

Biogeography and taxonomy of the Andean hummingbird genus *Haplophaedia* Simon (Aves: Trochilidae), with the description of a new subspecies from southern Ecuador

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Zusammenfassung

Biogeographie und Taxonomie der andinen Kolibrigattung *Haplophaedia* Simon (Aves: Trochilidae), mit der Beschreibung einer neuen Unterart aus Südecuador

Die vorliegende Studie präsentiert die Ergebnisse biogeographischer und taxonomischer Untersuchungen der andinen Kolibrigattung *Haplophaedia*, basierend auf der Auswertung der geographischen Variation morphometrischer und farblicher Gefiedermerkmale. Außerdem werden ökologische und ethologische Besonderheiten vorgestellt. In der historischen Taxonomie wurden zwei Gattungsvertreter unterschieden, *H. aureliae* (ssp. *aureliae*, *caucensis*, *floccus*, *galindoi*, *russata*, *affinis*, *assimilis*) und *H. lugens*. Aufgrund biogeographischer und morphologischer Befunde wird vorgeschlagen, die spezifische Validität von *H. assimilis* (ssp. *assimilis*, *affinis*) anzuerkennen. Beide Taxa sind von den nördlichen Populationen deutlich allopatrisch isoliert und unterscheiden sich von diesen vor allem in der geschlechtsmonomorphen Färbung der für die Gattung charakteristischen Federhöschen und dem sehr dunkelgrünen, kaum irisierenden Gefieder. Innerhalb des südlichen Verbreitungsgebietes von *H. aureliae* in S-Ecuador treten zudem abweichend gefärbte Teilpopulationen mit deutlicher weißer Fransenzeichnung auf der Ventralseite auf, die als neue Unterart, *H. aureliae cutucuensis* subsp. nov., beschrieben werden. Im Gegensatz zu anderen andinen Trochilidengruppen entstand *Haplophaedia* vermutlich präpleistozän in den Nebelwäldern der Nordanden und wanderte erst während der Eiszeiten in ähnliche Lebensräume der West- und Zentralanden ein.

1. Introduction

Among the trochiline hummingbirds, the pufflegs form a morphologically and ethologically differentiated Andean group comprising the genera *Eriocnemis* (Reichenbach, 1849) and *Haplophaedia* (Simon, 1919¹). As their most significant common plum-

age character, both taxa exhibit conspicuous thigh feathers almost completely covering the legs, the so-called puffs, and a unicoloured, forked tail. Bioacoustically, they share a similar song structure (K.-L. S., pers. obs.).

¹ Based on Simon (1921), we suggest this reference to represent the first citation of *Haplophaedia* as the often cited source Simon (1918; e.g. PETERS 1945, DEL HOYO et al. 1999) is questionable and rather appears to be an unofficial report (M. Théry, MNHNP, pers. comm.).

This paper reviews the biogeographical data and morphological affinities of *Haplophaedia*, currently comprising the two taxa *H. aureliae* and *H. lugens*, and substantiates the proposed specific validity of *H. assimilis*

(HEYNEN 1999). Based on geographical variation and allopatric occurrence in the southern range of *H. aureliae* (FJELDSÅ & KRABBE 1986, 1998), we describe a new subspecies from southern Ecuador.

2. Material and Methods

A total of 149 *Haplophaedia* skins were examined in the bird collections of various national and international scientific institutions (for details, see Acknowledgements). Plumage colours were either studied under natural light conditions or by means of an illuminating magnifying glass ($\times 10$). Descriptions of non-iridescent colours (capitalized, numbers in brackets) refer to SMITHE (1975), whereas iridescent (metallic) colours are given in general terms derived from subjective impressions. The plumage topography follows JOHNSGARD (1997). Immature birds, identified by cinnamon fringes in the dorsal plumage and more greyish parts in the throat plumage, were excluded from further morphological analysis. Morphometric characters (length of bill: 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 near-

est 0.1 mm.

In order to test for statistical significance between subpopulations ($n = 4$), specimens from one locality or adjacent collecting sites (excluding topographical borders like high mountain ranges) were grouped in pools (cf. VUILLEUMIER 1968) and compared with parametric test methods (*F*-test, student's *t*-test; significance level $p < 0.05$). For the calculation of statistics and for graphical imaging we used Excel 7.0 and SigmaPlot 5.0 respectively.

