

## BIOGEOGRAPHY OF *RAMPHOMICRON* BONAPARTE, 1850 (AVES: TROCHILIDAE)

André-A. Weller & Karl.-L. Schuchmann<sup>1</sup>

A. Koenig – Zoological Research Institute and Museum of Zoology, Ornithology,  
Working Group: Biology and Phylogeny of Tropical Birds, Adenauerallee 160, 53113 Bonn, Germany

**Resumen.** *Ramphomicron* es un género neotropical de colibríes, endémico de los Andes, al occidente de Venezuela hasta el norte de Bolivia. La insuficiencia en registros y observaciones durante las décadas pasadas a lo largo de la distribución del taxon se ha hecho evidente por la falta de información respecto a tópicos relevantes como la ecología, comportamiento, biogeografía y patrones morfológicos de este. Mediante el uso de caracteres morfológicos y de coloración tomados de pieles de estudio, se esclarece la situación biogeográfica, la variación geográfica y el basamento taxonómico de las especies *R. dorsale*, monotípica y *R. microrhynchum*, politépica. Ambas especies se caracterizan por poseer un pico extremadamente corto y un marcado dicromatismo sexual. Reconocemos tres subespecies para *R. microrhynchum*, de amplia distribución: *microrhynchum*, *albiventris* y *bolivianum*, ya que la forma *andicolum* de Venezuela debería ser incluida dentro de la raza nominal. Adicionalmente concluimos que la discontinuidad de registros para *R. microrhynchum* puede no haber sido únicamente ocasionada por brechas en colectas o destrucción reciente del hábitat montañoso, sino también como resultado de desventajas competitivas del género debido a su pequeño tamaño corporal y pico corto (por lo tanto acceso restringido a las flores). Desde un punto de vista filogenético, el taxon vecino más probable para *Ramphomicron* sería *Lesbia* Lesson, 1832, como lo indican rasgos comunes en la morfología (p.e. plumaje de las hembras) y la etología (cortejo).

**Abstract.** *Ramphomicron* is a Neotropical hummingbird taxon endemic to the Andes from western Venezuela to northern Bolivia. The relative paucity of records and observations throughout its range has been reflected during the past decades in the lack of sufficient information on relevant topics such as the ecology, behavior, biogeography, and morphological patterns of this taxon. Using color and morphometric characters besides distributional data taken from skin specimens, this study particularly aligns the biogeographical situation, geographical variation, and taxonomic background of the two involved species, the monotypic *R. dorsale* and the polytypic *R. microrhynchum*. Both taxa are characterized by, e.g., an extremely short bill and strong sexual dichromatism. Within the widespread *R. microrhynchum*, we recognize three subspecies (*microrhynchum*, *albiventris*, *bolivianum*) whereas the Venezuelan form *andicolum* should be included in the nominotypical race. Further we conclude that the discontinuity of records in *R. microrhynchum* may not be caused only by collecting gaps and recent destruction of the preferred high montane habitats but also may result from competitive disadvantages of *Ramphomicron* owing to its small body size and the short bill (i.e., restricted access to flowers). From a phylogenetic point of view the sister taxon of *Ramphomicron* is most likely *Lesbia* Lesson, 1832, indicated by common features both in morphology (e.g., female plumage) and ethology (display). Accepted 16 May 2002.

**Key words:** Trochilidae, *Ramphomicron*, South America, Andes, biogeography, taxonomy.

### INTRODUCTION

Among the New World avian taxa the nectar-feeding hummingbirds (Trochilidae) comprise the second largest family with some 328 species (Schuchmann 1999), mainly distributed throughout the Neotropics. Because of their enormous variety of habitats (e.g., Simpson 1979) the South American cordilleras can be considered as the center of hummingbird diversity (e.g., 160 spp. in Ecuador; Schuchmann 1999, Rahbek & Graves 2000). The Andean radiation of the subfamily Trochilinae, as well as of other avian groups

(Graves 1985), has been paralleled by a remarkable variation in phenotypical characters such as coloration, ornamental feathers, and biometry. For example, the latter is expressed in often strong interspecific or sexual differences in bill or tail shape and length, regarded as important features in trophic-ecological (i.e., bill morphology in relation to availability of food resources; e.g., Feinsinger & Colwell 1978, Kodric-Brown et al. 1984, Brown & Bowers 1985) or behavioral differentiation (i.e., signal function of ornamental rectrices during courtship or display, such as in *Agelaiocercus* or *Ocreatus*; Schuchmann et al., in press). Additionally, recent phylogenetic studies have pointed to the genetic diversification of Andean trochilid

<sup>1</sup> e-mail: kl.schuchmann.zfmk@uni-bonn.de

clades, suggesting that they are derived mainly from Amazonian lowland representatives (Bleiweiss 1998).

As in many other trochilid genera, no detailed study of the plumage variation and taxonomy of *Ramphomicron* has been undertaken since the middle of the 20th century (Zimmer 1952). Thus the aim of this paper is to summarize all presently available information on geographical variation in terms of color and morphometric aspects. Finally, we will discuss the biogeographical background and focus on the phylogenetic relationships to other trochilid groups.

## MATERIALS AND METHODS

A total of 145 specimens of *Ramphomicron* was examined using methods already employed in previous biogeographical studies (for details, see Schuchmann et al. 2000, 2001). Distributional analysis included mapping of collecting sites (after Paynter 1982, 1992, 1993, 1997; Stephens & Traylor 1983). Morphological analysis comprised color variation (if applicable, we used the terminology of Smithe 1975; names in brackets, capitalized) and measurement of mensural characters (bill from tip to operculum; wing chord; rectrices 1, 5). In order to test for statistical significance of differences between populations ( $n = 4$  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  $1^\circ$  latitude/longitude) were grouped in pools (cf. 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 dorsal plumage pattern (in males, greenish mixed with violet-blue) and shorter tail, were excluded from the statistical comparison.

## RESULTS

*General remarks.* Based on plumage morphology and strict allopatry, two species are presently distinguished, *Ramphomicron microrhynchum* and *R. dorsale*. Whereas the former taxon currently comprises four subspecies, the latter is monotypic (Fjelds  & Krabbe 1990, Schuchmann 1999). *R. dorsale* is restricted to the isolated mountain range of Sierra Nevada de Santa Marta, northern Colombia. *R. microrhynchum* is much more widespread throughout the northern and central Andes, occurring from the Cordillera de M rida of western Venezuela (*R. m. andicolom*), Co-

lombia to Ecuador and northwestern Peru (*R. m. microrhynchum*), and the central and eastern parts of the Peruvian Andes (*R. m. albiventre*) to locally northwestern Bolivia (*R. m. bolivianum*) (Fig. 1). All taxa are most commonly found above 2500 m (Fig. 2), inhabiting edges of humid forest, e.g., cloud and elfin forest (*Polylepis*), and adjacent sub-p ramo to p ramo from the subtropical to the temperate zone (Todd & Carriker 1922, Hilty & Brown 1986, Fjelds  & Krabbe 1990). They are uncommon to rare in their known ranges but may have been overlooked elsewhere (Schuchmann 1984, 1999; Ridgely & Greenfield 2001). Consequently, only a few observations have been published regarding habitat choice, breeding, and display behavior, namely of *R. microrhynchum* (Ruschi 1973, Mobbs 1978, Schuchmann 1990, Herzog et al. 1999).

