimen taken at Concepción (11°55'S, 75°17'W; MHNJP 3954) extends the species' known range 80 km northeastward.

The taxonomy of *L. nuna* has been controversial. Boucard (1891) described the form *boliviana* based on a single specimen from "Bolivia". Among

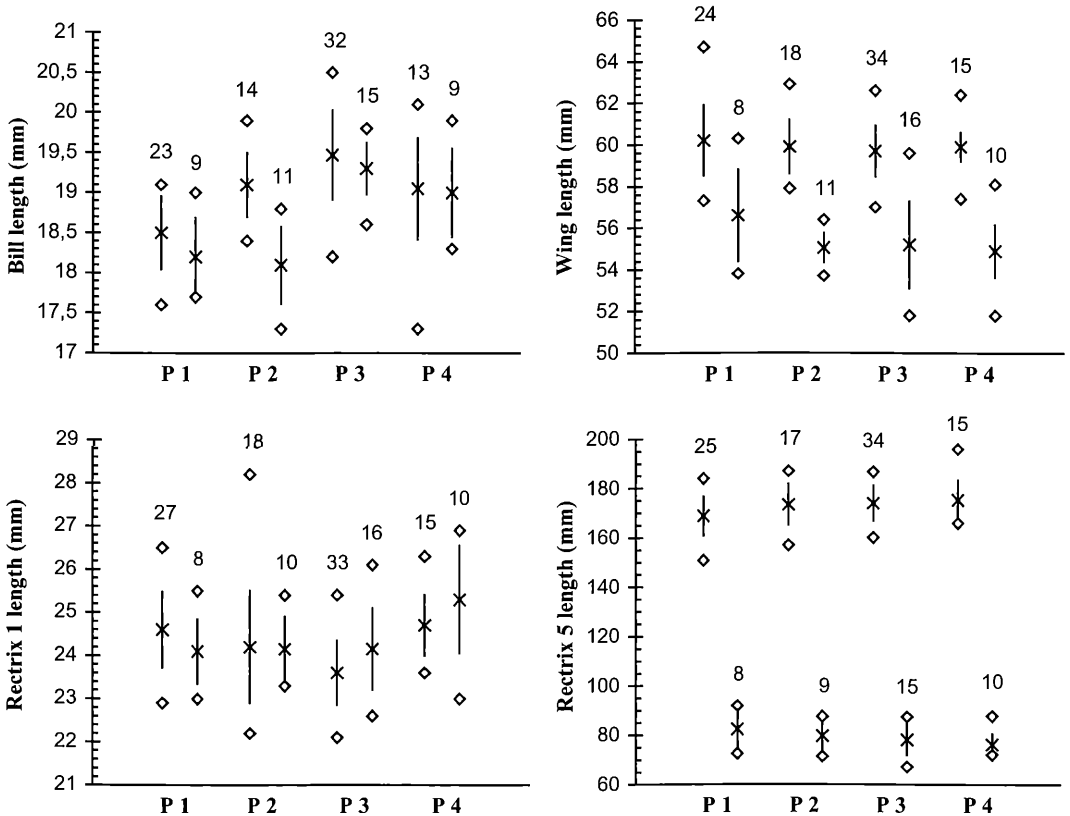

Fig. 4. Geographic variation of four morphometric characters in pools of *Lesbia v. victoriae* (cf. Fig. 1), showing means (×), extreme values (◇), standard deviations (bars), and numbers of study specimens. Left bars indicate males, right bars females.

others, Bond & Meyer des Schauensee (1943), Peters (1945) and Wolters (1982) maintained the subspecific validity of *L. n. boliviana*, whereas other taxonomists synonymized it with *L. n. nuna* (e.g., Zimmer 1951; Fjeldså & Krabbe 1990; Schuchmann 1999). A species record from depto. Cochabamba (Fjeldså & Krabbe 1990) likely refers to this population. According to Fjeldså (pers. comm.), the southern distributional limits are in northwestern prov. Chuquisaca (Sucre). We were unable to confirm records of supposed *L. n. nuna* from northwestern Bolivia (Hartert 1900, Bond & Meyer de Schauensee 1943).

Color variation. The male throat patch of both subspecies golden bronze to bronze-green. However, the outermost rectrices are mostly blackish (except for the bronze tips). The pale grayish outer web margins extend in typical adult representatives of the northern population only to about the basal half of r5 (rarely three-fifths, FMNH 222253), whereas they are reduced to approximately one third of the rectrix length in the southern population ("*boliviana*"). Among the specimens examined, we were unable to confirm the conclusion of Boucard (1891), who found the type of *boliviana* to be more "golden instead of grass green" than other *L. nuna* representatives from the Peruvian range.

Considering ventral characteristics, males have greenish belly feathers with inconspicuous pale fringes on the abdomen and under tail, which are buff to grayish in northern birds but rather cinnamon in southern ones. Females show dull bronze-green throat spots and buff to cinnamon abdominal parts. As in all other congeners, the throat plumage of immatures closely resembles that of adult females but is marked by more prominent, irregularly distributed greenish spots (Schuchmann 1983).

Morphometric variation. *L. nuna* is biometrically intermediate between *L. gouldii* and *L. victoriae* (Table 1). Local-scale statistical analysis of the adjoining central Peruvian populations of *L. gouldii huallagae* and *L. nuna* revealed significant differences for males in all mensural traits (e.g., bill, r5: $P<0.001$; females untested because of lack of data in *L. g. huallagae*).

Except for slightly longer innermost rectrices in males from Peru (r1: $P<0.05$), we found no significant differences in measurements between both populations. Zimmer (1930), on the basis of a single AMNH specimen from Bolivia, supposed that *boliviana* could be a valid taxon due to its longer bill but later withdraw his opinion (Zimmer 1951). Owing to the fairly poor collections in the species' Bolivian range (n=8, both sexes), only a single female from there was included in our analysis; its mensural characters fall within the range of northern females (Table 1). Nevertheless, evidence from both under parts and tail pattern suggests the subspecies *boliviana* to be maintained.

Lesbia gouldii Loddiges, 1832

Distribution and taxonomy. The total distribution of this species is shown in Fig. 2. In Colombia, the taxon is confined to the eastern and central Andes (*L. g. gouldii*: Meyer de Schauensee 1964, Hilty & Brown 1986) but, unlike some other high-Andean, supposedly closely related trochilids, such as *Ramphomicron* (Schuchmann 1999, Weller & Schuchmann 2002), is absent from the fairly isolated Sierra Nevada de Santa Marta. The Ecuadorian population known as *gracilis* is presently included in the nominate form (Schuchmann 1999, Ridgely & Greenfield 2001a). A single old record of *gouldii* exists from the adjacent Venezuelan Andes (Meyer de Schauensee & Phelps 1978), where Goering collected a specimen (BMNH 87.3.22.1355) labeled "Sierra Nevada, Mérida" as long ago as 1873. Hilty (2003) questions this record. In view of the lack of subsequent records it remains speculative whether the species has become extinct in this part of its range, or has been overlooked despite extensive collecting in the Mérida region. This observation is paralleled by the case of the Sapphire-vented Puffleg *Eriocnemis luciani*, a trochilid known from Venezuela only from a single 19th-century specimen taken at Páramo Conejos (Schuchmann et al. 2001).

