

Distribution of *Boissonneaua* taxa. Upper left birds, left-right: *B. flavescens tinochloria*, male and female; upper right birds, left-right: *B. f. flavescens*, female and male; lower left birds, top-bottom: *B. jardini*, male and female; lower right birds, top-bottom: *B. mathensii*, male and female.

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## BIOGEOGRAPHY AND GEOGRAPHIC VARIATION OF THE ANDEAN HUMMINGBIRD TAXON *BOISSONNEAUA* REICHENBACH, 1854 (AVES, TROCHILIDAE)

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**Resumen.** – Biogeografía y variación geográfica del taxón andino de colibríes *Boissonneaua Reichenbach, 1854* (Aves, Trochilidae). – Con la utilización de datos morfológicos y de distribución obtenidos de especímenes de museo, investigamos las afinidades biogeográficas y evolutivas en colibríes del grupo *Boissonneaua*. Junto con *Eriocnemis* y *Haplophaedia*, estos conforman el grupo de los calzaditos, debido a que presentan plumas tibiales agrandadas. Con respecto al número de taxa, este género es menos diferenciado en comparación con otros taxa de trochílidos andinos que comprenden *B. flavescens* (incl. *B. f. tinochlora*), *B. mathewsii* y *B. jardini*. Las especies habitan principalmente las zonas tropicales y templadas bajas, ascendiendo hasta una altura de 3000 m s.n.m. Desde el punto de vista morfológico, tienen un dicromatismo sexual poco pronunciado y, si comparamos los caracteres medibles, todos los taxa son parecidos. En lo que se refiere a coloración, *B. flavescens* y *B. mathewsii* son más similares entre sí que con respecto a *B. jardini* que posee un plumaje de colores más intensos entre el violeta y el verde-azul. Basados en evidencia biogeográfica y patrones de coloración, suponemos que el centro de origen de *Boissonneaua* se localiza en la pendiente oriental de los Andes (*B. flavescens*, *B. mathewsii*). Subsecuentes invasiones trans-andinas y eventos de aislamiento pueden haber disparado procesos de sub-especiación y especiación (*B. f. tinochlora*, *B. jardini*) a lo largo de la pendiente occidental de los Andes del Sur de Colombia y el Norte de Ecuador.

**Abstract.** – Using distributional and morphological data obtained from voucher specimens, we investigated biogeographic and evolutionary affinities of *Boissonneaua* hummingbirds. Together with *Eriocnemis* and *Haplophaedia*, this group forms the assemblage of pufflegs, due to their enlarged tibial tufts. With respect to the number of taxa, *Boissonneaua* is less differentiated compared to other Andean trochilid taxa, comprising *B. flavescens* (incl. *B. f. tinochlora*), *B. mathewsii*, and *B. jardini*. The species chiefly inhabit the tropical to lower temperate zone, ascending to 3000 m a.s.l. Morphologically, sexual dichromatism is poor, and all taxa resemble in mensural characters. In coloration, *B. flavescens* and *B. mathewsii* are more similar to each other than to *B. jardini* that has a more colorful violet to bluish-green plumage. Based on biogeographic evidence and coloration patterns, we suppose the center of origin of *Boissonneaua* to be located on the eastern Andean slope (*B. flavescens*, *B. mathewsii*). Subsequent trans-Andean invasion and isolation events may have

triggered subspeciation and speciation processes (*B. f. tinocblora*, *B. jardi*) along the western slope of the Andes in southern Colombia and northern Ecuador. Accepted 30 November 2000.

**Key words:** Boissonneaua, Trochilidae, Andes, biogeography, geographic variation.

## INTRODUCTION

Recent studies based on the biogeographic and morphological aspects of Andean trochilids (subfamily Trochilinae) have revealed that several genera apparently represent monophyletic lineages (review in Schuchmann 1999). As an example, the metaltails (*Metallura*) and thornbills (*Chalcostigma*) have been identified as sister groups (Schuchmann & Heindl 1997, Heindl & Schuchmann 1998). Another trochiline clade that most probably can be derived from a common ancestor comprises the pufflegs (*Eriocnemis*, *Haplophaidia*) and supposed related taxa (*Helianthus*, *Ocreatus*, *Urosticte*) as they share various morphological and ethological traits (e.g., Schuchmann 1987, Schuchmann *et al.* 2000). This paper deals with the geographic variation and biogeography of *Boissonneana* (Reichenbach, 1854), which has several features in common with the pufflegs but also with such genera as *Aglaeactis* and *Urochroa*.

Similarly to *Eriocnemis*, members of the genus *Boissonneana* exhibit a rather aggressive territorial behavior (Mobbs 1972, Kattan & Murcia 1985) and often forage by clinging to flowers (Hilty & Brown 1986). Other ethological parallels with the pufflegs and the *Aglaeactis-Urochroa* sub-unit include the open wing presentation after perching, display behavior, and plumage morphology. The bioacoustic repertoire of *Boissonneana* is most similar to that of *Aglaeactis*. For example, the song of both taxa consists of high, sharp pitches, producing a rather metallic sound (Miller 1963, Fjelds  & Krabbe 1990; Schuchmann, pers. obs.).

Contrary to the dark greenish basic plumage and enlarged tibial tufts exhibited by the

pufflegs, *Boissonneana* species are more variable in coloration, possess reduced feathering on the thighs and show conspicuous cinnamon axillaries and under wing-coverts similar to *Aglaeactis*. The bicolored tail pattern resembles that of *Urochroa*.

## MATERIAL AND METHODS

A total of 274 *Boissonneana* skins was examined in the bird collections of various national and international scientific institutions (for details, see Acknowledgments). Plumage colors were either studied under natural light conditions (sun light, indirect light) or by means of a magnifying illuminated glass (x 10). Descriptions of non-iridescent colors (capitalized, numbers in brackets) refer to Smithe (1975) whereas iridescent (metallic) colors are given in general terms derived from subjective impression. As spectrophotometric tests on qualitative aspects of both structural and pigment colors in hummingbirds produced intolerably high standard deviations, this method was not applied in this study. The plumage topography follows Johnsgard (1997). Immature birds, chiefly identified by cinnamon fringes in ventral plumage and cinnamon malar stripes, were excluded from further morphological analysis. Mensural characters (bill length: distance from tip to proximal end of operculum; wings: unflattened position; tail: rectrices 1, 5 = r1, r5) were measured with a digital caliper to the nearest 0.1 mm.