Compared with other trochilid taxa endemic to the Andes, the genus *Ramphomicron* is characterized by an unusual combination of morphological features. In relation to body size and body length, the bill is among the shortest of all hummingbirds, averaging only 10–13 mm. *Ramphomicron* is strongly sexually dichromatic. Males exhibit a characteristic oval to v-shaped glittering throat patch and a deeply bifurcated tail. Their dark-colored upperparts and rectrices contrast strongly with the chiefly greenish underparts. Females are greenish above and show extended whitish-buff parts ventrally, spotted with greenish discs.

*Ramphomicron dorsale* Salvin & Godman, 1880

*Distribution and status.* The Black-backed Thornbill *R. dorsale* must be considered a restricted-range species, being recorded from only a few localities in the Santa Marta mountains (e.g., Meyer de Schauensee 1964, Hilty & Brown 1986; Fig. 1). Since the range is covered by the Santa Marta National Park (EBA), the species is currently not classified as vulnerable (BirdLife International 2000) but may qualify as such if there is a future habitat decrease (Schuchmann 1999).

Of all taxa of the genus, *R. dorsale* has the widest altitudinal range (Fig. 2). The uppermost record of 4600 m in La Guajira (P ramo de Chirigua; e.g., AN-SP # 159801) lies above those recorded for any member of *R. microrhynchum*. As indicated by an immature specimen collected at 900 m (La Concepci n) in February, seasonal altitudinal migration may occur to an unknown extent (Todd & Carriker 1922, Meyer de Schauensee 1949, Fjelds  & Krabbe 1990).

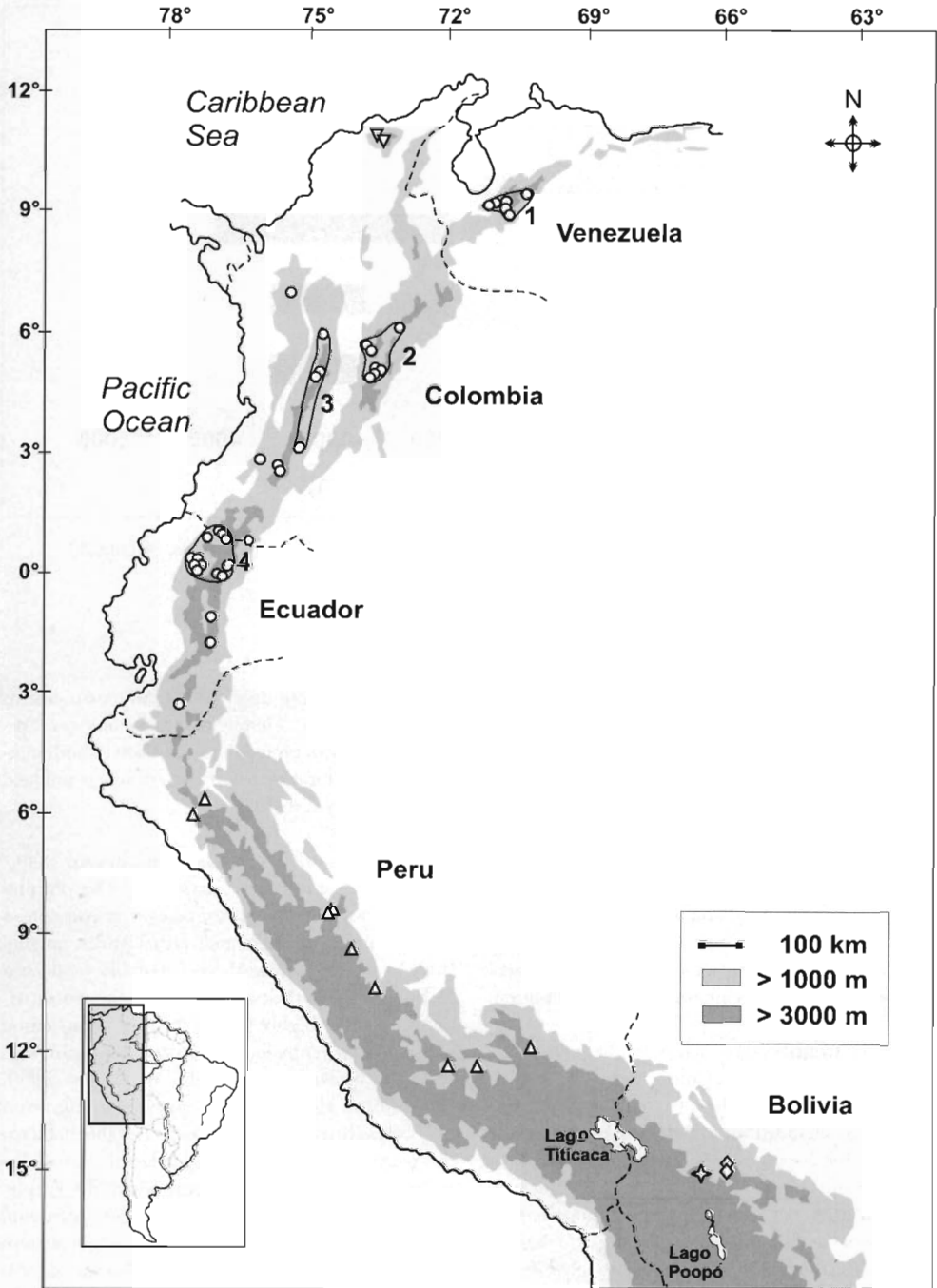


FIG. 1. Distribution of *Ramphomicron*, based on study skins and literature data (see Appendix): *R. dorsale* (inverted triangles), *R. m. microhynchum* (circles), *R. microhynchum albiventris* (triangles), *R. microhynchum bolivianum* (squares), and supposed hybrid *Ramphomicron* x *Adelomyia* (star).