Although the overwhelming majority of records of *L. g. pallidiventris* come from both slopes surrounding the central Río Marañon drainage (Fig. 2), three specimens (two adults, one immature) were collected by Hocking much further south in central depto. Huánuco, at Chavinillo (09°47'S, 76°35'W; MHNJP 4060) at the headwaters of the Marañon, and on the eastern bank of the Río Huallaga in the Panao region at Huancapata (09°50'S, 76°00'W; ANSP 176409-410). This is even more remarkable because these localities occur within the distributional range of the central Peruvian form currently known as *L. nuna eucharis* (Fig. 2; see below). However, the specimens in question are in all morphological characters clearly referable to the subspecies *pallidiventris*.

L. gouldii is most commonly found above 2000 m, but there exists a remarkable altitudinal variation between the populations (Fig. 3). *L. n. pallidiventris* shows the widest altitudinal range, exceptionally descending to the tropical zone of the Andean foothills in depto. Amazonas at only 650 m (at Chachapoyas area, LSUMZ 75168), but ascending to more than 3000 m in deptos. Cajamarca and La Libertad (e.g., Tayabamba).

The name *chlorura* (Gould, 1871) was occasionally applied (Zimmer 1930; Wolters 1982) for the population from the Andes of depto. Huánuco, currently regarded as *eucharis* (Schuchmann 1999). To date, the distribution of this form has remained unclear. More concrete information was provided only by Zimmer (1951), who suggested the holotype originating from "the mountains southeast of Huánuco" (1951: 47). However, almost all Peruvian specimens under study labeled as "*L. nuna eucharis*" or "*L. nuna chlorura*" were collected on the rain shadow slope south of Cordillera Carpish, located just on the opposite bank of Río Huallaga northwest of the city of Huánuco, except for two FMNH skins (# 66753-66754) originating from the so-called "Huánuco mountains" (Paynter 1983).

Curiously, the holotype of "*Lesbia eucharis*" (Bourcier & Mulsant, 1848) has been claimed to be both in the possession of the Natural History Museum, Tring (formerly BMNH; Warren 1966) and the American Museum of Natural History (Greenway 1978). Clearly, this fact raises various questions about the identity and origin of both specimens, which to our knowledge has not been sufficiently answered to date. The BMNH specimen (# 1888.7.25.185) was obtained by Gould from

J. Bourcier (Warren 1966) and is labeled "San Buenaventura, New Grenada", which likely refers to a locality near Bogotá, Colombia (not located in Paynter 1997). The AMNH type (# 38104), apparently also originating from Bourcier but later deposited in the Elliot collection, is tagged simply "New Grenada". In this context we prefer to follow Zimmer's argument (1951, for which see the detailed discussion), who states that for several reasons the latter specimen in fact represents the type examined by Gould; in any case, it remains unclear "who first accredited the bird to Colombia" (Zimmer 1951: 47). Nevertheless we disagree with Zimmer, who claimed that the *eucharis* type came from the Andes near Huánuco in central Peru (1951: 47). Because both type specimens of *L. eucharis* appear to be of uncertain geographic origin (but most likely from Colombia; cf. Zimmer 1951, Greenway 1978), a thorough character study was undertaken to re-evaluate the status of these individuals (see below). Subsequently, the findings were compared to those obtained for the other *Lesbia* taxa. This approach seemed necessary to us because (a) an earlier, superficial examination of the BMNH type revealed that it is unlikely to be a member of the *Lesbia nuna* or *gouldii* group, respectively, and (b) as a consequence, such a finding would effect the current taxonomy of one these groups (namely *L. gouldii*).

Diagnosis of "*Lesbia eucharis*". Zimmer's (1951) discussion of *eucharis* (based on the AMNH specimen), the only detailed study of this critical form after Elliot's (1878) revision, lacks evidence from other than a few morphological characters, such as bill shape (broken in that type), and coloration of the under tail and gorget. Therefore, his statement that "the type is clearly a member of the *nuna* group" needs to be questioned. Our results, based on both type specimens, contradict Zimmer's conclusion in several points.

In general appearance, both male specimens resemble *L. victoriae* rather than *L. gouldii* (the taxon complex used, in fact, for comparison by Zimmer). As already explained in the species accounts, in this sex the main distinguishing characters between both species (*L. nuna* is ignored for geographic reasons) refer to the gorget, tail coloration, abdomen, under tail, and, not least, to the mensural data. The following character descriptions, if not mentioned otherwise, refer to both types:

(1) The throat patch is emerald green mixed with golden green, but more v-shaped instead of rounded and slightly extended towards the lower throat, resembling that of *L. v. victoriae*.
(2) The four inner rectrix pairs are terminally richly emerald to golden green (not as deeply bronze-green as in typical *L. victoriae*), with the greenish areas successively reduced from r1 to r4, but not reaching the same extent as in *L. gouldii*. The bluish green subterminal coloration is reminiscent of *L. victoriae*.
(3) Like *L. gouldii*, the outermost rectrix pair (r5) is marked by a relatively broad and light bronze-green tip. The pale, creamy-colored bases of the outer webs reach about half of the length of r5.
(4) The under tail coverts exhibit golden green centres, more conspicuous than in most *L. victoriae* examined, but narrower than in typical *L. gouldii*.
(5) Abdomen and margins of the under tail coverts are True Cinnamon (139), nearly the same as those of *L. v. victoriae*. Additionally, the BMNH specimen exhibits some grayish fringes at the belly centre.
(6) Regarding the biometrics as a character unit, the two males are very similar in mensural dimensions but intermediate between *L. victoriae* and *L. gouldii* (Table 1). Although the AMNH type lacks the bill tip, Zimmer (1951) referred this bird to the *L. nuna* (= *L. gouldii*) group but concluded from the (fairly long) remaining part of the bill that it could not belong to the subspecies *nuna*, *gouldii*, *gracilis* or *pallidiventris*. However, contrary to this author our results indicate that the sum of morphological characters of *eucharis* do not agree to any presently known population of *Lesbia* (e.g., based on tail coloration or bill length; Table 1). Taking into further consideration that the often synonymized form *L. chlorura*, of which the type is unfortunately lost, also seems to lack major plumage features of the Huánuco specimens (e.g., the latter with considerably shorter tail; Gould 1871, cf. Table 1), we conclude that the population of the Andes of central Peru is presently left without a valid taxon name.