In order to test for statistical significances between subpopulations ( $n \geq 4$ ), specimens from adjacent collecting sites (excluding topographical borders like high mountain ranges, mostly within 1° lat./long.) were grouped in

TABLE 1. Mensural characters of *Boissonneaua* taxa based on data obtained from skins, showing mean values  $\pm$  SD, ranges, and sample sizes (in parentheses).

Taxon	Sex	Bill (mm)	Wing (mm)	Rectrix 1 (mm)	Rectrix 5 (mm)
<i>B. flavescens</i>	M	21.1 $\pm$ 0.8 (43)	76.3 $\pm$ 2.2 (47)	39.5 $\pm$ 1.5 (45)	49.9 $\pm$ 1.5 (45)
		19.5–23.2	70.6–80.6	36.1–43.3	45.9–52.8
	F	20.9 $\pm$ 0.9 (29)	71.6 $\pm$ 2.0 (31)	39.3 $\pm$ 1.6 (27)	46.2 $\pm$ 1.6 (26)
		18.7–23.0	67.2–75.1	34.0–42.0	42.9–48.6
<i>tinoclora</i>	M	21.3 $\pm$ 0.7 (18)	75.4 $\pm$ 1.3 (17)	37.6 $\pm$ 1.2 (18)	48.4 $\pm$ 1.3 (18)
		20.2–22.8	73.0–77.9	35.9–39.4	45.8–50.8
	F	21.4 $\pm$ 0.7 (9)	71.6 $\pm$ 1.1 (9)	39.3 $\pm$ 1.6 (8)	45.1 $\pm$ 1.5 (9)
		20.4–22.9	69.8–73.0	36.6–41.1	41.4–47.4
<i>B. mathewsii</i>	M	21.0 $\pm$ 0.8 (43)	76.3 $\pm$ 1.3 (40)	39.9 $\pm$ 1.6 (45)	48.6 $\pm$ 1.6 (42)
		19.0–22.7	73.7–79.5	36.0–44.4	44.9–52.6
	F	21.1 $\pm$ 1.1 (30)	71.5 $\pm$ 1.5 (28)	39.8 $\pm$ 1.6 (31)	44.6 $\pm$ 1.1 (31)
		18.5–22.9	68.5–75.0	37.0–43.0	41.5–46.9
<i>B. jardini</i>	M	22.4 $\pm$ 0.6 (26)	76.1 $\pm$ 1.4 (26)	40.3 $\pm$ 1.5 (26)	48.8 $\pm$ 1.3 (26)
		20.8–23.4	73.3–78.9	37.6–42.9	46.8–51.7
	F	23.0 $\pm$ 0.7 (23)	70.6 $\pm$ 1.3 (22)	39.8 $\pm$ 1.4 (23)	44.5 $\pm$ 1.2 (23)
		21.7–24.8	68.4–73.1	37.6–41.9	41.9–46.3

pools (cf. Vuilleumier 1968) and compared using parametric methods (*F*-test, student's *t*-test; significance level  $P < 0.05$ ). For calculation of statistics and for graphical imaging we used MS Excel 7.0 and SigmaPlot 5.0, respectively.

Coordinates and altitudes of collecting sites (see Appendix 1) derived from specimens labels, unless already mentioned by the collector, were obtained from ornithological gazetteers (Paynter 1982, 1993, 1997; Stephens & Traylor 1983) or the "International Travel Map, South America North West" (scale: 1: 4,000,000).

## RESULTS

*Characteristics.* The genus *Boissonneaua* comprises three species, *B. flavescens*, *B. jardini*, and *B. mathewsii* [we follow Zimmer (1951) in spelling the specific name "*mathewsii*" as, con-

trary to the original description by Bourcier (1847), the correct name of the collector is Mathews]. These are medium-sized trochilids, averaging 11–13 cm in length and 7–8 g, somewhat larger than most members of *Haplophaedia* and *Eriocnemis* (Schuchmann *et al.* 2000). In contrast to many other trochiline groups, sexual dimorphism is relatively slight, involving differences in gorget coloration and morphometry; females have on average slightly longer bills, shorter wings, and shorter outer rectrices than males (compare Table 1, Figs 1 and 2). As a typical morphological trait of the genus, both sexes exhibit conspicuous cinnamon axillaries (True Cinnamon, 139,  $\times$  Robin Rufous, 340) that may have a territorial function as signal patches when the wings are extended (Schuchmann, pers. obs.).

In comparison to body size, the bill length of *Boissonneaua* species is rather short

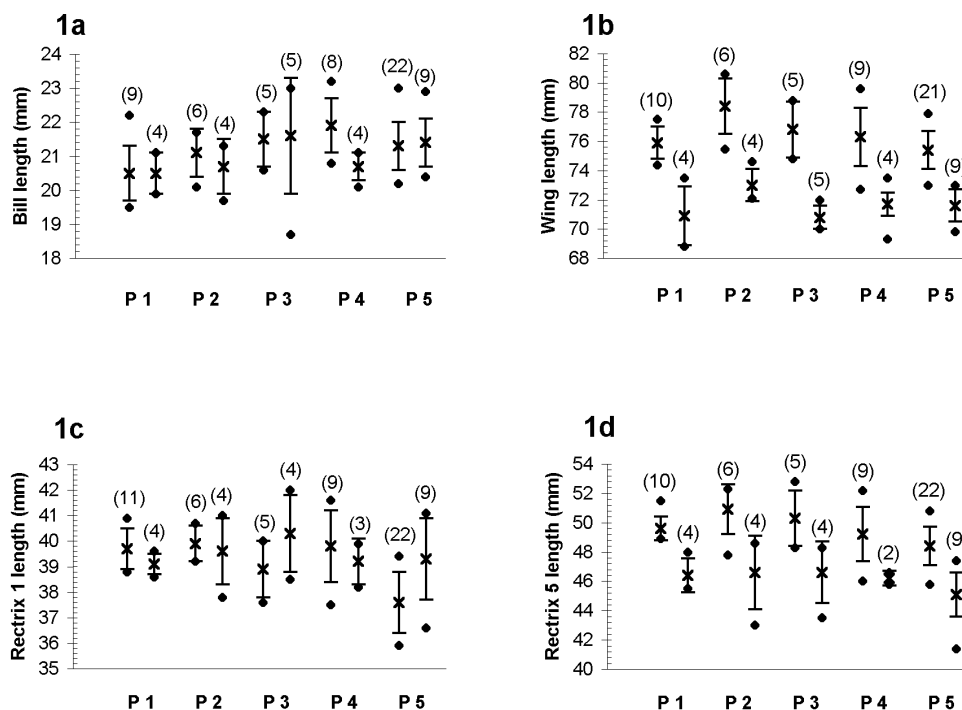


FIG. 1. Mean  $\pm$  s.d., minimum and maximum values of biometric characters (bill, wings, rectrices) in pools of *Boissonneana f. flavescens* (pools 1–4) and *B. f. tinochlora* (pool 5). Left bars showing males, right bars females (numbers in brackets); cross points indicate single specimens. Localities (from N to S), pool 1: La Culata, Valle, Páramo Tambor, Sierra Nevada, Los Nevados; pool 2: Buenos Aires, Hacienda las Vegas, La Corcova; pool 3: Cañon del Mt. Tolima, Tijeras, Belen; pool 4: Alto de las Cruces, Cerro Munchique, Cocal; pool 5: Intag, Pachijal, Guala, Río Saloya, Tandyapa, Mindo, Milligalli, Río Tandapi, Canzacoto, Corazón; for coordinates and altitudes, see Appendix 1.