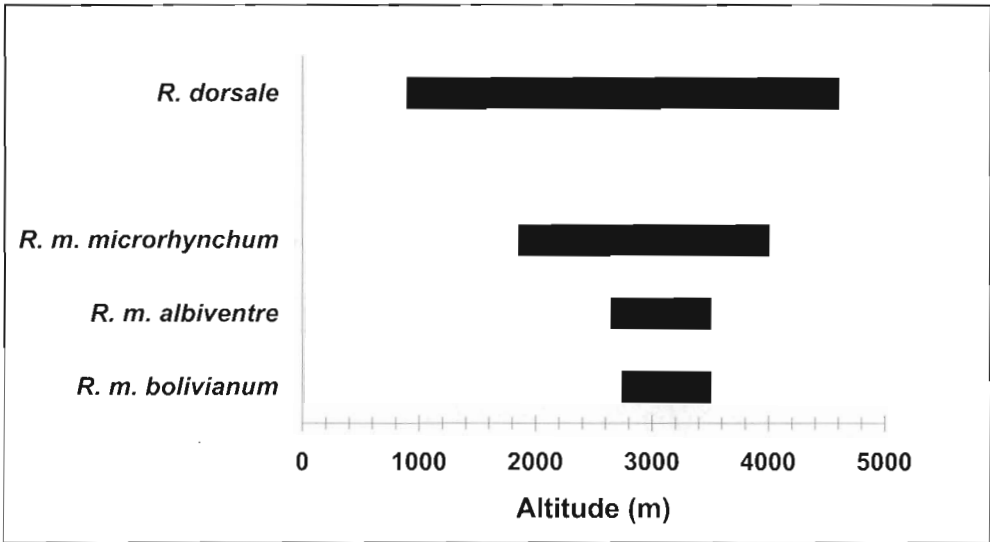


FIG. 2. Altitudinal range of *Ramphomicron*, based on study skins and literature data (see Appendix).

*Color characters.* The male has a velvety blackish dorsal plumage and tail, sometimes with a golden green or dark bluish tinge (cf. Todd & Carriker 1922), and blackish to terminally copper-purplish uppertail coverts; throat patch golden; breast to belly greyish-green to iridescent green, more cinnamon towards abdomen; undertail coverts dark brown with pale buff fringes. The female has bronze-green upperparts with coppery uppertail coverts and bluish- to blackish-purple rectrices with white tips, enlarged in the outermost rectrices; below, whitish with bronze-green spots; discs of undertail coverts olive-green to blackish-green.

*Mensural characters.* Table 1 lists the biometric data of all *Ramphomicron* taxa. Unfortunately, for statistical analysis only three adults (two males, one female) could be included in this study. Typically for the genus the bill is extremely short (12.5–12.9 mm) in both sexes of *R. dorsale* but, unlike *R. microrhynchum*, is slightly decurved at the tip. Moreover, males have longer wings and especially rectrices (e.g., r5) than females, thus contributing to a more strongly bifurcated tail. The rectrices are terminally broadened compared with *R. microrhynchum*. An immature male (ICN # 21674, initially labelled as female) has a similar bill (12.9 mm) and wing length (57.3 mm) as

both adult males but differs in the tail measurements (e.g., r5: 46.5 mm). Despite the small number of specimens examined, geographical variation in both morphological and morphometric characters is unlikely, due to the very restricted range.

*Ramphomicron microrhynchum* Boissonneau, 1840  
*Distribution, status, and taxonomy.* The Purple-backed Thornbill *R. microrhynchum* is widespread throughout the northern and central Andes, ranging from Venezuela and northern Colombia southward to Bolivia. Nevertheless, the species' known distribution appears highly patchy throughout its entire range, with currently four recognized subspecies (e.g., Hilty & Brown 1986, Fjeldså & Krabbe 1990, Schuchmann 1999; Fig. 1). However, since the taxon may be easily overlooked even in favorable habitats, this pattern does not necessarily reflect the actual distributional situation. Some areas where the Purple-backed Thornbill occurs are now under protection, such as the Parque Nacional Sierra Nevada in western Venezuela and the Parque Nacional Natural de Puracé in southwestern Colombia (Schuchmann 1999).

The northernmost subspecies, *R. m. andiculum* (Simon, 1921) is an endemic of western Venezuela. It has been recorded exclusively from the Andes of

Mérida and Trujillo, separated from *R. m. microrhynchum* by the Táchira depression. Recent taxonomic studies have maintained the subspecies *andicolum* (Meyer de Schauensee & Phelps 1978, Fjeldså & Krabbe 1990), contradicting earlier workers such as Chapman (1926) and Zimmer (1952) who doubted the validity of this taxon.

The nominate race shows a rather scattered distribution throughout Colombia, where it occurs in all three Andean ranges (Fig. 1). Two female specimens from the Páramo Frontino, Cauca (USNM # 436288, 436290) probably represent the north-westernmost species record. The southern limits are in northern Peru (Piura; Fjeldså & Krabbe 1990), but the majority of specimens have been collected in the Andes of Colombia and northern Ecuador (see Appendix). In central and southern Ecuador the species is known from only a few localities, such as more recent observations in the Parque Nacional Podocarpus (Rasmussen *et al.* 1996, Ridgely & Greenfield 2001).

Fjeldså & Krabbe (1990) indicate that the Peruvian subspecies *R. m. albiventris* comprises several allopatric populations, with their northern distributional limits in southern Piura. However, within our study we were able to examine only northwestern individuals from two localities in Cajamarca (Cutervo, Taulis). The southeastern populations occur locally along the eastern Andean slope between Huánuco and Cuzco and seem to be separated from the northwe-

stern ones by the upper Río Marañón valley. The southernmost records of *albiventris* are from Bosque Ampay, Apurímac, and Cordillera Vilcanota, Cuzco (Fjeldså & Krabbe 1990; this study).

The holotype of *R. m. bolivianum* taken at Copacata (depto. Cochabamba, Bolivia) by C. Cordier (ZFMK # 81367; Schuchmann 1984) has remained the only specimen of this subspecies collected to date. However, during recent ornithological surveys the species was recorded from two nearby localities in the Cotacajes drainage where several female-type birds were observed in low *Cleome* (Capparidaceae) shrubs (Herzog *et al.* 1999). For reasons of geography, we tentatively include these records in the race *bolivianum*. In addition, a supposed hybrid specimen of *Ramphomicron* × *Adelomyia* from the depto. La Paz (Colección Boliviana de Fauna # 02688; paper in prep.) indicates the occurrence of this subspecies further northwest in the Cordillera Quimza Cruz. A detailed evaluation of the affinities of *bolivianum* is included in the following morphological analysis.

*Color characters.* Compared with *R. dorsale*, the main differences are found in the upperparts both of males and females. Males have a shining bluish-violet head (including neck; malar and auricular area more blackish-purple) and dorsal plumage and shorter uppertail coverts, with a rather clinal variation among the subspecies. In the nominotypical form, *andicolum* and *albiventris*, the basic coloration is True

TABLE 1. Biometric characters of *Ramphomicron microrhynchum* and *R. dorsale*, based on study skins; given are means ± s.d., sample sizes (in brackets), and ranges.