Color variation in *L. gouldii*. The major discriminating color characters of the *L. gouldii* subspecies are summarized in Table 2. A clinal north-south variation is reflected in the general plum-

age (for a detailed description, see Zimmer 1930), including the male gorget patch, which is on average more emerald green in *gouldii* but rather golden to bronze-green in Peruvian birds. The subspecies *gracilis* is intermediate in these characters and additionally marked by rich buff to cinnamon abdominal parts and fringes of belly feathers and under tail coverts, contrasting with the more pale buff tinge of *gouldii* and *pallidiventris* (Simon 1902; Zimmer 1930). Females of *L. gouldii* differ from adult males by the rich buff under tail coverts, often bearing inconspicuous traces of dull green or bronze-green centrally. As in *Ramphomicron* females (Weller & Schuchmann 2002), the creamy-whitish coloration of the outer webs in r5 extends almost to the feather tip.

Zimmer (1930) noted that males of the race *pallidiventris* differ in the amount of greenish color visible on the upper surface of the outer rectrices. Further individual variation is diagnosable in two specimens (LSUMZ, male # 91885, female # 91886) from Tayabamba, depto. La Libertad, marked by their extremely bronze body plumage. However a third specimen (female, LSUMZ 91884) has merely a weak bronze-green coloration. For geographic reasons, we tentatively assign the specimens concerned to *pallidiventris*, for which this locality represents the southernmost range limit. Further collecting data may show that this population merits taxonomic status.

As demonstrated above, the fairly distinctive population from central Peru (Fjeldså & Krabbe 1990) has not been appropriately acknowledged in the previous taxonomic literature. Based on tail characteristics, it is included in the *L. gouldii* complex. For biogeographic reasons, we recommend naming it as:

Lesbia gouldii huallagae, ssp. nov.

Diagnosis. Differs from other *L. gouldii* members by more bronze-green coloration, conspicuous light fringes in the ventral plumage of adult males, and very pale abdominal parts (similar to *L. g. pallidiventris*); in size, by longer bill (Table 3).

Holotype. Adult male, BMNH reg. no. 1946.49.416; collected at Hacienda Huarapa, depto. Huánuco, Peru, 9100 ft. (ca. 2785 m), on 5 December 1939 by A. Morrison.

Description of holotype. Bill blackish, relatively short (15 mm); head including auricular area, back, rump and upper tail coverts shining bronze-green; tail strongly forked, with exposed parts of r1-r4 shining golden green, and rectrix bases blackish green; r5 with inner webs basically purplish-black to dark golden bronze, becoming bright bronze-green towards tip, and outer webs with basal two-thirds grayish white, and terminal third blackish green except for bronze tip; gorget glittering emerald to golden green; remaining under parts weakly bronze-green with whitish buff fringes, except for flanks; abdomen whitish buff; under tail coverts centrally greenish with pale buff fringes.

Female. Cotype, adult, FMNH reg. no. 67751; collected at Chinchao, depto. Huánuco, Peru, 1740 m, on 3 November 1922 by J. T. Zimmer.

Description of cotype. Upper parts golden green to bronze-green; tail much shorter than in male (Table 1); inner four rectrix pairs emerald to bronze-green, at base more bluish to purplish black; r5 similar but outer webs mostly pale buff,

Table 3. Statistical differences in two mensural characters of male Gould's Trainbearer *Lesbia gouldii*. Specimens numbers for bill/rectrix 5 length, *L. g. gouldii*: n=21/21; *L. g. gracilis*: n=30/28; *L. g. aureliae*: n=14/13; *L. g. pallidiventris*: n=50/51; *L. g. huallagae*: n=7/6. Significance levels (Student's *t*-test, two-tailed): ***=$P<0.001$; **=$P<0.01$; *=$P<0.05$; n.s.=not significant. Taxon names reflect taxonomy concept as presented in this study; asterisk indicates subsp. nov.

Lesbia gouldii ssp.		*gouldii*	*gracilis*	*aureliae**	*pallidiventris*	*huallagae**
		Rectrix 5 length				
gouldii	Bill length		***	n.s.	***	***
gracilis				**		
*aureliae**				–		
pallidiventris				n.s.		
*huallagae**				*	n.s.	–

towards tip blackish to bronze-green; under parts basically whitish with golden to bronze-green spots, largest along the flanks; belly centre, abdomen, under tail coverts tinged pale buff.

Range. Andes of central depto. Huánuco, Peru, where it occurs on both slopes of the upper Río Huallaga valley, mainly in the Cordillera Carpish, and at the adjacent headwaters of the Río Marañon (one record).

Etymology. This taxon is named for its biogeographic center, the upper Huallaga drainage.

Remarks. The most distinctive plumage characters of *L. g. huallagae* – the bronze plumage sheen and the ventral fringes in males – have never been credited by previous authors to individuals of the Huánuco population, because the discussion of the affinities of "*chlorura*" or "*eucharis*," namely by Zimmer (1930, 1951), chiefly focused on a single type rather than on specimens actually originating from central Peru. For this study, we were able to examine a total of 10 specimens, among them only one adult female and two immatures, from six localities (see Appendix), deposited in the collections of BMNH, FMNH, and LSUMZ. Immature males look much alike adult females, but usually have a paler abdomen and more greenish under tail coverts. Although males resemble those of *L. nuna* in the coloration of the throat patch, the relatively bright green coloration of the central rectrices in *L. g. huallagae* differs strikingly from that of the congener. Thus, this taxon is included in the *L. gouldii* group for morphological (i.e., tail characteristics, morphometrics) and geographic reasons.

Another population of *L. gouldii* with stable character differences occurs in southern Ecuador, but has been neglected to date from a taxonomic point of view. The individuals in question are marked by a distinct plumage and tail morphology and should be recognized as:

Lesbia gouldii aureliae, ssp. nov.

Diagnosis. Differs from all other *L. gouldii* members by the strongly golden bronze coloration of the basic plumage, and from *L. g. gracilis* by the paler, more cream-buff instead of cinnamon-buff abdomen and the longer tail in males.

Holotype. Adult male, BMNH reg. no. 1902.3.13. 2138; collected at Guishapa (= Paguishapa), prov. Oña, Ecuador, 2000 m, on 23 May 1899 by P. O. Simons.

Description of holotype. Bill blackish, relatively short (12.4 mm); upper parts, chest, belly, flanks, and wing coverts strongly shining golden bronze to bronze-green; tail strongly forked, with exposed parts of r1-r4 shining emerald green, and rectrix bases and lower halves blackish green to golden green; r5 with basal half of inner webs purplish-black, the remaining part blackish golden green with bright bronze-green tip, and outer webs with basal two-thirds whitish buff, and terminal third purplish black except for bronze tip; gorget glittering deep golden green; abdominal parts cream-buff; under tail coverts bronze with pale cinnamon bases and fringes.