and varies from c. 20.5–22 mm in *B. flavescens* to c. 22.5–23 mm in *B. jardini* (means for both sexes). All other biometric characters are very similar among the taxa (Table 1).

The members of *Boissonneana* are found in Andean humid to wet forests and cloud forests (e.g., Hilty & Brown 1986, Fjeldsâ & Krabbe 1990). They inhabit the tropical to lower temperate zone, between 350–3000 m. *B. jardini* is usually found at lower altitudes than the other taxa, occasionally below 1000 m (e.g., data in Meyer de Schauensee 1949; this study), with an overall range between 350–2200 m (Heynen 1999). Near Mindo,

northwestern Ecuador (00°02'S, 78°48'W), this species was found to be uncommon around 700 m (Schuchmann, pers. obs.). Recorded densities of *B. flavescens* and *B. jardini* in southern Colombia (La Planada) and Ecuador (Mindó) vary from 1–2 pairs/km<sup>2</sup> but may be underestimated due to their secretive feeding habits. Unlike members of *Haplophaidia* (Schuchmann 1977), *Boissonneana* species forage preferably in the mid and upper level vegetation (canopy).

*Distribution and taxonomy.* The range of *Boissonneana* extends over several parts of the north-

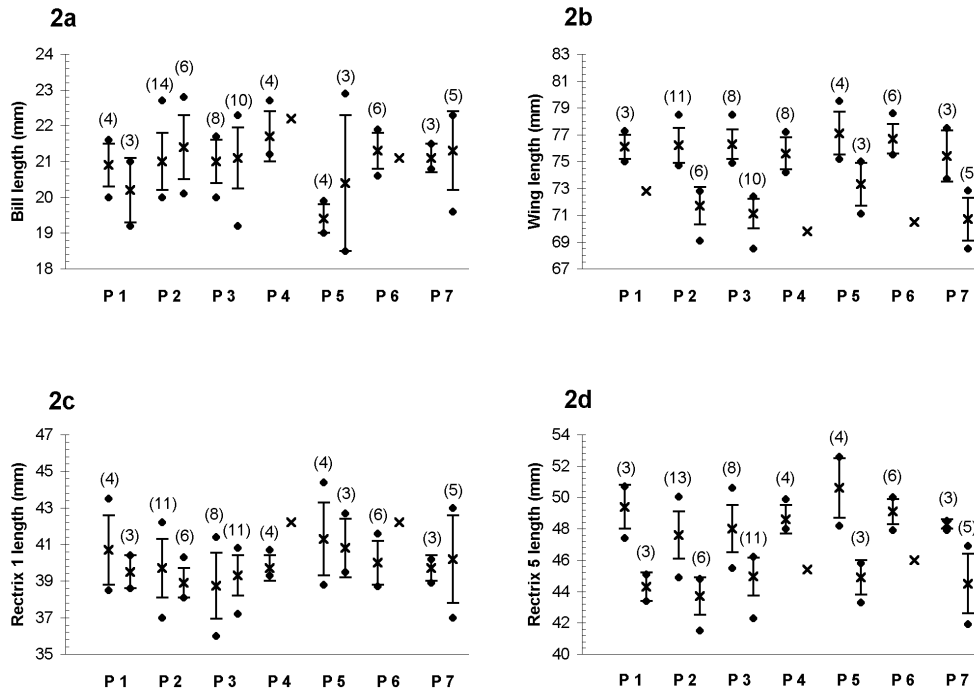


FIG. 2. Mean  $\pm$  s.d., minimum and maximum values of biometric characters (bill, wings, rectrices) in pools of *Boissonneaua mathewsii*. Left bars showing males, right bars females (numbers in brackets); cross points indicate single specimens. Localities (from N to S), pool 1: Huila, Quito, Intag, Tambillo; pool 2: Cuyujúa, Río Oyacachi (El Chaco), Baeza; pool 3: Baños, Cayandedel, Macas; pool 4: El Chiral, Nudo de Cajanuma; pool 5: Tambillo, Levanto, Cutervo, Taulis; pool 6: Cushi, Rumicruz, Utcuyacu, Garita del Sol; pool 7: Idma, Huyro, San Miguel Bridge, Machu Picchu, Huaisampillo; for coordinates and altitudes, see Appendix 1.

ern Andes from northern Colombia and western Venezuela southward to western Ecuador and northwestern to central Peru. In spite of this relatively wide distribution, only four taxa are currently known, one polytypic and two monotypic species (listed from N to S; sequence of taxa maintained throughout section “Species of *Boissonneaua*”; in brackets behind author’s name: type locality):

*Boissonneaua flavescens* Loddiges, 1832

*B. f. flavescens* Loddiges, 1832 (Popayán, Colombia) – W Venezuela (Táchira, Mérida, Lara) and N to SW Colombia (all three cordilleras).

*B. f. tinochlora* Oberholser, 1902 (West side of Corazón, Ecuador) – SW Colombia (Nariño) to NW Ecuador (locally along eastern slope).

*Boissonneaua jardini* Bourcier, 1851 (Nanegal, Ecuador)  
SW Colombia to N Ecuador.

*Boissonneaua mathewsii* Bourcier, 1847 (*ex* Loddiges MS) (Peru)  
NW Ecuador to W and S Peru.