Taxon	Sex	Mensural characteristics (mm)				
		Bill	Wing	Rectrix 1	Rectrix 5	R5 - R1
<i>R. m. microrhynchum</i>	M	10.4 ± 0.5 (69) 8.5 - 11.3	51.4 ± 1.7 (67) 46.0 - 55.2	25.8 ± 1.0 (70) 23.4 - 28.1	48.0 ± 4.0 (61) 44.2 - 52.8	22.2 ± 1.9 (61) 18.8 - 26.8
	F	10.3 ± 0.5 (30) 9.4 - 11.3	46.1 ± 1.5 (31) 43.2 - 49.1	24.4 ± 0.9 (31) 22.3 - 25.9	30.6 ± 1.3 (29) 27.7 - 33.7	6.2 ± 1.5 (29) 2.7 - 8.7
<i>R. m. albiventris</i>	M	10.7 ± 0.5 (17) 9.9 - 12.1	50.8 ± 1.3 (18) 48.1 - 52.8	26.3 ± 0.8 (16) 24.6 - 28.0	45.2 ± 2.0 (10) 42.4 - 48.1	18.2 - 2.0 (9) 15.6 - 21.4
	F	10.5 ± 0.5 (12) 9.7 - 11.4	47.2 ± 1.5 (10) 45.1 - 50.0	24.7 ± 1.5 (11) 22.6 - 27.6	30.7 ± 1.7 (11) 28.8 - 33.9	6.0 ± 1.6 (10) 3.5 - 9.5
<i>R. m. bolivianum</i>	M	10.7 (1)	50.0 (1)	25.3 (1)	43.7 (1)	18.4 (1)
<i>R. dorsale</i>	M	12.3 - 12.9 (2)	58.5 - 58.9 (2)	27.7 - 28.5 (2)	51.8 - 52.5 (2)	24.0 - 24.1 (2)
	F	12.7 (1)	50.8 (1)	25.3 (1)	34.8 (1)	9.5 (1)

Violet (172), the latter subspecies with more blue or Spectrum Violet (72) centrally. In race *bolivianum*, this tone (72) extends over all dorsal parts, including the head, thus giving the taxon the most bluish sheen of all races. The longer uppertail coverts are fringed blackish-blue in all races. The rectrix coloration changes slightly from north to south, showing dark purplish with some coppery in *andicolum* and *microrhynchum*, and more blackish purple in *albiventre* and *bolivianum*. In subadult males, freshly molted outer rectrices appear more dark to blackish golden-green (*R. m. albiventre*, Huancapata, FMNH # 299099).

Earlier taxonomists such as Zimmer (1952) restricted their description of the geographical variation in *R. microrhynchum* to the ventral plumage. Indeed several color characters of certain diagnostic value can be recognized, although differences can be weak and not always stable within taxa groups, thus indicating polymorphism at the subspecific level. In particular, this refers to the color differences in the throat patch and undertail coverts. Simon (1921) distinguished male *R. m. andicolum* from nominate birds on the basis of their golden gorget patch tipped with brilliant green feathers, and the deeper rufous fringes of their undertail coverts. As subsequently stated by Zimmer (1952), both characters are rather insufficient diagnostic features for *andicolum* but, according to our analysis, a rather golden iridescent gorget holds better for *albiventre*. Some males of *andicolum* have a similar golden sheen on the gorget (e.g., USNM # 190500) whereas others have decidedly more brilliant green iridescence or exhibit single glittering green feathers laterally (e.g., SMF # 65627). Besides color aspects, the gorget shape depends on individual variation which cannot be clearly referred to geographical populations (partly due to small sample numbers). Most individuals exhibit a long oval glittering patch but others have it more rounded. One male from southeastern Peru (BMNH # 1946.49.447, *R. m. albiventre*, Hacienda Huarapa) has an extremely narrow throat patch combined with unusual glittering golden discs.

More significant color differences between populations than those in the throat plumage exist in the lower underparts of males. One good characteristic of most males of *albiventre* which we found was apparently overlooked in former revisions is the strongly bronzy sheen on chest, belly and flanks, distinguishing the taxon from all other races. However, this character is not present in two male *albiventre* from the Huánuco area (BMNH # 1946.49.447, FMNH

# 299099), instead they have shining golden-green underparts. In addition, these birds are purplish-violet dorsally, not exhibiting the more bluish tinge found in other *R. m. albiventre* individuals.

In *andicolum* males, the margins of the (mostly) purplish-centered undertail coverts vary from buff-grey (e.g., three specimens in COP collection) to strongly buff or cinnamon (e.g., USNM # 356547), thus blurring the distinction from nominotypical birds. The abdominal feathers and undertail coverts of *albiventre* are fringed on average paler greyish (Bond 1954) whereas they are more cinnamon-rufous in the northern genus members and in the single male of *bolivianum*. Based on the combination of the above-mentioned dorsal and ventral characters, we include north-western Peruvian specimens from Taulis (AMNH collection), as well as those from adjacent Cutervo (ZFMK), in *R. m. albiventre*, contrary to Zimmer (1952) who considered specimens from both localities as *R. m. microrhynchum*.

Females of all races usually have golden-green on head and back but may exceptionally show bluish-green iridescence (*R. m. albiventre*, BMNH # 1946.49.448). Unfortunately for morphological comparison, to date no female of *bolivianum* has been collected. Fjeldså & Krabbe (1990) mention that some *R. microrhynchum* females exhibit whitish lower back feathers. As indicated by Hartert (1900) and our study, this character refers rather to subadult birds (e.g., in ZFMK # 9323, or with additional buffish tinge, such as in ZFMK # 9322), which have sometimes been misidentified as adult females. Ventrally, the plumage is basically whitish and more or less tinged buffy (similar to Pale Pinkish Buff, 121D; reduced in *albiventre*) in the northern subspecies, with smaller golden to bronzy-green spotting on throat and abdomen but enlarged greenish discs on flanks and belly. Zimmer (1952) also pointed out that nominate females usually have more prominent green throat spots than other conspecifics. However, according to Todd (1942) we found that female *andicolum* are almost indistinguishable from those of the nominate form.

Unlike in males, tail and uppertail coverts of female *R. microrhynchum* are more coppery-purplish, and the shorter undertail coverts are completely cinnamon, while the longer ones have at least same-colored broadened margins. The outer rectrices (r4, r5) show broad whitish tips which in r5, in contrast to the rounded pattern of immatures (see below), extend more towards the feather base on the outer than on the inner webs.

Immature males look much like females in most plumage characters but may show (in advanced sub-adult stage) an incompletely developed bluish-violet back and corresponding head feathers. As long as they lack the complete throat patch of adult males or have only a few single glittering gorget feathers, they can be most easily distinguished from females by their enlarged, shining throat spots, broader greenish to purplish centers of undertail coverts, and a generally more whitish than cinnamon ringe in the ventral plumage.

*Mensural characters.* *R. microrhynchum* is characterized by an extremely short bill (c. 2.5 mm shorter than in *R. dorsale*) but medium-length wings and tail feathers (see Table 1). Sexes are dimorphic in various characters since males have on average much longer wings (e.g., nominate race with mean difference = 5.3 mm) and outer rectrices (r5, m.d. = 17.6 mm). The pro-

longation of the latter results in a remarkable mean tail bifurcation of 22.3 mm in males. Individual variation in this sex is most conspicuous in the bill, with a minimum length of 8.5 mm (ZFMK # 9324, Carpintero, Venezuela) and a maximum of 11.3 mm (AMNH # 111716, Lagunaeta, Colombia). In the nominate race, the mean bill-wing ratio is 0.20 (*R. dorsale*, n = 2: 0.22).