Female. Cotype, adult, BMNH reg. no. 725; collected at Cuenca, prov. Azuay, Ecuador, 2200 m, on 10 May 1899 by P. O. Simons.

Description of cotype. Upper parts, wing coverts and flanks shining golden to bronze-green; tail much shorter than in male; bases of inner webs of r1-4 purplish black, remaining parts emerald green to bronze-green (darker in r4); inner webs of r5 and terminal fifth of outer webs purplish black, their tips inconspicuously tipped dark bronze; under parts mainly whitish, with shining bronze-green to (rarely) emerald green spots; belly centre, lateral fringes, abdomen, and under tail coverts buff to pale cinnamon, the latter sometimes with bronze-green centres.

Range. Andes of southern Ecuador from prov. Azuay to prov. Loja.

Etymology. Refers to the enhanced golden bronze tinge of the plumage.

Remarks. Individual variation in *L. g. aureliae* is minor. The characteristic bronze coloration holds for 27 (90 %) of the 30 specimens under study, whereas the remaining ones are more golden green (e.g., female, BMNH 979, Guachanamá). In addition, five individuals (16.7 %) have more buff- or cinnamon-colored abdominal parts (e.g., male, AMNH 167036, El Paso; female, BMNH 1902.3.13. 2135, Paguishapa). Three specimens from the southern range of *L. g. gracilis*, two from Hacien-

da Talahua, prov. Bolívar (BMNH 1902.313.2133-2134; female, male), and a further male from Riobamba, prov. Chimborazo (BMNH 1902.313.2132), approach the coloration of *aureliae*, since they are more bronze than typical representatives of *gracilis* (totally n=45). However, other color features (e.g., abdomen), as well as the tail length of the two males in question (94.7, 97.8 mm; Table 1), are closer to the characteristics of the latter taxon than to those of *aureliae*.

Morphometric variation. Significant changes in male characters exist across the range of *L. gouldii* (Tables 1, 3). For example, bill and wing length are greater in the northern (Colombia, *gouldii*) and southern populations (S Ecuador to Peru, *aureliae, pallidiventris*), whereas the taxon occurring in the intervening area, *gracilis*, is smallest in these characters. The average bill length is only 12.0 mm in males of the latter, but longest in those of *huallagae* (15.3 mm). Similarly, males of *gracilis* exhibit the shortest outer tail feathers (100 mm). Thus, they differ on average strikingly ($P<0.001$) from the r5 length of the adjacent form *aureliae* (113.2 mm; all means), although three males of the latter (=23 %, totally n=13) fall within the range of *gracilis*.

Compared with males, females of all populations usually show slightly smaller mensural characters, with the exception of r5, which reaches only about half of the male length. For *L. g. huallagae* we were able to include only one female specimen (cotype, see above) in this study. Immature males of all taxa, often found misidentified as females, are recognizable by their longer wings (similar to adult males, >50 mm) and rectrices (r5 usually >65 mm).

Taxonomic decisions

The complexity of the taxonomic history of *Lesbia* is reflected in Table 4. In our study, decisions on the validity of taxa are chiefly based on morphological evidence. This is not only due to the lack of other comparative data (e.g., bioacoustics, molecular biology), but also to the allopatric or parapatric occurrence of *L. gouldii* and *L. nuna*. Hence an assessment of species limits under such conditions – a common problem for Neotropical bird taxa – requires the identification of "core characters", which may play an important role in the intraspecific recognition, or the amount of variation in a set of characters (Hu et al. 2000). In *Lesbia*, a combination of color and biometric characteristics provides to us a sufficient basis for the resurrection of *L. gouldii* to specific status, in addition to the previously recognized taxa *L. nuna* and *L. victoriae*.

The taxonomy and species concept used in this study are paralleled by similar approaches applied to widespread Andean and Neotropical genera of hummingbirds and other bird families. For trochilids, well-studied examples are represented by the allo- and superspecies found in the pufflegs *Haplophaedia*, the metaltails *Metallura*, the sunangels *Heliangelus*, and the topazes *Topaza* (e.g., Graves 1980, 1990, Heindl & Schuchmann 1998, Schuchmann et al. 2000, Hu et al. 2000). Similar species limits have been set in view of "leapfrog-pattern" in Andean tody-tyrants *Poecilotriccus* (Tyrannidae; Johnson & Jones 2001, Johnson 2002). Differences in external morphology among closely related Andean taxa are often paralleled by genetic differentiation, indicating a higher divergence than can be expected from plumage patterns (e.g., Arctander & Fjeldså 1994, Chesser 1999, García-Moreno & Fjeldså 2000, Cuervo et al. in press). Vice versa, striking color differences may not be an indication for a more distant relationship, e.g., in groups with complex character combinations such as brush-finches (García-Moreno & Fjeldså 1999, Cadena 2003). We believe that the former case may apply to *L. gouldii* and *L. nuna*, and favor to treat them as distinct species.

The case of "*Lesbia eucharis*" is just one of the many examples of a critical re-assessment of an old but – in terms of a correct intrageneric classification – fairly neglected avian taxon. As repeatedly demonstrated in recent studies on hummingbird taxonomy and hybridization (e.g., Graves 1990, 2001, Weller & Schuchmann 1997, Weller 1999, 2001), various aspects (i.e., morphology of supposedly related taxa, specimen history) have to be considered in order to decide whether specimens with an unusual plumage pattern and uncertain collecting data represent aberrations or immatures of existing species, valid taxa, or even hybrids.

In general, individuals in *Lesbia* with color or morphometry irregularities are rare. A prominent example of plumage variation in *L. victoriae* is represented by the above-mentioned AMNH specimen (# 59747). Simon (1921) described under the former species name "*Lesbia gracilis*"

(= *L. gouldii*) the taxa "*labilis*" and "*longicauda*" (both currently included in *L. gouldii pallidiventris*) on the basis of slightly different tail characteristics. However, these differences express individual variation at the subspecific level rather than they justify the taxonomic separation of the concerning specimens (cf. Peters 1945, Zimmer 1951). By contrast, several biometric characters and the tail morphology of "*L. eucharis*" are not matched by other congeners, suggesting that the type specimens are unlikely to be variants of any previously described taxon of this genus. There is also no evidence of artificial color alterations in iridescent plumage parts (e.g., due to light or chemical exposure) as observed by Graves (1991) for hummingbird specimens under unfavorable museum storage conditions.

The fairly speculative suggestion on the origin of the AMNH type of *L. eucharis* by Zimmer (1951) is neither clearly matched by the collectors' information for both specimens (including the BMNH type) nor by the actual external morphology and distribution of *Lesbia* as shown in this paper. We presume that both specimens were likely collected in Colombia rather than in Peru, as known for many other unique hummingbird types from the commercial "Bogotá collections" (Berlioz & Jouanin 1944). Although there is one case of a putative valid but extinct trochilid species (*Heliangelus zusii*, Graves 1993) known from just a single Bogotá trade skin, it seems unlikely that any still existing population of the fairly common genus *Lesbia* has been overlooked in Colombia, despite the long-lasting pressure of collecting (mainly for the fashion industry) between the late 18th and early 20th centuries. Consequently, the possibility remains that *L. eucharis* is a hybrid.