The historic generic classification reveals several changes in taxonomic treatment. *Bois-*

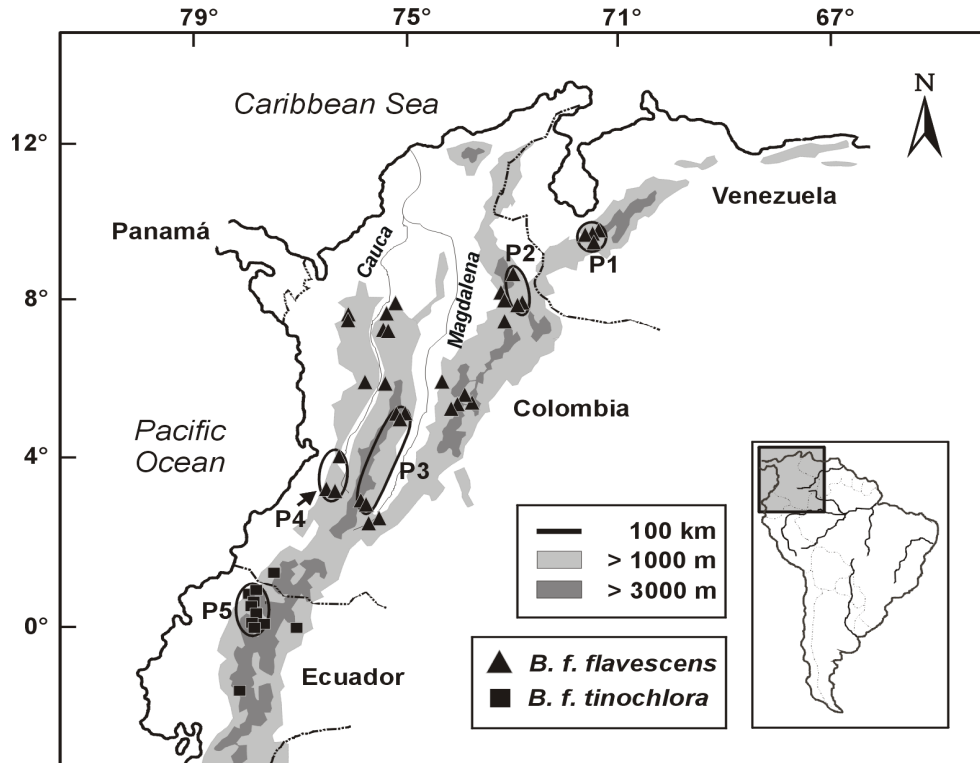


FIG. 3. Geographic distribution of *Boissonneana flavescens*, based on data obtained from skins and literature (Meyer de Schauensee 1949).

*sonneana* was first described by Reichenbach (1854, March), just a few months before Gould (1854, October) introduced the name *Panoplites*. This appellation was subsequently maintained by other taxonomists, e.g., by Elliot (1878), Salvin (1892), and Salvadori & Festa (1900). Obviously due to the plumage pattern, Gould (1861) placed this genus close to the genera *Thalurania* and *Florisuga*. Mulsant *et al.* (1866) included the taxa *jardini* and *flavescens* in the genera *Florisuga* (subgenus: *Galeria*; *G. jardinei*) and *Callidice* (*C. flavescens*), respectively. Later, Mulsant (1875) described the taxon *mathewsii* first as the type species for the new subgenus *Alosia* (under genus *Panoplites*) but merged it thereafter into *Chytolaema* (Mulsant & Verreaux 1876). However, more mod-

ern classifications (e.g., Hartert 1900, Simon 1921: *Boissonneauxia*; Peters 1945) have referred all three species to the original generic name.

Due to the low number of taxa at the species level there had been only minor nomenclatural changes. Simon (1921) questioned the separate status of *B. flavescens tinochlora* towards the nominate form. Likely, this statement induced Chapman (1926) to confirm the subspecific validity of *tinochlora*.

#### Species of *Boissonneana*

##### *Boissonneana flavescens*

*Diagnosis.* The Buff-tailed Coronet (*B. flavescens*) has a largely greenish plumage, chiefly with shining golden green on the back and

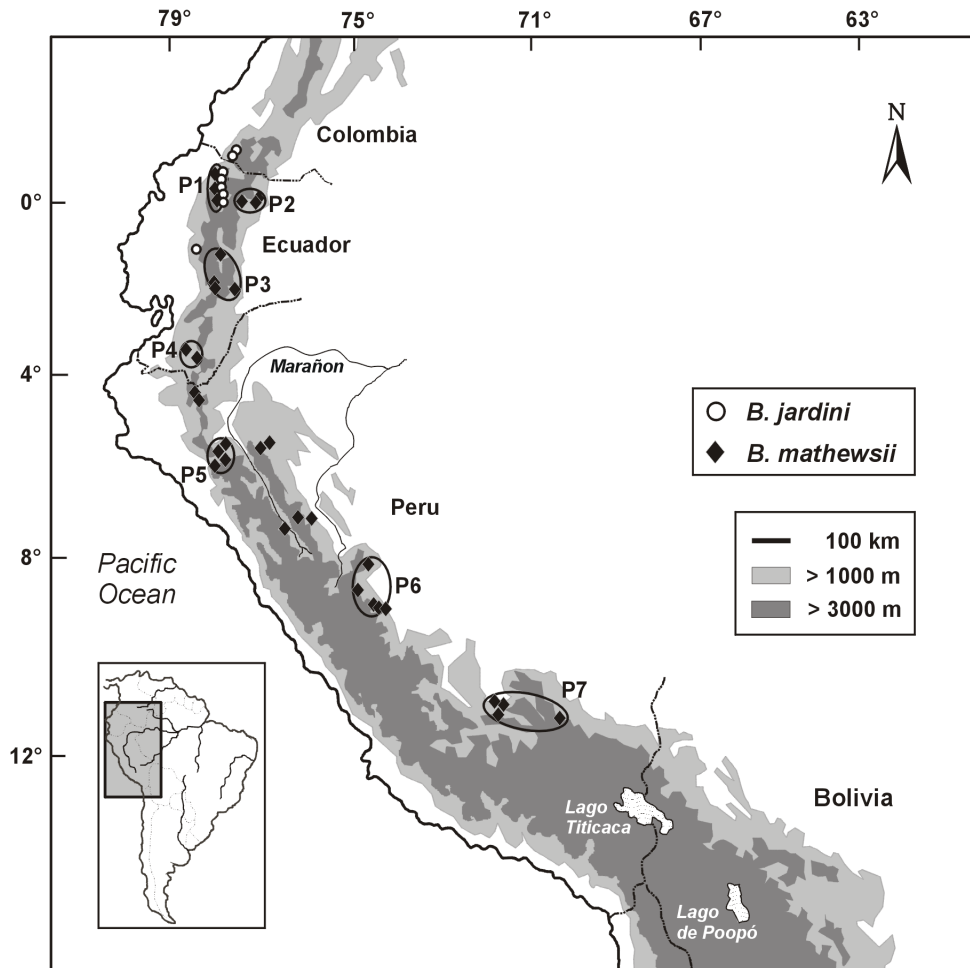


FIG. 4. Geographic distribution of *Boissonneaua jardini* and *B. mathewsii*, based on data obtained from skins and literature (Meyer de Schauensee 1949, Zimmer 1951).