In general, geographical character shifts are minor and restricted to males, although it should be noted that sample sizes of some populations, particularly of females, were rather small and thus insufficient for any statistical analysis. Within the northern species range we used four pools (Fig. 3) for intraspecific comparison: in Venezuela, the Andes of Mérida (ssp. *andicolum*, pool 1; males, females); in Colombia (ssp. *microrhynchum*), the Cordillera Oriental (pool 2; males, females) and the Cordillera Central (pool 3, males, females) and the Cordillera Central (pool 3,

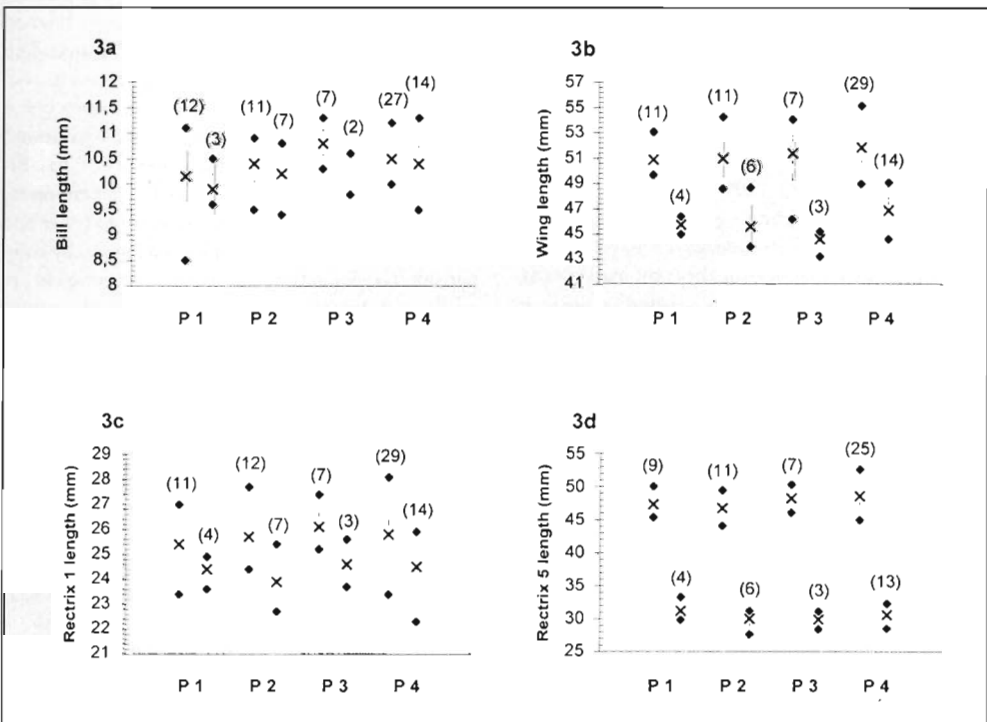


FIG. 3. Variation of mensural characters in different geographical pools of *Ramphomicron m. microrhynchum*; shown are means  $\pm$  s.d., minimum and maximum values. Left bars indicate males, right bars females (sample sizes in brackets); for location of pools, see Fig. 1.

males), and the northern Ecuadorian Andes (ssp. *microrhynchum*, pool 4; males, females). As a result we found a clinal variation in bill and wing length, both characteristics showing a slight increase from northern to southern populations. Males from Venezuela (pool 1) are partly smaller than those from the Cordillera Central (bill;  $P < 0.05$ ) and from Ecuador (bill, wings;  $P < 0.05$ ). Individuals from the Cordillera Oriental (pool 2) have on average shorter outermost rectrices ( $P < 0.05$ ) than those from Ecuador (pool 4). On the other hand, no significant differences were detected between female pools.

Owing to the low specimen numbers, combined with scattered collecting sites in *R. m. albiventre*, we rejected subdividing this population into pools. This subspecies can be morphometrically distinguished from nominate birds only by its shorter outer rectrices (r5,  $P < 0.01$ ) and hence a reduced tail bifurcation ( $P < 0.001$ ). The mensural data of the *R. m. bolivianum* male type specimen fall within the range of male *albiventre* (Table 1). Notable differences in most characters when compared to the first description of *bolivianum* (Schuchmann 1984) can either be explained by what distance was measured (e.g., type culmen length: 7 mm) or by the more precise digital measuring in this study (wings, r5).

## DISCUSSION

Within the Andean hummingbird assemblage the systematic affinities of *Ramphomicron* have been variously evaluated. Considering the combination of external morphological characters – including the short bill, tail morphology, and strong sexual dimorphism – the genus was either placed close to the metaltails (*Metallura*, *Chalcostigma*; e.g., Zimmer 1952) or to the trainbearers (*Lesbia*) and comets (*Sappho*, *Polyonomus*; Schuchmann 1999) or next to both groups (Fjeldså & Krabbe 1990). Previously, *Chalcostigma* was even included in *Ramphomicron* (e.g., Wyatt 1871, Taczanowski 1884). However, the latter taxon most likely represents a sister group of *Lesbia*, with whom it shares not only several important plumage characters (i.e., brilliant male throat patch, female and immature ventral plumage) but also as a common ethological feature the display behavior (namely with *L. nuna*; Schuchmann 1999). The supposed close relationship between these taxa is further stressed by the existence of an intergeneric hybrid, *Ramphomicron microrhynchum* × *Lesbia victorae* (Graves 1997), formerly known as *Zodalia ortonii* (Lawrence, 1869).

The most prominent characteristic of *Ramphomicron* (particularly *R. microrhynchum*) is the unusually short bill, having the minimum length in all hummingbirds. Among other high-altitude hummingbirds a similarly reduced bill length, with an even shorter bill in relation to body size (as measured by bill-wing length ratio), is found only in *Oxygogon* (in *O. g. guerinii* males: c. 0.18, with average bill length c. 13 mm and wing length c. 70 mm; unpubl. data), a páramo-inhabiting species of the northern Andes. Except for Trochilinae members with an extreme bill elongation, such as *Ensifera*, these ratios average for hummingbirds with medium-length bills c. 0.33–0.45 (e.g., compare mensural data of amazilinae trochilids, Weller 1998, and pufflegs, Schuchmann *et al.* 2000, 2001). Such a bill length reduction, together with a decrease in body size when compared to several other trochilids with similar distribution patterns and habitat requirements (e.g., most *Eriocnemis* pufflegs, *Heliangelus* sunangels; Schuchmann *et al.* 2001, unpubl. data), is possibly a limiting factor of the population density, which can be deduced from the discontinuous recording and the relative rareness of *Ramphomicron* throughout its entire range. This may be caused primarily by a restricted access to available long-corolla flowers, although *R. microrhynchum*, like other trochilids, might use holes made by flower-piercers (*Diglossa* sp.) at the basal part of corollae. Secondly, it may result from (increased) competition for food resources within the preferred cloud forest and sub-páramo habitat (for altitudes, see Fig. 2). By comparison, *Oxygogon* is more frequently recorded in appropriate habitats (up to > 5000 m), probably owing to a less competitive situation among trochilids in the higher-elevation páramo zone where it feeds almost exclusively from *Espeletia* flowers (e.g., Schuchmann 1999). Although no quantitative studies exist to alight the interspecific competition among *Ramphomicron* and sympatric trochilid taxa, the strong interference of body size and bill size (length, shape) with regard to the coexistence of trochilid species has been demonstrated for various ecological situations of Neotropical communities (e.g., Snow & Snow 1972, Kodric-Brown *et al.* 1984).