Until now only a few cases of hybridization involving *Lesbia* species have been published. At the intergeneric level, one prominent example is

Table 4. Historical taxonomy of *Lesbia*. Bold-marked taxa indicate nomenclatural changes compared to preceding authors, or newly described ssp. (*).

First description	Peters (1945)	Zimmer (1951)	Schuchmann (1999)	this study
Trochilus victoriae Bourcier & Mulsant, 1846	*L. v. victoriae*	*L. v. victoriae*	*L. v. victoriae*	*L. v. victoriae*
Trochilus eucharis Bourcier & Mulsant, 1848	*L. victoriae eucharis*	*L. nuna eucharis*	*L. nuna eucharis*	hybrid *L. v. victoriae* ? *L. g. gouldii*
Lesbia aequatorialis Boucard, 1893	*L. victoriae aequatorialis*	*L. v. victoriae*	*L. v. victoriae*	*L. v. victoriae*
Psalidoprymna juliae Hartert, 1899	*L. victoriae juliae*	*L. victoriae juliae*	*L. victoriae juliae*	*L. victoriae juliae*
Psalidoprymna berlepschi Hellmayr, 1915	*L. victoriae berlepschi*	*L. victoriae berlepschi*	*L. victoriae berlepschi*	*L. victoriae berlepschi*
Trochilus gouldii Loddiges, 1832	*L. nuna gouldii*	*L. nuna gouldii*	*L. nuna gouldii*	*L. g. gouldii*
Trochilus gracilis Gould, 1846	*L. nuna gracilis*	*L. nuna gracilis*	*L. nuna gracilis*	*L. gouldii gracilis*
Psalidoprymna pallidiventris Simon, 1902	*L. nuna pallidiventris*	*L. nuna pallidiventris*	*L. nuna pallidiventris*	*L. gouldii pallidiventris*
–		–		*L. gouldii aureliae**
–				*L. gouldii huallagae**
Lesbia chlorura Gould, 1871	*L. nuna chlorura*	*L. nuna eucharis*	*L. nuna eucharis*	hybrid *L. v. victoriae* ? *L. g. gouldii*
Ornismya nuna Lesson, 1832	*L. n.*	*L.*	*L.*	*L.*
Lesbia boliviana Boucard, 1891	*L. nuna boliviana*	*L. n. nuna*	*L. n. nuna*	*L. nuna boliviana*

"Lesbia ortoni" Lawrence (= *"Zodalia glyceria"* Gould), now regarded as a hybrid between the Black-tailed Trainbearer and the Purple-backed Thornbill, *L. victoriae* × *Ramphomicron microrhynchum* (Graves 1997). Additionally, specimens described as "*Chalcostigma purpureicauda*" (Hartert 1898) or "*Zodalia thaumasta*" (Oberholser 1902) may in fact represent hybrids of *L. victoriae* and the Long-tailed Sylph *Aglaiocercus kingi* (Fjeldså & Krabbe 1990, Schuchmann 1999), although a modern revision of the specimens concerned is needed (Berlioz & Jouanin 1944). Based on the occasional occurrence of *Lesbia* specimens with aberrant plumage characteristics from the "Bogotá collections", Berlioz & Jouanin (1944) supposed intrageneric hybridization between *L. nuna* (= *gouldii*) and *L. victoriae* and referred them to "*Trochilus (= Lesbia) eucharis*" (see Zimmer 1951, Fjeldså & Krabbe 1990). However, at present it is unclear where these specimens have been deposited or if they still even exist.

Accordingly, our findings point to a hybrid origin also for the *L. eucharis* "types" (i.e., mensural data, Table 1). Since *L. gouldii* and *L. victoriae* are widely sympatric in Colombia only along the central Cordillera Oriental, the *eucharis* birds probably came from the Bogotá region. The intermediate tail morphology and morphometry, combining features of both species, strongly indicate that they are hybrids of these taxa rather than intergeneric hybrids, as the character set clearly weighs against the likelihood of any species from a different trochilid genus being one of the parents (see Graves 1990).

Biogeographic and phylogenetic aspects

The distributional and morphological patterns of the trainbearers reflect both specific and subspecific speciation events related to macro- and micro-scale environmental changes (e.g., *sensu* refuge theory, Haffer 1967; see also Remsen 1984, Cracraft 1985, Fjeldså 1992, 1995, Bleiweiss 1998, García-Moreno et al. 1999, Schuchmann et al. 2001). Apart from these general effects, other specific factors, such as sexual selection in the male's plumage, have likely played an important role in the evolutionary divergence of *Lesbia*. For example, the latter is pronounced in the convergent development of signal characters, such as the elongation or patterning of the outer rectrices in the trainbearers.

At the lower taxonomic level, the apparent parapatry or even sympatry of the two subspecies *L. gouldii pallidiventris* and *L. g. huallagae* is of particular interest, given the fact that we found no evidence for hybridization. Although the single *pallidiventris* record from the Marañon headwater region might be simply explained by seasonal migration originating from the central upper valley, the same might not be true for two specimens (including one immature) from the Panao region in the eastern Huallaga drainage. Assuming that the local endemic form *huallagae* could establish itself prior to *pallidiventris*, records of the latter may point to a more recent invasion under favourable ecological conditions via the uppermost Marañon valley. They could also be an indication of a relict population (Panao region) that was initially separated from the main population by environmental changes, e.g., due to an increasing aridity of the upper Huallaga valley during past geohistoric epochs (i.e., glacial phases). However, the additional occurrence of *L. g. huallagae* on the right river bank (Hacienda Chismay, FMNH 66753-754) may indicate that this region, at least, has no significant importance as a dispersal barrier for this species in more recent times. Alternatively, both taxa might have been able to invade the eastern Andes of Huánuco by passing the headwaters of Río Huallaga along the Cordillera Huayhuash, although at present this interpretation lacks evidence from collecting data.

Some implications of the evolutionary history can be drawn from some morphological characteristics (strong sexual dimorphism, body sizes, tail pattern) shared by *Lesbia* with only two other Andean trochilid genera, *Ramphomicron* and *Sappho*. The polytypic taxon *Ramphomicron* (two species) is distributionally focused to the northern Andes (Weller & Schuchmann 2002) and has in common with *Lesbia* the female-type plumage (under parts whitish speckled with green; r5 reduced in length and with extended pale outer webs) and the fairly short bill (especially *L. gouldii*). The female pattern is also present in the Red-tailed Comet *Sappho sparganura*, but with regard to other characters, for example biometry (wing and r5 length), this taxon is closer to *L. nuna* and *L. victoriae*. Since external morphology data suggest that *Lesbia*, *Ramphomicron* and *Sappho* may be monophyletic, a detailed study comparing the life history data of all three taxa is in preparation.