underparts whereas the gorget and some feathers on belly and flanks are more iridescent. The belly, flanks, and lateral parts of the rump exhibit buffy subterminal bars and fringes (Pale Pinkish Buff, 121D). Both characters are also pronounced in the gorget of females. Similarly, this buff coloration is dominant in the outer three rectrices while their tips and upper margins as well as the innermost two rectrix pairs are dark golden green. Usually, in females the golden green of

the rectrix tips is reduced or absent from the inner webs. The discs of under tail-coverts are slightly darker than the central tail feathers but more variable in coloration showing greenish to greyish brown centers (Light Drab, 119C, to Drab-Grey, 119D) with buffy fringes. As found in many species of pufflegs, the feather thighs are completely whitish. Immature birds have the malar area characteristically Cinnamon (123A) as well as the fringes on chin, gorget, and belly (here



becoming partly Clay colored, 123B).

*Distribution and variation in plumage characters.* Although the species occurs in all parts of the northern Andes (Fig. 3), only two subspecies can be recognized. In Colombia, subpopulations of the nominate race inhabit both slopes surrounding the Cauca valley (Cordillera Occidental, Cordillera Central) and the western slope of Cordillera Oriental northeast of the central Magdalena valley but seem to be absent from the upper east region (compare Hilty & Brown 1986). The Venezuelan range extends over the Andes of Mérida from southwestern Táchira to southwestern Lara (compare Sánchez Osés 1995); this subpopulation may be isolated from that of northeastern Colombia by the arid Táchira depression. Altogether, there is evidence for the occurrence of at least four allopatric subpopulations within the nominate form (western, central, eastern Andes, Andes of Mérida).

From Nariño southward to western Ecuador, *B. f. flavescens* is replaced by *B. f. tinochlora*. Based on specimen records, these taxa are separated apparently by the arid valley of Río Patia. *B. f. tinochlora* can be distinguished from the northern race only by the coloration of the belly and inner rectrices, which is slightly darker buff. Additionally, in *tinochlora* the greenish rectrix tips are broader than in *flavescens*, especially in females. However, intergradation in tail coloration between both subspecies is found at the southern end of the Western Cordillera. According to our results, Chapman (1917) reported 17 nominotypical birds (AMNH) from the vicinity of Popayán, upper Cauca valley (type locality, 02°27'N, 76°36'W), showing intermediate characters (buffy tinge, extension of greenish tips), a state he referred to as yet unfinished “parallel evolution” towards *B. f. tinochlora*.

Other color differences represent individual variation, e.g., the intensity of ventral contrast. One adult *B. f. flavescens* female from Cali

(ZFMK # 81.385) has conspicuous Cinnamon (123A) subterminal bars and fringes in the underparts. Similarly, the portions of buffy or whitish fringes vary in both males and females of *B. f. tinochlora*.

*Variation in mensural characters.* Table 1 summarizes the biometric data for all taxa of *Boissonneana*. Figure 1 gives an overview for the four tested morphometric characters from different pools of *B. f. flavescens*. Generally, for this taxon the data distribution appears relatively homogeneous whereas greater differences occur between sexes. We found strong sexual dimorphism in wing length (Fig. 1b) where females average 4–5.5 mm less than males of the same pool (approximate means in males: 76–78.5 mm; in females: 71–73.5 mm). Likewise, in males the outermost rectrices (r5, Fig. 1d) are significantly longer in all pools (approximate means in males: 49–51 mm; in females: c. 46–46.5 mm). In contrast, males and females show similarities in bill length (Fig. 1a: means in both sexes c. 20.5–22 mm; except pool 4, *f. flavescens*) and rectrix 5 length (but note the discontinuity in means, Fig. 1d).

Despite the extensive geographic range covered, only a few trends can be diagnosed among distinct subpopulations. In *B. f. flavescens*, the bill length varies clinally, increasing from northern to southern pools (Fig. 1a). Males of *B. f. tinochlora* are on average slightly smaller in all morphometric characters, with significant differences only in the length of the innermost tail feathers (Fig. 1c: e.g., pool 5 < pools 1, 2, 4,  $P < 0.001$ , t-test); female *tinochlora* are more like those of the nominate form.

#### *Boissonneana mathensii*

*Diagnosis.* In similarity to *B. f. flavescens*, the Chestnut-breasted Coronet (*B. mathensii*) has golden green upperparts and iridescent greenish spots on gorget. The subterminal bars and fringes of the latter are darker, usually True

Cinnamon (139) in the center, becoming laterally Robin Rufous (340).

Most obviously, both taxa differ in the lower ventral plumage and tail. The coloration of chest and belly in *B. mathewsii* can be described as Dark Chestnut (32) or Amber (36; more in females and immatures). The undertail coverts are paler Cinnamon (39) whereas the tail is darker colored again, showing a mixture of Antique Brown (37) × Tawny (38). As in *B. flavescens*, the outer rectrices are tipped with bronze-green. Moreover, the puffs vary in coloration from Clay Color (123B) to Yellow Ocher (123C).

*Distribution and variation in plumage characters.* *B. mathewsii* occurs from northern Ecuador to southern Peru (Fig. 4) at altitudes between 1000 to almost 3000 m (e.g., Rumicruz, Peru, 10°44'S, 75°55'W), thus reaching the widest latitudinal distribution of all generic members. Most records within the southern range refer to the eastern Andean slopes. At the northwestern distributional limits in Ecuador, the taxon also inhabits the western slope as far as Chimborazo. In Peru, it is found in the central Andes southward to Cajamarca, and along the eastern slope to Cuzco.

With respect to the origin of the type, Bourcier (1847) only mentioned that the concerning specimen came from “Le Pérou”. Referring to the travel itinerary of the collector Mathews, Zimmer (1951) suggested Chachapoyas as a restricted type locality, one of the sites visited by Mathews.

While comparing an extensive skin series from Ecuador with Peruvian birds, Zimmer (1951: 23) stated that “no regional distinctions are evident”. Our analysis of qualitative plumage characters also revealed no conspicuous differences even among widely separated subpopulations. Generally, variations exist at the individual level. Likewise, sexual dimorphism is extremely low, which makes it quite difficult to differentiate among males

and females based on color features alone. Usually, males exhibit enlarged greenish discs on the gorget while the subterminal bars and feather borders are more prominent in females. As an additional mark already noted by Zimmer (1951), the belly coloration may be slightly paler in some females (more dark Amber, 36).