The previously valid subspecies of *R. microrhynchum* have often been maintained on the basis of subtle morphological differences (e.g., coloration of undertail coverts; Zimmer 1952). In the case of *R. microrhynchum andicolum*, our results suggest that these differences are unstable when compared to *R. m. microrhynchum*, and consequently this taxon



should be included in the nominotypical form. In contrast, we retain the Central Andean form *R. m. albiventre*, being aware of a certain geographical variation, i.e., as expressed by the color anomalies of two males and a female (BMNH # 1946.49.447–448; FMNH # 299099) from the Huánuco region of central eastern Peru. Nevertheless, without additional skin material at hand we are unable to assign these specimens to a new taxonomic form; instead, our results may encourage further collecting efforts in this zoogeographically important region (see also Zimmer 1930, Morrison 1948).

The broad occurrence of similar phenotypes in the main Andean distribution range of *Ramphomicron* means that assessing the biogeographical center of the genus is rather difficult. For instance, a golden glittering throat patch is expressed both in the northern and southern populations of *R. microrhynchum*, and even enhanced in *R. dorsale*. As also found in other Andean trochilid taxa like *Eriocnemis* (*E. nigrivestis*; Schuchmann *et al.* 2001) and *Heliangelus* (*H. regalis*), the blackish male plumage of *R. dorsale* most likely represents a derived character. The latter species is a relict endemic of the Sierra Nevada de Santa Marta, which has long been known as an important center of avian endemism, due to its much older geological history than the Andes and its isolation from the main ridges of the northern cordilleras (e.g., Todd & Carriker 1922, Cracraft 1985).

However, there is indication that *Ramphomicron* likely originated in the central Andes of southern Peru or northern Bolivia rather than somewhere in the northern Andes, which is supported by biogeographical and morphological evidence. A southern evolutionary center, such as that suggested for the trochilid genera *Chalcostigma*, *Metallura*, and *Ocreatus* (Fjeldså 1992, Schuchmann & Heindl 1997, Heindl & Schuchmann 1998, Schuchmann *et al.*, in press), is indicated by the dorsal pattern. Additional evidence comes from the closely related genus *Lesbia*, which has its center most probably in southern Peru (Schuchmann & Weller, in prep.). If we consider a hypothetical greenish-backed *Ramphomicron* ancestor (see female-type plumage), the bluish-violet sheen found in the populations from Peru and Bolivia (*albiventre*, *bolivianum*) would be more likely to occur as an apomorphic character than the deep purplish coloration of the northern representatives of male *R. microrhynchum* or the blackish tone of male *R. dorsale*. Independent of the supposed origin, the minor phenotypical variation within the main range of *Ram-*

*phomicron* may result from both rapid radiations across different parts of the Andes and moderate long-term alterations of environmental conditions in high-altitude Andean zones (according to the “stable area” theory, Fjeldså 1995). Additionally, there is evidence for a considerable loss of timberline habitat due to human activities since post-glacial times (e.g., Kessler 1995, Fjeldså & Kessler 1996). Besides the competition interference mentioned above, this could partly explain the relatively patchy distribution pattern currently observed in *Ramphomicron*.

## ACKNOWLEDGMENTS

We are grateful to the curators and staff of the following museums and research institutions for either permitting access to their bird collections during our studies or for lending specimens: American Museum of Natural History, New York (AMNH); The Academy of Natural Sciences, Philadelphia (ANSP); The Natural History Museum, Tring (BMNH); Colección Ornitológica Phelps, Caracas (COP); Field Museum of Natural History, Chicago (FMNH); Instituto de Ciencias Naturales, Bogotá (ICN); Museo de Historia Natural “Javier Prado”, Lima (MHNJP); Naturhistorisches Museum, Basel (NHMB); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Forschungsinstitut Senckenberg, Frankfurt/Main (SMF); Staatliches Museum für Naturkunde, Stuttgart (SMNS); and Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). This project was financially supported by the German Science Council (Deutsche Forschungsgemeinschaft, DFG, Schu 766/5-3), the Brehm-Fonds for International Bird Preservation, Bonn, a Frank Chapman Collection Study Grant (AMNH) and a Jessup Award (ANSP). Further, the ANSP kindly provided accommodation for AAW. We also thank M. Linares, Universidad de los Andes, Bogotá, for valuable logistical support, Carlos Sánchez-Osés, ZFMK, for the Spanish abstract, and W. Bock, New York, G. Graves, Smithsonian, Washington D.C., and B. Hillcoat, Neuss, for critical comments on the manuscript.

## REFERENCES

- BirdLife International. 2000. Threatened birds of the world. Barcelona.
- Bleiweiss, R. 1998. Origins of hummingbird faunas. *Biol. J. Linn. Soc.* 65: 63–76.
- Boissonneau, J. 1840. *Ornismya microrhyncha*. *Rev. Zool.* 2: 354.