Acknowledgments. We are grateful to the scientific staff of the bird divisions of the following natural history museums and institutions for either lending specimens or permitting access to their skin collections: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, Tring (BMNH); Field Museum of Natural History, Chicago (FMNH); Instituto de Ciencias Naturales, Bogotá (ICN); Museum of Natural Science, Zoology, Louisiana State University, Baton Rouge (LSUMZ); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museo de Historia Natural "Javier Prado", Lima (MHNJP); Naturhistorisches Museum, Basel (NHMB); National Museum of Natural History, Smithsonian Institution, Washington D.C. (NMNH); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main (SMF); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). This project was financially supported by the German Science Council (Deutsche Forschungsgemeinschaft, Schu 766/5-3), the Brehm-Fonds for International Bird Conservation, Bonn, a Frank Chapman Collection Study Grant (AMNH), and a Jessup Award (ANSP). The ANSP kindly provided accommodation for AAW, and M. Linares, Universidade de los Andes, Bogotá, gave valuable logistical support. We express our thanks to W. Bock, New York, J. Fjeldså, Copenhagen, B. Hillcoat, Neuss, and A. T. Peterson, Lawrence, for critical comments on the manuscript and an earlier draft, respectively. A. Schmitz-Ornes, ZFMK, kindly translated the summary into Spanish.

Summary

Biogeography and taxonomy of the widespread Andean trochilid genus *Lesbia* LESSON, 1833 are analyzed based on distributional data and morphological characters of skin specimens. The Black-tailed Trainbearer, *L. victoriae*, and the Green-tailed Trainbearer, *L. nuna*, are currently recognized as two species, but morphological evidence (tail pattern, biometrics) reveals that another taxon, Gould's Trainbearer, *L. gouldii*, previously included in the latter, should be considered as a distinct species. The type specimens of "*L. eucharis*", until recently treated as a subspecies of *L. nuna* from Huánuco, central Peru, come from the northern Andes and are most likely hybrids of *L. gouldii* × *L. victoriae*. Further, the central Peruvian population of Gould's Trainbearer should be recognized as a new subspecies, *L. gouldii huallagae* subsp. nov., marked by the strongly bronze-green coloration and conspicuous pale fringes in the male ventral plumage. Another new taxon, *L. gouldii aureliae* subsp. nov., is described from southern Ecuador and mainly characterized by its remarkable golden bronze coloration. This study also confirms the taxonomic separation of *L. nuna boliviana* and *L. gouldii* (formerly *nuna*) *gracilis*, but the validity of *L. victoriae aequatorialis* is not supported by mensural data. Morphological similarities (female-type plumage, tail pattern, body size relations) indicate a close relationship of *Lesbia* with the thornbills *Ramphomicron* and the Red-tailed Comet *Sappho sparganura*.

Resumen

Se analiza la biogeografía y taxonomía del ampliamente distribuido género andino *Lesbia* LESSON, 1833 en base a los datos de distribución y caracteres morfológicos de ejemplares de Museo. El Colacintillo Colinegro, *L. victoriae*, y el Colacintillo Coliverde, *L. nuna*, son actualmente reconocidos como dos especies, pero evidencias morfológicas (aspectos de la cola, datos biométricos) revelan que otro taxón, El Colacintillo de Gould, *L. gouldii*, previamente incluido en el último, debería considerarse como una especie distinta. Los ejemplares tipo de "*L. eucharis*", de Huanuco, Perú central, hasta hace poco tomados como parte de la subespecie *L. nuna*, proveniente del norte de los Andes son posiblemente híbridos de *L. gouldii* × *L. victoriae*. Adicionalmente, la población de Perú central del Colacintillo de Gould debería ser considerada como una nueva subespecie, *L. gouldii huallagae* subsp. nov., debido a la fuerte coloración bronce-verde y bordes conspicuamente pálidos en el plumaje ventral de los machos. Otro taxón, *L. gouldii aureliae* subsp. nov., es descrito para el sur de Ecuador y se caracteriza principalmente por su coloración especialmente dorado-bronce. Este estudio también confirma la separación taxonómica de *L. nuna boliviana* y *L. gouldii* (anteriormente *nuna*) *gracilis*, pero se descarta la validez de *L. victoriae aequatorialis*. Similitudes morfológicas (plumaje tipo hembra, tipo de cola, relaciones de tamaño del cuerpo) indican una relación cercana de *Lesbia* con las Picoespinas *Ramphomicron* y la Cometa Coliroja *Sappho sparganura*.

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Appendix

Localities and altitudes (either obtained from specimen labels or ornithological gazetteers) of study skins and additional data from Meyer de Schauensee (1949), listed from N to S. Coordinates refer to Paynter (1982, 1992, 1993, 1997), Stephens & Traylor (1983), or the Alexandria Digital Library Gazetteer (http://www.alexandria.ucsb.edu; n. loc. = not located).