*Variation in mensural characters.* *B. mathewsii* is similar in morphometric traits to *B. flavescens* except in rectrix length (c. 1.5 mm shorter on average in both sexes; Table 1, Fig. 2). Thus the tail bifurcation is less pronounced than in the sister taxon (Table 1). Males and females differ significantly in the length of wings (approximate means in males: 75.5–77 mm; in females: 70.5–73.5 mm) and outer rectrices (r5, in males: 47.5–50.5 mm; in females: 43.5–45 mm), partly resulting from the fact that the intrasexual variation is relatively low in these features (Figs 2b and 2d). Bill length (Fig. 2a) and rectrix length (r1, Fig. 2c) seem to vary independently from the range, perhaps as a result of sampling bias or insufficient sample size. We did not find any indication of clinal progression for biometric characters along a geographic gradient.

#### *Boissonneaua jardini*

*Diagnosis.* Among the members of the genus, the Velvet-purple Coronet (*B. jardini*) shows the most conspicuous plumage pattern along with the most obvious sexual dimorphism. Depending on the light conditions, both sexes are characterized by the velvet-like coloration of head, neck, and upper gorget that appear blackish under most angles (e.g., seen from above). Viewed frontally, the crown and center of the gorget are iridescent violet (similar to True Violet, 172, × Spectrum Violet, 72).

Dorsally, the back is predominantly turquoise (Cyan, 164; seen from above) and velvet Dark Green in coloration (162A; seen

from behind), respectively, becoming stronger golden green towards the rump. In contrast to this pattern, the discs of the tail coverts, inner rectrices, and outer webs and tips of the external rectrices are usually relatively dull brownish green (~ Brownish Olive, 29, or very dark Olive, 30) whereas the central portions of the four outer rectrix pairs are whitish. Occasionally, the central tail feathers are tinged Cinnamon-Brown (33; e.g., one female, ZFMK # 8828). The undertail coverts have whitish fringes and, at times, portions of the centers.

In the underparts of adult males, glittering violet (True Violet, 172, × Spectrum Violet, 72) extends from the lower gorget to the abdomen, separated from the blackish gorget by a more or less pronounced turquoise (~ iridescent Cyan, 164, × Turquoise Blue, 65) belt across the lower throat. Towards the flanks, the violet coloration grades into glittering Dark Green (262) × Emerald Green (163). Females can be distinguished from males by the presence of more Cyan (164) colored spots on throat and belly, and the scaled appearance of the ventral plumage caused by broader pale greyish brown (Light Drab, 119C) subterminal bars and fringes. In immatures, belly and flanks are more greyish brown (fringed Drab-Grey, 119D, towards the abdomen). Unlike *B. flavescens* and *B. mathensii*, the feather thighs in both males and females have a Pale Pinkish Buff (121D) coloration.

*Distribution and variation in plumage characters.* The principal center of distribution for *B. jardini* is the Andes of northern and northwestern Ecuador (Fig. 4), particularly in the provinces of Imbabura and Pichincha. Unlike *B. flavescens* and *B. mathensii*, this trochilid is exclusively confined to the western Andean slope. The southern distributional limits are apparently in the province of Bolívar (southernmost specimen locality: Hacienda Porvenir, c. 01°21'S, 79°04'W). Northward, the

taxon has been recorded rarely from Cerro Tatamá (Chocó) and Nariño, southwestern Colombia (Heynen 1999). Throughout the range we found no variation in any color characters (compare Chapman 1926).

*Variation in morphometric characters.* In bill length, *B. jardini* is different from the other two species, reaching higher mean values in both sexes. As shown in Table 1, bill length in males varies from 20.8–23.4 mm (mean: 22.4 mm), and is slightly greater in females (21.7–24.8 mm, mean: 23.0 mm). On the strength of concurrent rectrix length (r1, r5; Table 1), the average tail bifurcation is very similar to *B. mathensii* (mean in males: 8.5 mm, *B. j.*, vs 8.3 mm, *B. m.*; in females: 4.7 mm, both taxa) but rather distinct from that of *B. flavescens* (*B. f. flavescens*, mean in males: 10.3 mm; in females: 6.4 mm).

We were not able to detect intraspecific variation across the range, perhaps due to the clustered collecting sites in northern Ecuador, small sample sizes of measured southern specimens, or lack of further comparative material. However, the mensural data obtained for the two southernmost males from Hacienda Porvenir indicate the absence of strong differences between this subpopulation and northern individuals.

## DISCUSSION

Compared with many other Andean hummingbird genera, the genus *Boissonneaua* is not only fairly continuously distributed in the northern and central Andes (Figs 3–4) but shows an unusual differentiation pattern. Intraspecific plumage variations and interspecific morphometric shifts are relatively slight compared to the well-marked differences in species coloration (see Plate). These findings differ from those obtained for other ecologically comparable trochilid groups with higher speciation rates such as the starfrontlets (*Coe-*

*ligena*, e.g., Zimmer 1951, Schuchmann & Züchner 1997), metaltails (Schuchmann & Heindl 1997, Heindl & Schuchmann 1998), and pufflegs (*Haplophaedia*, Schuchmann *et al.* 2000). Therefore, besides the question as to which causes may have triggered speciation events in *Boissonneana* it is also important to consider the origin of the taxa involved. The hypothetical model discussed below shows that the recent distributional and morphological data from *Boissonneana* representatives can only partly explain their current biogeographic patterns. As supposed for other trochilid genera with an Andean focus of distribution (e.g., *Amazilia*, Weller 2000a; *Saucerrotia*, Weller 2000b; *Haplophaedia*, Schuchmann *et al.* 2000; *Chlorostilbon*, Bündgen 1999), the genus may have evolved in Plio-Pleistocene refuges, perhaps as a result of forest fragmentation during glacial periods (cf. Haffer 1967, 1970).

The absence of local endemics or restricted-range taxa together with a similar phenotypical occurrence within all species indicates on the one hand that radiation processes must have taken place very fast, with more or less parallel range extensions over several parts of the Andes. This scenario could explain the distribution and plumage patterns of *B. flavescens* and *B. mathewsii*. Both are characterized by only minor (*flavescens*) or negligible (*mathewsii*) intraspecific differences although their subpopulations partly occur in different and relatively isolated mountain ranges. Second, the fact that all three *Boissonneana* species are widely sympatric in northern Ecuador indicates a clear differentiation in biological requirements, with the restriction that *B. jardini* initially could have evolved in lower altitude habitats than the congeners, subsequently invading the higher submontane zone. In this context, the remarkable coloration pattern of *B. jardini* appears more derived whereas *B. flavescens* and *B. mathewsii* exhibit relatively plesiomorphic characters.