- Bonaparte, C. L. J. L. 1850. *Conspectus generum avium*. Vol. 1. Leyden.
- Bond, J. 1954. Notes on Peruvian Trochilidae. *Proc. Acad. Nat. Sci. Philad.* 106: 165–183.
- Brown, J. H., & M. A. Bowers 1985. Community organization in hummingbirds: relationships between morphology and ecology. *Auk* 102: 251–269.
- Chapman, F. 1926. The distribution of bird life in Ecuador. *Bull. Am. Mus. Nat. Hist.* 55.
- Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Orn. Monogr.* 36: 49–84.
- Feinsinger, P., & R. K. Colwell. 1978. Community organization among Neotropical nectar-feeding birds. *Amer. Zool.* 18: 779–796.
- Fjeldså, J. 1992. Biogeographic patterns and evolution of the avifauna of relict high-altitude woodlands of the Andes. *Steenstrupia* 18: 9–62.
- Fjeldså, J. 1995. Geographical patterns of neoendemic and older relict species of Andean forest birds: the significance of ecologically stable areas. Pp. 89–102 in Churchill, S. P., Balslev, H., Forero, E., & J. L. Luteyn (eds). *Biodiversity and conservation of Neotropical montane forests*. The New York Botanical Garden, Bronx, New York.
- Fjeldså, J., & M. Kessler. 1996. Conserving the biological diversity of *Polylepis* woodlands of Peru and Bolivia. A contribution to sustainable natural resource management in the Andes. NORDECO, Copenhagen.
- Fjeldså, J., & N. Krabbe. 1990. *Birds of the high Andes*. Zoological Museum, University of Copenhagen, Copenhagen, Denmark.
- Graves, G. R. 1985. Elevational correlates of speciation and intraspecific geographic variation in plumage of Andean forest birds. *Auk* 102: 556–579.
- Graves, G. R. 1997. Diagnoses of hybrid hummingbirds. 3. Parentage of *Lesbia ortoni* Lawrence. *Proc. Biol. Soc. Washington* 110: 314–319.
- Heindl, M., & K.-L. Schuchmann. 1998. Biogeography, geographical variation and taxonomy of the Andean hummingbird genus *Metallura* GOULD, 1847. *J. Ornithol.* 139: 425–473.
- Herzog, S. K., Fjeldså, J., Kessler, M., & J. A. Balderrama. 1999. Ornithological surveys in the Cordillera Cocapata, depro. Cochabamba, Bolivia, a transition zone between humid and dry intermontane Andean habitats. *Bull. Brit. Orn. Cl.* 119: 162–177.
- Hilty, S. L., & W. L. Brown. 1986. *A guide to the birds of Colombia*. Princeton.
- Kessler, M. 1995. Present and potential distribution of *Polylepis* (Rosaceae) forests in Bolivia. Pp. 281–294 in Churchill, S. P., Balslev, H., Forero, E., & J. L. Luteyn (eds). *Biodiversity and conservation of Neotropical montane forests*. The New York Botanical Garden, Bronx, New York.
- Kodric-Brown, A., Byers, G. S., & D. F. Gori. 1984. Organization of a tropical island community of hummingbirds and flowers. *Ecology* 65: 1358–1368.
- Lawrence, G. N. 1869. Character of some new South American birds, with notes on rare and other little known species. *Ann. Lyc. Nat. Hist.* 9: 265–275.
- Meyer de Schauensee, R. 1949. The birds of the Republic of Colombia. *Caldasia* 5, no. 23: 381–644.
- Meyer de Schauensee, R. 1964. The birds of Colombia and adjacent areas of South and Central America. Narberth, Penn.
- Meyer de Schauensee, R., & W. H. Phelps, Jr. 1978. *A guide to the birds of Venezuela*. Princeton.
- Mobbs, A. J. 1978. Thornbill Hummingbirds (Part I). *Avic. Mag.* 84: 17–19.
- Morrison, A. 1948. A list of birds observed at the Hacienda Huarapa, Department of Huanuco, Peru. *Ibis* 90: 126–128.
- Paynter, R. A., Jr. 1982. *Ornithological gazetteer of Venezuela*. Museum of Comparative Zoology, Cambridge, Mass.
- Paynter, R. A., Jr. 1992. *Ornithological gazetteer of Bolivia*, 2nd edition. Museum of Comparative Zoology, Cambridge, Mass.
- Paynter, R. A., Jr. 1993. *Ornithological gazetteer of Ecuador*, 2nd edition. Museum of Comparative Zoology, Cambridge, Mass.
- Paynter, R. A., Jr. 1997. *Ornithological gazetteer of Colombia*, 2nd edition. Museum of Comparative Zoology, Cambridge, Mass.
- Rahbek, C., & G. R. Graves. 2000. Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proc. R. Soc. Lond. (B)* 267: 2259–2265.
- Rasmussen, J. E., Rahbek, C., Poulsen, B. O., Poulsen, M. K., & H. Bloch. 1996. Distributional records and natural history notes on threatened and little known birds of southern Ecuador. *Bull. Brit. Orn. Cl.* 116: 26–46.
- Ridgely, R. S., & P. J. Greenfield. 2001. *The birds of Ecuador*. Vol. 1. Status, distribution, and taxonomy. Cornell, Ithaca.
- Ruschi, A. 1973. *Beija-flores*. Museu de Biologia Prof. Melo-Leitão. Santa Teresa, Brazil.
- Salvin, O., & F. D. Godman. 1880. On the birds of the Sierra Nevada de Santa Marta, Colombia. *Ibis*, IV. series, vol. 4: 169–178.
- Schuchmann, K.-L. 1984. Two hummingbird species, one a new subspecies, new to Bolivia. *Bull. Brit. Orn. Cl.* 104: 5–7.
- Schuchmann, K.-L. 1990. Biologie, Haltung und Pflege wenig bekannter Kolibriarten - Teil I. *Trochilus* 11: 45–51.
- Schuchmann, K.-L. 1999. Family Trochilidae (Hummingbirds). Pp. 468–680 in del Hoyo, J., Elliott, A., & J. Sargatal (eds). *Handbook of the birds of the world*, Vol. 5: Barn-owls to hummingbirds. Barcelona.

- Schuchmann, K.-L., & M. Heindl. 1997. Biogeographie, geographische Variation und Taxonomie der andinen Kolibrigattung *Chalcostigma* REICHENBACH, 1854. *Mitt. Zool. Mus. Berl.* 73, Suppl.: Ann. Ornithol. 21: 131–153.
- Schuchmann, K.-L., Weller, A.-A., & I. Heynen. 2000. Biogeography and taxonomy of the Andean hummingbird genus *Haplophaedia* Simon (Aves: Trochilidae), with the description of a new subspecies from Ecuador. *Ornithol. Anz.* 39: 17–42.
- Schuchmann, K.-L., Weller, A.-A., & I. Heynen. 2001. Biogeography and taxonomy of the Andean genus *Eriocnemis* (Aves: Trochilidae). *J. Ornithol.* 142: 433–481.
- Schuchmann, K.-L., Weller, A.-A., & D. Jürgens, D. In press. Biogeography and ecology of *Ocreatus* hummingbirds (Aves: Trochilidae). *Ecotropica*.
- Simon, E. 1921. Histoire naturelle des Trochilidae (synopsis et catalogue). Paris.
- Simpson, B. B. 1979. Quaternary biogeography of high montane regions of South America. Pp. 157–188 in Dullman, W. (ed.). *The South American Herpetofauna: its origin, evolution and dispersal*. Monogr. Mus. Nat. Hist. 7. Lawrence.
- Smithe, F. B. 1975. *Naturalist's color guide*. American Museum of Natural History. New York.
- Snow, B. K., & D. W. Snow. 1972. Feeding niches of hummingbirds in a Trinidad valley. *J. Anim. Ecol.* 41: 471–485.
- Stephens, L., & M. A. Traylor, Jr. 1983. *Ornithological gazetteer of Peru*. Museum of Comparative Zoology. Cambridge, Mass.
- Taczanowski, L. 1884. *Ornithologie du Pérou*. Vol. 1., Rennes.
- Todd, W. E. C. 1942. List of hummingbirds in the collection of the Carnegie Museum. *Ann. Carnegie Mus.* 29: 271–370.
- Todd, W. E. C., & M. A. Carriker, Jr. 1922. The birds of the Santa Marta region of Colombia: A study in altitudinal distribution. *Ann. Carnegie Mus. Pittsburgh* 14.
- Vuilleumier, F. 1968. Population structure of the *Astenes flammula* superspecies (Aves: Furnariidae). *Breviora* 297: 1–21.
- Weller, A.-A. 1998. *Biogeographie, geographische Variation und Taxonomie der Gattung Amazilia* (Aves: Trochilidae). Unpubl. Ph.D. thesis, Rhein. Friedrich-Wilhelms Univ., Bonn.
- Wyatt, C. W. 1871. Notes on some of the birds of the United States of Columbia. *Ibis*, III. series, vol. 1: 373–384.
- Zimmer, J. T. 1930. Birds of the Marshall Field Peruvian Expedition 1922–1923. *Field Mus. Pub. Chicago, Zool.* 17: 233–480.
- Zimmer, J. T. 1952. *Studies of Peruvian birds*. No. 62. The hummingbird genera *Patagona*, *Sappho*, *Polyonomus*, *Ramphomicron*, *Metallura*, *Chalcostigma*, *Taphrolesia*, and *Agelaiocercus*. *Am. Mus. Novit.* 1595: 1–29.