L. v. victoriae, COLOMBIA: Vetas, Santander, 3000 m, 07°20'N, 72°50'W; Mutiscua, Norte de Santander, 2650 m, 07°18'N, 72°45'W; Guicán, Nevado El Tablón, Boyacá, altitude ?, 06°27'N, 72°25'W; Lagunillas, Boyacá, 3300-3400 m, 06°15'N, 72°38'W; Pacho, Las Palmas, Cundinamarca, 1860 m, 05°08'N, 74°10'W; páramo NW Suesca, Cundinamarca, 2635 m, 05°06'N, 73°48'W; Represa del Sisga, Cundinamarca, 2500 m, 05°05'N, 73°43'W; Zipaquirá, Vda. Empatizada, Cundinamarca, 2650 m, 05°02'N, 74°00'W; San Francisco, Cundinamarca, 1500 m, 04°58'N, 74°18'W; Subachoque, Cundinamarca, 2685 m, 04°56'N, 74°11'W; La Mar, Cundinamarca, 2680 m, 04°55'N, 74°10'W; Chia, Guaimaral, Cundinamarca, 2562 m, 04°52'N, 74°02'W; Guasca, Cundinamarca, 2720 m, 04°52'N, 73°52'W; La Planada, Cundinamarca, 2650 m, 04°48'N, 74°24'W; Anolaima, Cundinamarca, 1500 m, 04°46'N, 74°28'W; La Herrera, Cundinamarca, 2650 m, 04°42'N, 74°18'W; (vicinity of) Bogotá, Cundinamarca, 2600-2900 m, 04°36'N, 74°05'W; Monserrate, páramo "El Granizo", Bogotá, Cundinamarca, 3250 m, 04°36'N, 74°04'W; Villavicencio, Cundinamarca, altitude ?, ca. 04°36'N, 74°04'W; Choachi, Cundinamarca, 04°36'N, 74°04'W, 1966 m, 04°32'N, 73°56'W; Chipaque, Cundinamarca, 2600-2900 m, 04°27'N, 74°03'W; Quetame, Cundinamarca, 1530 m, 04°20'N, 73°51'W; Iles, Nariño, 2985 m, 00°58'N, 77°32'W; Cumbal, Nariño, 3050-3350 m, 00°54'N, 77°47'W; Derrumbe, near Puerres (00°53'N, 77°30'W), Nariño, altitude ?, n. loc.; Chorreado, Nariño, 3000 m, 00°50'N, 77°25'W; ECUADOR: San Gabriel, Carchi, 2870 m, 00°36'N, 77°49'W; Nono, Pichincha, 2730 m, 00°04'S, 78°35'W; Volcan Pichincha, Pichincha, 3200-3400 m, 00°10'S, 73°33'W; Hacienda El Garzón, Pichincha, 3050 m, n. loc.; Faldas, Pichincha, altitude, n. loc.; Cumbaya, Pichincha, 2300 m, 00°12'S, 78°26'W; Quito, Pichincha, >2800 m, 00°13'S, 78°30'W; Valle Tumbaco, Pichincha, 2400 m, 00°13'S, 78°24'W; Chillo Valley, Pichincha, 2500 m, ca. 00°20'S, 78°27'W; Pampa de Limpios, Pichincha, 3700 m, 00°37'S, 78°28'W; páramo of Cotopaxi, Cotopaxi, altitude ?, 00°40'S, 78°26'W; San Agustín, Cotopaxi, 3100 m, 00°41'S, 78°32'W; E of Pilaló, Cotopaxi, 3600 m, 00°59'S, 79°01'W; Chimborazo, Chimborazo, ca. 3000-4000 m, 01°28'S, 78°48'W; Riobamba, Chimborazo, 2750-3000 m, 01°40'S, 78°38'W; Cajabamba, Chimborazo, 3200 m, 01°42'S, 78°45'W; Laguna de Colta, Chimborazo, 3100 m, 01°44'S, 78°45'W; mountains above Chambo, Chimborazo, 2900-3300 m, 01°44'S, 78°35'W; Hacienda El Paso, Azuay, altitude ?, 03°22'S, 79°05'W; Bestion, Rio Chingata, SE Oña (03°32'S, 79°10'W), Azuay, 3075 m, n. loc.

L. victoriae juliae, ECUADOR: 25 km SSE Jimbura, Loja, 3050 m, 04°47'S, 79°24'W; PERU: E side Huancabamba-Canchaque pass, Piura, 2600 m, n. loc., between 05°14'S, 79°28'W – 05°24'S, 79°36'W; La Lejía, Amazonas, 2745 m, 06°10'S, 77°31'W; Atuén, Amazonas, ca. 3200 m, 06°45'S, 77°42'W; Cajamarca, Cajamarca, 3050 m, 07°10'S, 78°31'W; Bambamarca, Cajamarca, 3050 m, 07°24'S, 77°42'W; Cajabamba, Cajamarca, 2745-3050 m, 07°37'S, 78°03'W; Huamachuco, La Libertad, 3170 m, 07°48'S, 78°04'W; La Caldera, La Libertad, 3550 m, 08°13'S, 77°15'W; Santa Clara, Ancash, 3000 m, 08°28'S, 77°25'W; Yanac, Ancash, 4000 m, 08°37'S, 77°52'W.

L. victoriae berlepschi, PERU: Cayna, Huánuco, 3320 m, 10°11'S, 76°20'W; Palca, Junín, 2700-2800 m, 11°21'S, 75°31'W; Tarma, Junín, 3000-3500 m, 11°25'S, 75°42'W; Huancavelica, Huancavelica, 3650 m, 12°46'S, 75°02'W; Anta, Cuzco, 3500 m, 13°29'S, 72°09'W.

L. n. nuna, PERU: Concepción, Junín, 3650 m, 11°55'S, 75°17'W; Colcabamba (including Hacienda Chacas, Tayacaja), Huancavelica, 2600-2980 m, 12°20'S, 74°42'W; Yauli, Junín, 3355 m, 12°47'S, 74°49'W; Lircay, Huancavelica, 3250 m, 12°56'S, 74°43'W; Huanta, 4 km E Chota, Ayacucho, 3500 m, 12°56'S, 74°15'W; Chospiyoc, Cuzco, 3050 m, 13°16'S, 72°21'W; above Ollantaytambo, Cuzco, 2750 m, 13°16'S, 72°16'W; Cachupata, Cuzco, 3555 m, 13°17'S, 71°22'W, Paucartambo, Cuzco, 2865-3000 m, 13°18'S, 71°40'W; Huatoccto, Cuzco, altitude ?, 13°20'S, 71°35'W; above Ahuayro, Apurímac, 2440 m, 13°22'S, 73°52'W; Pisac, Cuzco, 3070 m, 13°26'S, 71°51'W; Ninabamba, Apurímac, 2135 m, 13°28'S, 73°49'W, Capana, Cuzco, 3500-4000 m, 13°28'S, 71°25'W; Anta, Cuzco, 3500 m, 13°29'S, 72°09'W; Marcapata, Cuzco, 3150 m, 13°30'S, 70°65'W; Cuzco, Cuzco, 3400 m, 13°31'S, 71°59'W; Hacienda La Laguna, Apurímac, 3040 m, 13°38'S, 73°19'W; Bosque Paraguay, near Piyai, 3350 m, ca. 14°47'S, 72°41'W.

L. nuna boliviana, BOLIVIA, La Paz: Sorata, 3500 m, 15°47'S, 68°40'W; Valley Milipaya, (near?) Sorata, 2450-3660 m, n. loc.; NE side Mt. Sorata, Nevado Illampu, altitude ?, ca. 15°50'S, 68°34'W; Chicani, altitude ?, 16°28'S, 68°04'W.

Lesbia g. gouldii, VENEZUELA: Sierra Nevada, Mérida, 2400-2700 m, 08°33'N, 71°03'W; COLOMBIA: Pamplona, Norte de Santander, 2340 m, 07°23'N, 72°39'W; mountains of Pacho, Cundinamarca, altitude ?, ca. 05°06'N, 74°10'W; Represa del Sisga, Cundinamarca, 2500 m, 05°05'N, 73°43'W; Gachancipá, Cundinamarca, 2600 m, 05°00'N, 73°53'W; La Mar, Cundinamarca, 2680 m, 04°55'N, 74°10'W; Tabio, Cundinamarca, 2643 m, 04°55'N, 74°06'W; Est. La Caro, Cundinamarca, 2540 m, 04°52'N, 74°02'W; Chia, Guaimaral, Cundinamarca, 2562 m, 04°52'N, 74°02'W; (vicinity of) Bogotá, Cundi-

namarca, 2600-2900 m, 04°36'N, 74°05'W; Choachí, Cundinamarca, 1966 m, 04°32'N, 73°56'W; Finca Mátega, Vda. Quimasata, Une, Cundinamarca, 2000 m, 04°24'N, 74°02'W; Est. Termales, Páez, Nevado del Huila, Cauca, 2800-2970 m, 02°48'N, 75°57'W; Popayàn, Cauca, altitude ?, 02°27'N, 76°36'W; Volcan Puracé, Cauca, 2600-3050 m, 02°21N', 76°23'W.