This pattern is similar to the conspicuous morphological changes observed in west Andean populations of other widespread trans-Andean trochiline taxa, e.g., *Haplophaedia* (*H. lugens* vs *H. aureliae*, *H. affinis*; cf. Schuchmann *et al.* 2000), *Urochroa* (*U. b. bougueri* vs *U. bougueri leucura*), and *Coeligena* (e.g., *C. wilsoni*, *C. coeligena obscura* vs *C. coeligena* ssp.).

With respect to the origin of the genus *Boissonneana*, the preceding assumptions let us suppose that the ancestral population evolved on the eastern slope of the Andes. If *Aglaeactis* and *Urochroa* are considered – based on morphological, behavioral, and biogeographic affinities – as sister groups of *Boissonneana* within a monophyletic lineage, this suggests that a proto-*Boissonneana* could have originated either from the Peruvian (proto-*mathewsii*) or Ecuadorian Andes (proto-*flavescens*). Subsequently, the ancestral population was separated into the precursors of *B. mathewsii* and *B. flavescens*. The latter form possibly evolved in the eastern Cordillera of the northern Andes and later extended its range across the central and western Cordillera and northeastward to the Andes of Mérida. The Venezuelan subpopulation is not differentiated from the nominate race which indicates a relative continuity and lack of disturbance of the species habitat during glacial epochs rather than a recent invasion. Interestingly, this pattern is similar to that found in some other montane forest-bound trochilids (e.g., *Eriocnemis*, Heynen 1999; *Chlorostilbon*, Bündgen 1999) but not to those known for several submontane taxa (e.g., *S. saucerrottei*, *S. viridigaster*; Weller 1998, 2000b) or for páramo species (e.g., *Oxygogon guerini*). Considering the southern extent of the range of *B. flavescens*, the subspecific validity of the race *tinochlora* should be maintained although the differences are fairly weak. Secondary contact with the nominate form is indicated by intergradation in tail morphology at the southern end

of the Cordillera Occidental (i.e., Cerro Munchique).

*B. jardini* appears more derived than its congeners in the extent and coloration of iridescent or otherwise highly contrasted plumage parts. However, the basic pattern of belly and rectrices suggests a closer relationship with *B. flavescens*. Thus we conclude that this taxon most likely evolved from southern derivatives of the *B. flavescens* lineage rather than from representatives of *B. mathewsii*. Based on its restricted range the taxon may have arisen in a very local refugium located in southern Nariño or Pichincha. Generally, this region seems to represent an important center of endemism for the pufflegs *Eriocnemis* (e.g., *E. nigriventris*, Heynen 1999) and *Haplophaidia* (*H. lugens*, Schuchmann et al. 2000).

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APPENDIX 1. Localities of study specimens and additional records from literature, listed from N to S (compare Figs 3–4).

*B. flavescens* (including data from Meyer de Schauensee 1949; coordinates after Paynter 1982, 1993, 1997):

Colombia, Cordillera Oriental: Buenos Aires, Norte de Santander, 1830–2045 m, 08°01'N, 72°58'W; Las Ventanas, Norte de Santander, 2000–3000 m, 07°48'N, 73°06'W; Ramírez, Norte de Santander, 2500 m, 07°48'N, 73°05'W; Páramo de San Pedro, Norte de Santander, > 3000 m, 07°47'N, 73°03'W; Portrerras, Norte de Santander (?), 2150 m, 07°34'N, 73°03'W; Cachirí, Santander, 1890 m, 07°30'N, 73°01'W; Surata, Santander, 1740 m, 07°22'N, 73°00'W; La Corcova, Santander, 2030 m, 07°15'N, 72°54'W; Bucaramanga, Santander, 1000 m, 07°08'N, 73°09'W; Hacienda las Vegas, Santander, 07°04'N, 72°56'W; La Pica, Santander, 2800 m, 06°45'N, 72°45'W; Villeta, Cundinamarca, 842 m, 05°01'N, 74°28'W; vicinity of Bogotá, Cundinamarca, ca. 04°36'N, 74°05'W; Fómeque, Cundinamarca, 2000 m, 04°29'N, 73°54'W; El Peñón, Cundinamarca, 2880 m, 04°26'N, 74°18'W; El Roble, Cundinamarca, 2475 m, 04°23'N, 74°19'W; Fusagasugá, Cundinamarca, 1830–2135 m, 04°21'N, 74°22'W;

Colombia, Cordillera Central: Valdivia, Antioquia, 2200 m, 07°05'N, 75°27'W; Ventanas, Antioquia, 2000 m, 07°05'N, 75°27'W; Hacienda Potreros, Antioquia, 1980 m, 06°39'N, 76°09'W; Medellín, Antioquia, 1538 m, 06°15'N, 75°35'W; Santa Elena, Antioquia, 2750 m, 06°13'N, 75°30'W; Sabaneta, Antioquia, 1700 m, 06°09'N, 75°36'W; Río Negro, Antioquia, 2120 m, 06°09'N, 75°22'W; El Zancudo, Caldas, 2400 m, 05°05'N, 75°30'W; Cañon del Mt. Tolima, Tolima, 1700–2200 m, 04°40'N, 75°19'W; Laguneta, Quindío, 2700 m, 04°35'N, 75°30'W; Toche, Tolima, 2000 m, 04°32'N, 75°25'W; Popayán, Cauca, 1760 m, 02°27'N, 76°36'W; Tijeras, Huila, 2500 m, 02°22'N, 76°16'W; Moscopán, Huila, 2300 m, 02°20'N, 76°05'W; Belén, Huila, 2135 m, 02°15'N, 76°05'W; Almaguer, Cauca, 2312 m, 01°55'N, 76°50'W; Andalucía, Huila, 2310 m, 01°54'N, 75°40'W; La Candela, Huila, 1525–1675 m, 01°50'N, 76°20'W; Buena Vista, Huila, 01°50'N, 75°57'W;

Colombia, Cordillera Occidental: Cerro Tatamá, Risaralda, Chocó, Valle del Cauca, 850–2450 m, 05°00'N, 76°05'W; Bitaco, Valle del Cauca, 1350 m, 03°36'N, 76°36'W; Alto de las Cruces,

Valle del Cauca, 2200 m, ca. 03°30'N, 76°38'W; Cali, Valle del Cauca, 957 m, 03°27'N, 76°31'W; La Florida, Cauca, 2200–2400 m, 02°35'N, 76°55'W; Cerro Munchique, W of Popayán, Cauca, 2425–2540 m, 02°32'N, 76°57'W; Cocal, Cauca, 1225 m, 02°31'N, 76°57'W.