APPENDIX. Localities and altitudes (either obtained from specimen labels, ornithological gazetteers or the Alexandria Digital Library Gazetteer, <http://fat-albert.alexandria.ucsb.edu:8827/gazetteer/>) of study skins and additional records from literature (Todd & Carriker 1922, Meyer de Schauensee 1949, Herzog *et al.* 1999), listed from N to S (coordinates after Paynter 1982, 1992, 1993, 1997; Stephens & Traylor 1983; n. loc. = not located):

*Ramphomicron dorsale*, Colombia: Cuchilla San Lorenzo, Magdalena, 1900–2300 m, ca. 11°10'N/74°07'W; La Concepción, La Guajira, 900 m, 11°03'N/73°27'W; Páramo de Chirigua, La Guajira, 4600 m, 10°56'N/73°22'W; Sierra Nevada de Santa Marta, Magdalena/Cesar, 2700–2750 m, ca. 10°50'N/73°40'W.

*R. m. microrhynchum*, Venezuela: Conejos, Mérida, 3000 m, 08°50'N/71°15'W; Páramo de Santo Domingo, Mérida, 3000 m, 08°45'N/70°47'W; Carpintero, Mérida, 3000–4000 m, 08°42'N/71°05'W; Páramo Escorial, Mérida, 2500 m, 08°38'N/71°05'W; Sierra Moñtanas, Mérida, 3000 m, c. 08°36'N/71°00'W; Los Nevados, Mérida, 3000 m, 08°28'N/71°04'W; Cumbre Cerro El Retiro, ca. La Revancha, Táchira, 2800 m, 07°30'N/72°20'W.

Colombia: Páramo Frontino, Antioquia, 3600 m, 06°28'N/76°04'W; Páramo de Agüero, Boyacá, 3050–3500 m, 05°59'N/73°05'W; Páramo de Sonson, Antioquia, 2530–2745 m, 05°43'N/75°15'W; Pacho, Cundinamarca, 1860 m, 05°08'N/74°10'W; Zipaquirá, Vda. Empalizada, Cundinamarca, 2650 m, 05°02'N/74°00'W; Páramo de Santa Isabel, Risaralda (?), 3650 m, 04°47'N/75°26'W; Páramos de Bogotá, Cundinamarca, altitude ?, ca. 04°36'N/74°05'W; Laguneta, Quindío, 2100–3150 m, 04°35'N/75°30'W; Páramo de Choachí, Cundinamarca, 3000–3500 m, 04°33'N/73°58'W; San Miguel, Cundinamarca, 2470 m,

04°27'N/74°18'W; El Peñon, Cundinamarca, 2880 m, 04°26'N/74°18'W; La Aguadita, Cundinamarca, 2000 m, 04°25'N/74°20'W; El Roble, Cundinamarca, 2450 m, 04°23'N/74°19'W; Est. Terminales, Páez, Nevado del Huila, Cauca, 2800–2970 m, 02°48'N/75°57'W; W of Popayán (Micay), Cauca, 3150 m, 02°46'N/76°55'W; El Crucero, Cauca, 3200 m, 02°22'N/76°39'W; Paletará, Cauca, 3000 m, 02°10'N/76°26'W; Río Patía, Cauca, altitude ?, n. loc.; Cerro Pax, Nariño, 3050 m, 00°23'N/77°26'W;

Ecuador: S of road Maldonado-Tulcán, S Río de La Plata, Carchi, 3400 m, ca. 00°40'N/78°02'W; El Pun, Carchi, 2600–2800 m, 00°40'N/77°37'W; San Francisco, Carchi, altitude ?, 00°50'N/77°41'W; Intag, Imbabura, altitude ?, 00°24'N/78°36'W; Santo Domingo, Pichincha, altitude ?, 00°07'N/78°48'W; Cordillera Alaspungo, Pichincha, 3600 m, 00°00'N/78°36'W; Mindo, Pichincha, altitude ?, 00°02'S/78°48'W; El Castillo, Pichincha, altitude ?, n. loc. (near Mindo); Nono, Pichincha, 2730 m, 00°04'S/78°35'W; Nono to Pichincha, Pichincha, 3050–3350 m, n. loc.; Volcán Pichincha, Pichincha, 3350–4000 m, 00°10'S/78°33'W; Cam. Paylón, Pichincha, altitude ?, n. loc. (ca. Vn. Pichincha); Oyacachi, Napo, 2500 m, 00°10'S/78°07'W; Quito, Pichincha, ca. 2820 m, 00°13'S/73°30'W; ravines near Quito, n. loc.; Lloa, Pichincha, 3577 m, 00°15'S/78°35'W; Papallacta, Napo, 3150 m, 00°22'S/78°08'W; Cuyujúa, Napo, 2400 m, 00°24'S/78°02'W; Maspá, Napo, 2600 m, 00°25'S/78°01'W; Runtún, Tungurahua, 2000–2800 m, 01°26'S/78°24'W; Zuña, Morona-Santiago, 3500 m, 02°12'S/78°16'W; Taraguacocha, El Oro, < 3400 m, 03°40'S/79°40'W.

*R. microrhynchum albiventris*, Peru: Cutervo, Cajamarca, 2650 m, 06°22'S/78°51'W; Taulis, Cajamarca, 2670 m, 06°54'S/79°03'W; Hacienda Huarapa, 26 km NE of Huánuco (09°55'S/76°14'W), Huánuco, 2745 m, n. loc.; Millpo, E of Tambo de Vacas, Huánuco, 3600 m, ca. 09°42'S/75°47'W; Huancapata, Huánuco, 2750 m, 09°50'S/76°00'W; Rumicruz, Pasco, 2960 m, 10°44'S/75°55'W; Huacapistana, Junín, 2745–3050 m, 11°14'S/75°29'W; Cachupata, Cuzco, 3555 m, 13°17'S/71°22'W; Pomayaco, near Ahuayro (13°22'S/73°52'W), Apurímac, 2745 m, n. loc.; Bosque Ampay, Apurímac, 2800 m, 13°38'S/72°57'W.

*R. microrhynchum bolivianum*, Bolivia, Cochabamba: Kari Mayo, ca. 2750–3500 m, 16°45'S/66°41'W; Puyani, 2900 m, 16°47'S/66°42'W; Cocapata, 3300 m, 16°57'S/66°43'W.