Coordinates and altitudes of collecting sites (see Appendix) derived from specimen labels, unless already mentioned by the collector, were obtained from ornithological gazetteers (PAYNTER 1992, 1993, 1997; PAYNTER & TRAYLOR 1983; STEPHENS & TRAYLOR 1983) or the "International Travel Map, South America, North West" (1993; scale: 1:4 000 000).

3. Results

3.1 General remarks

Haplophaedia species occur in mountain ranges of extreme eastern Panama and in the Andes from Colombia and Ecuador to northeastern Peru and western Bolivia (Fig. 1; Plates 1, 2). As typical forest-inhabiting taxa, they are restricted to wet tropical and subtropical forests in the submontane and montane zone between 900 and 3500 m, a habitat generally known as cloud

forest, but usually below 2500 m (Fig. 2). Although often very local in distribution, these trochilids can generally be regarded as fairly common to abundant, at least in the northern parts of their distributional range (e.g., RIDGELY 1976, FJELDSÅ & KRABBE 1990). The westernmost representative, *H. lugens*, is sometimes considered as vulnerable, based on the paucity of records throughout its range and its restriction to the highly endangered ecosystems of hu-

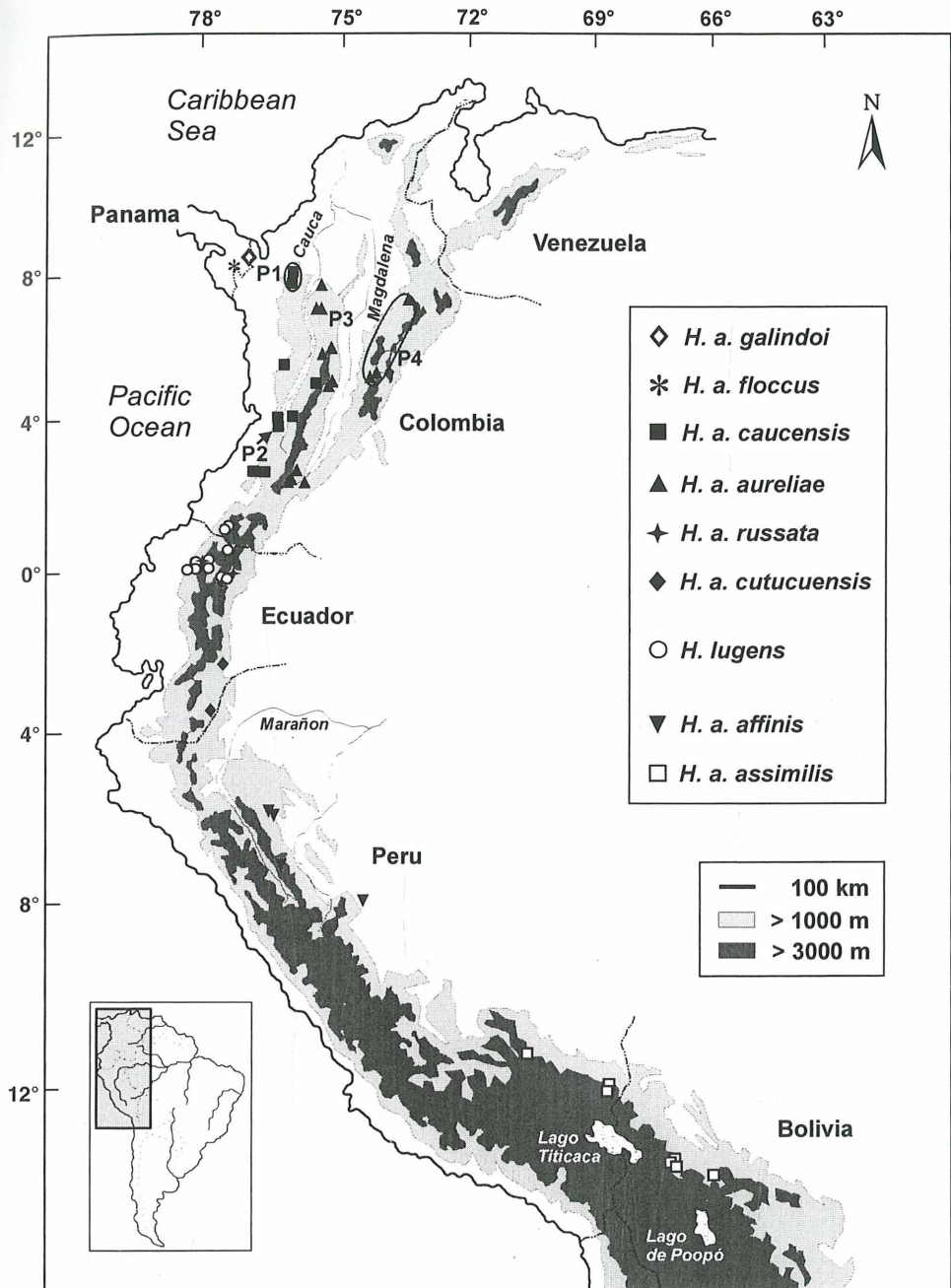


Fig. 1: Geographical distribution of all *Haplophaedia* taxa, based on data obtained from skins and literature (COLLAR et al. 1992, MEYER DE SCHAUENSEE 1949, ZIMMER 1951; for details of localities, see Appendix); encircled are male pools (see also Fig. 3). Abb. 1: Geografische Verbreitung der Taxa von *Haplophaedia* basierend auf Balguntersuchungen und Literaturangaben (COLLAR et al. 1992, MEYER DE SCHAUENSEE 1949, ZIMMER 1951; Fundorte s. Appendix); eingezeichnet sind Männchen-Pools (s. a. Abb. 3).