*B. flavescens tinochlora*, Colombia: Ricaurte, Nariño, 1190 m, 01°13'N, 77°59'W; Ecuador: Intag, Imbabura, 1200 m, 00°24'N, 78°36'W; Pachijal (= Río Tambillo), Pichincha, 00°18'N, 78°59'W; Pacto, Pichincha, 1400 m, 00°12'N, 78°52'W; Gualea, Pichincha, 1500 m, 00°07'N, 78°50'W; Nieble, Pichincha, 2300 m, 00°06'N, 78°31'W; Río Saloya, Pichincha, 1680–1830 m, 00°01'N, 78°57'W; Tandayapa, Pichincha, 2500 m, 00°01'S, 78°46'W; Mindo, Pichincha, 1260–2125 m, 00°02'S, 78°48'W; Milligalli, Pichincha, 1800 m, 00°16'S, 78°36'W; Río Tandapi, Pichincha, 00°25'S, 78°47'W; Canzacoto, Pichincha, 1850–1975 m, 00°26'S, 78°45'W; Antisana, Napo, 00°30'S, 78°08'W; Corazón, western slope, Pichincha, 2750 m, 00°32'S, 78°39'W; Volcán Sumaco, Napo, 00°34'S, 77°38'W; Illiniza, Pichincha, Cotopaxi, 00°40'S, 78°42'W; Pallatanga, Chimborazo, 1500 m, 01°59'S, 78°57'W; Citado, Chimborazo (?), 2386 m, not located, probably (near) Río Citado, 02°12'S, 78°50'W.

*B. jardini* (including data from Chapman 1926, Meyer de Schauensee 1949; coordinates after Paynter 1993, 1997):

Colombia: Buenavista, Nariño, 350 m, 01°29'N, 78°05'W; Ricaurte, Nariño, 1190 m, 01°13'N, 77°59'W; San Pablo, Nariño, 1830 m, 01°06'N, 78°01'W; Nóvita Trail, Nariño, 2160 m, not located;

Ecuador: Intag, Imbabura, 1200 m, 00°24'N, 78°36'W; Pachijal (= Río Tambillo), Pichincha, 00°18'N, 78°59'W; Gualea, Pichincha, 1500 m, 00°07'N, 78°50'W; Nanegal, Pichincha, 1400 m, 00°07'N, 78°46'W; Nanegal Chico, Pichincha, 1500 m, 00°02'N, 78°37'W; San Tadeo, Pichincha, 1500 m, 00°01'N, 78°48'W; Mindo, Pichincha, 1200–1830 m, 00°02'S, 78°48'W; Nono, Pichincha, 2730 m, 00°04'S, 78°35'W; Río San Pedro, Pichincha, 2450–2600 m, 00°06'S, 78°23'W; Guápulo, Pichincha, 2960 m, 00°12'S, 78°29'W; Cumbayá, Pichincha, 2450 m, 00°12'S, 78°26'W; Tumbaco, Pichincha, 2400 m, 00°13'S, 78°24'W; Hacienda Porvenir, Bolívar, 1800 m, not located, probably near Hacienda Talahua, 01°21'S, 79°04'W.

*B. mathewsii* (including data from Chapman 1926, Zimmer 1951; coordinates after Stephens & Traylor 1983, Paynter 1993):

Ecuador: Intag, Imbabura, 1200 m, 00°24'N, 78°36'W; Huila, Pichincha, 1000–1500 m, 00°03'N, 78°53'W; Río Oyacachi, below El Chaco, Napo, 1615 m, 00°23'S, 77°49'W; Cuyujúa, Napo, 2400 m, 00°24'S, 78°02'W; Tambillo, Pichincha, 2785 m, 00°25'S, 78°32'W; Baeza, Napo, 1375–1900 m, 00°27'S, 77°53'W; Volcán Sumaco, Napo, 00°34'S, 77°38'W; Baños, Tungurahua, 2000–2200 m, 01°24'S, 78°25'W; Cayanded, Chimborazo, 1375 m, 02°07'S, 78°59'W; Huigra, Chimborazo, 1220 m, 02°17'S, 78°59'W; Pagua forest, Chimborazo, 1900 m, not located (above Huigra); Junction Río Chanchán, Río Chiguancay, Guayas, Chimborazo, 850 m, not located (near Huigra); Chunchi, Chimborazo, 2260 m, 02°17'S, 78°59'W; Macas, Morona-Santiago, 1015 m, 02°19'S, 78°07'W; El Chiral, El Oro, 1225–1950 m, 03°38'S, 79°41'W; Nudo de Cajanuma, Loja, 2500 m, 04°05'S, 79°12'W;



Peru: Chaupe, Cajamarca, 1800 m, 05°10'S, 79°10'W; Lomo Santo, Cajamarca, 1525 m, not located, above Jaen, 05°42'S, 78°47'W; Tambillo, Cajamarca, 1770–2440 m, 06°10'S, 78°45'W; La Lejía, Amazonas, 2745 m, 06°10'S, 77°31'W; Levanto, Amazonas, 2745 m, 06°16'S, 77°49'W; Cutervo, Cajamarca, 2650 m, 06°22'S, 78°51'W; Chugur, Cajamarca, 2750 m, 06°40'S, 78°45'W; Taulís, Cajamarca, 1650–3000 m, 06°54'S, 79°03'W; Utcubamba, La Libertad, 2000 m, 08°13'S, 77°08'W; Hacienda Nuevo Loreto, San Martín, 1200 m, 08°15'S, 76°52'W; San Pedro, Ancash, 1830 m, 08°34'S, 77°27'W; Cushi, Pasco, 1820 m, 09°51'S, 75°37'W; Rumicruz, Pasco, 2960 m, 10°44'S, 75°55'W; Utcuyacu, Junín, 1465 m, 11°12'S, 75°28'W; Chilpes, Junín, 1830 m, 11°19'S, 75°16'W; Garita del Sol, Junín, 1755 m, 11°17'S, 75°21'W; Idma, Cuzco, 1525 m, 12°53'S, 72°49'W; Huyro, Cuzco, 1465 m, 12°58'S, 72°36'W; San Miguel Bridge, Cuzco, 1845 m, 13°06'S, 72°38'W; Machu Picchu, Cuzco, 1830–2600 m, 13°07'S, 72°34'W; Huaisampillo, Cuzco, 2745 m, 13°14'S, 71°26'W.

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