L. gouldii gracilis, ECUADOR: Pelagallo, Pichincha, 1500-2000 m, 00°09'N, 78°32'W; above Puéllaro, Pichincha, 2450 m, 00°04'N, 78°24'W; Camino de Mindo, Pichincha, 3000 m, ca. 00°02'S, 78°48'W; Volcán Pichincha, Pichincha, 3200-3700 m, 00°10'S, 78°33'W; Camino Paylón, Pichincha, altitude ?, n. loc. (ca. Volcán Pichincha); Quito, Pichincha, 2820 m, 00°13'S, 73°30'W; Valle de Tumbaco, Pichincha, 2400 m, 00°13'S, 78°24'W; Lloa, Pichincha, 3000 m, 00°15'S, 78°35'W; Papallacta, Napo, 3150 m, 00°22'S, 78°08'W; western slope of Corazón, Pichincha, 2750 m, 00°32'S, 78°39'W; Hacienda Talahua, Bolívar, 4000 m, 01°21'S, 79°04'W; Baños, Tungurahua, 1800 m, 01°24'S, 78°24'W; Runtún, Tungurahua, 3000 m, 01°26'S, 78°24'W; Volcan Chimborazo, Chimborazo, altitude ?, 01°28'S, 78°48'W; Guaillabamba, Riobamba, Chimborazo, 4000 m, ca. 01°40'S, 78°38'W; Ceche, Chimborazo, 2925 m, 02°11'S, 78°51'W; Hacienda Jalancay, Chimborazo, 1675 m, n. loc. (near Chunchi, 02°17'S, 78°55'W).

L. gouldii aureliae, ssp. nov., ECUADOR: Cuenca, Azuay, 2200 m, 02°53'S, 78°59'W; Cumbe, Azuay, 2500 m, 03°07'S, 79°01'W; Hacienda El Paso, Rio Charcay, Azuay, 2820 m, 03°22'S, 79°05'W; between Loja and Cuenca, Azuay ?, altitude ?, n. loc.; Paguishapa, Loja, 1800-2000 m, 03°35'S, 79°20'W; Loja, Loja, 2150-2200 m, 04°00'S, 79°13'W; Guachanamá, Loja, 2500 m, 04°02'S, 79°53'W; nudo de Cajanuma, Loja, 2300-2400 m, 04°05'S, 79°12'W; 2 km SW Utuama, 5 km SE Zozoranga, Loja, 2400 m, 04°23'S, 79°49'W.

L. gouldii pallidiventris, PERU, western Andes: El Tambo, Piura, 2865 m, 05°20'S, 79°30'W; 10 km E Canchaque, Piura, 2600 m, 05°24'S, 79°36'W; El Espino, Piura, altitude ?, 05°41'S, 79°18'W; Quebrada Lanchal, Piura, 2850 m, 05°41'S, 79°15'W; Chira, Cajamarca, 2290 m, 06°16'S, 78°42'W; Cutervo, Cajamarca, 2550-2650 m, 06°22'S, 78°51'W; Montaña de Chuli, 6 km NE Chota (06°33'S, 78°39'W), Cajamarca, 2745 m, n. loc.; Chugur, Cajamarca, 2745 m, 06°40'S, 78°45'W; Seques, Lambayeque, altitude ?, 06°54'S, 79°18'W; Taulis, Cajamarca, 2670 m, 06°54'S, 79°03'W; Cajamarca, Cajamarca, 2720-3000 m, 07°10'S, 78°31'W; Baños del Inca, Cajamarca, 2800 m, 07°10'S, 78°28'W; Sunchubamba, Cajamarca, 2500 m, 07°29'S, 78°24'W; Bosque de Suro, Sunchubamba, Cajamarca, 2650 m, 07°29'S, 78°24'W; Algamarca, Cajamarca, 3000 m, 07°36'S, 78°15'W; Cajabamba, Cajamarca, 2745-3050 m, 07°37'S, 78°03'W; Araqueda, Cajamarca, 2700 m, 07°40'S, 78°12'W; Succha, La Libertad, 2700 m, 07°54'S, 77°41'W; Maynapall, La Libertad, altitude ?, 07°56'S, 78°36'W; PERU, eastern Andes: Bagua Grande (Chachapoyas road), Amazonas, 650 m, 05°47'S, 78°26'W; La Lejia, Amazonas, 2745 m, 06°10'S, 77°31'W; Molinopampa, Amazonas, 2407 m, 06°11'S, 77°37'W; Ventilla, Amazonas, 2500 m, 06°11'S, 77°33'W; Uscho, Amazonas / San Martín, 1525 m, 06°11'S, 77°13'W; Bosque Millpo, Amazonas, 2600 m, 06°12'S, 77°35'W; Chachapoyas, Amazonas, 2330 m, 06°13'S, 77°51'W; Puma-Urcu, Amazonas, 3000 m, 06°16'S, 77°51'W; Levanto, Amazonas, 06°16'S, 77°49'W; Santa Rosa de Huayabamba, Amazonas, 1500 m, 06°22'S, 77°25'W; Leimebamba, Amazonas, 2135 m, 06°41'S, 77°27'W; San Pedro, SE of Leimebamba, Amazonas, 2625-2865 m, n. loc.; Pataz, La Libertad, 2745 m, 07°44'S, 77°37'W; Cochabamba, La Libertad, 2300 m, 07°49'S, 77°53'W; Soquián, La Libertad, 2000 m, 07°51'S, 77°41'W; Tayabamba, La Libertad, 3250 m, 08°17'S, 77°18'W; Chavinillo, Huánuco, 3355 m, 09°47'S, 76°35'W; Huancapata, Huánuco, 2745 m, ca. 09°50'S, 76°00'W.

L. gouldii huallagae, ssp. nov., PERU, Huánuco: Hacienda Huarapa, 26 km NE of Huánuco, 2745 m, n. loc.; Chinchao, 1740 m, 09°38'S, 76°04'W; Cordillera Carpish, western slope, 2165 m, 09°40'S, 76°09'W; above Acomayo, below Bosque Zapatagocha, 2550 m, 09°40'S, 76°03'W; Quebrada Shugush, km 30 Huánuco-La Union road, 3100 m, 09°46'S, 76°48'W; Hacienda Shismay, 3200 m, 09°58'S, 76°10'W.