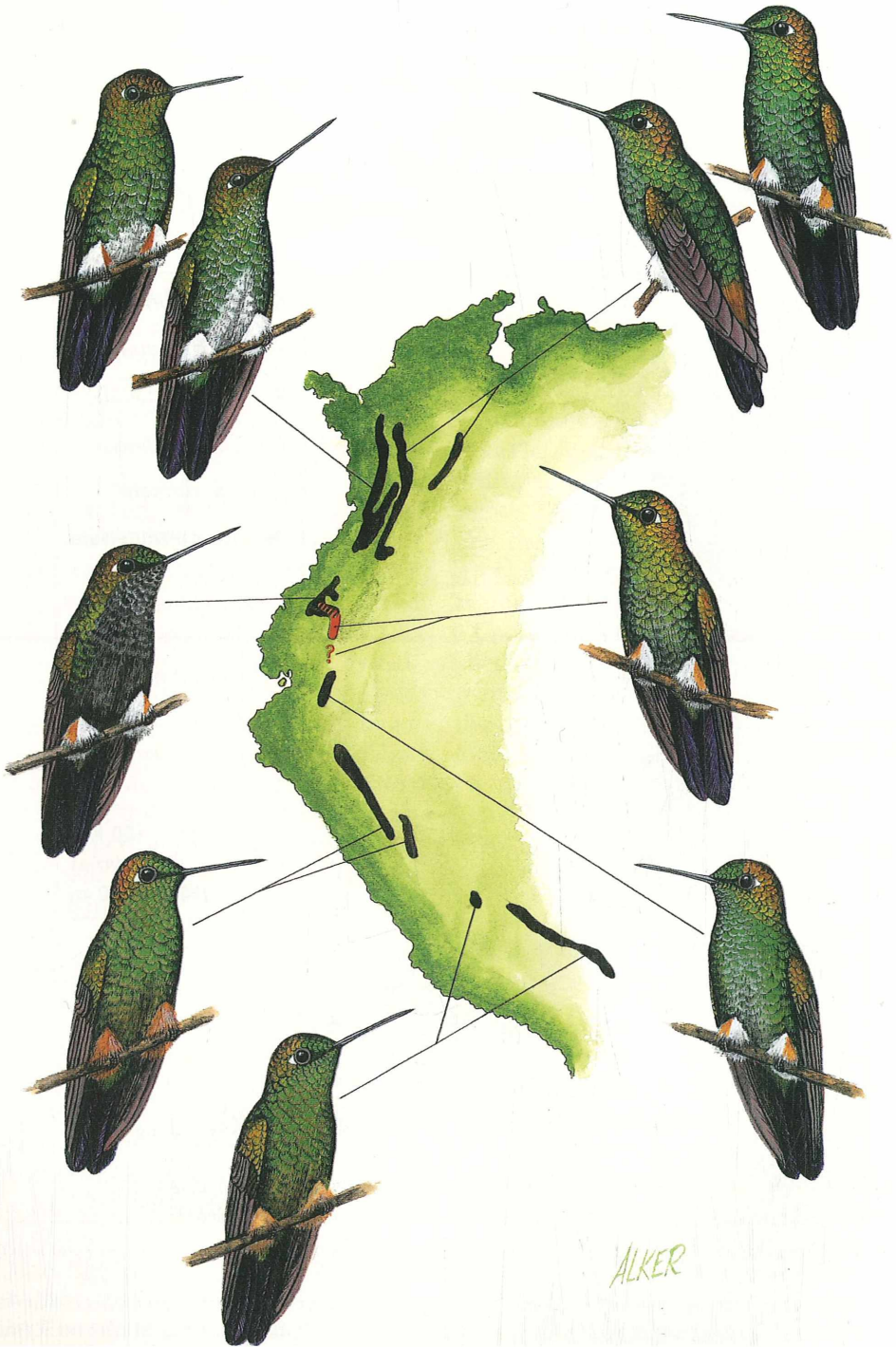




Plate 2: Distribution of *Haplophaedia* taxa (Panama, NW Colombia). Two left birds, top-bottom: *H. aureliae floccus*, ♂ and ♀; two right birds, top-bottom: *H. aureliae galindoi*, ♂ and ♀. Tafel 2: Verbreitung von *Haplophaedia*-Taxa (Panama, NW-Kolumbien). Links: *H. aureliae floccus*, ♂ (oben) und ♀ (unten); rechts: *H. aureliae galindoi*, ♂ (oben) und ♀ (unten).

- ◁ Plate 1: Distribution of *Haplophaedia* taxa (C Colombia to Bolivia). Two upper left birds, top-bottom: *H. aureliae caucensis*, ♂ and ♀; two upper right birds, top-bottom: *H. a. aureliae*, ♂ and ♀; middle right: *H. aureliae russata*, ♂; lower right: *H. aureliae cutucuensis*, ssp. nov., ♂; middle left: *H. lugens*, ♂; two lower left birds, top-bottom: *H. assimilis affinis*, ♂, and *H. a. assimilis*, ♂. Tafel 1: Verbreitung von *Haplophaedia*-Taxa (Zentralkolumbien bis Bolivien). Oben links: *H. aureliae caucensis*, ♂ (oben) und ♀ (unten); oben rechts: *H. a. aureliae*, ♂ (oben) und ♀ (unten); Mitte rechts: *H. aureliae russata*, ♂; unten rechts: *H. aureliae cutucuensis*, ssp. nov., ♂; Mitte links: *H. lugens*, ♂; unten links: *H. assimilis affinis*, ♂, und *H. a. assimilis*, ♂.

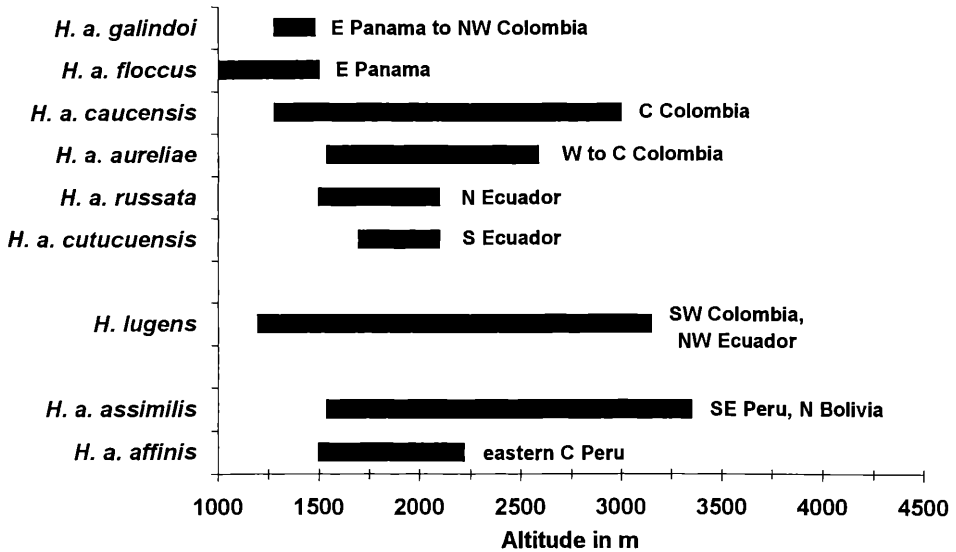


Fig. 2: Altitudinal range of all *Haplophaedia* taxa, based on data obtained from skins and literature (COLLAR et al. 1992, MEYER DE SCHAUENSEE 1949, ZIMMER 1951); for details, see Appendix. Abb. 2: Vertikalverbreitung der Taxa von *Haplophaedia*, basierend auf Balguntersuchungen und Literaturangaben (COLLAR et al. 1992, MEYER DE SCHAUENSEE 1949, ZIMMER 1951); s. a. Appendix.

mid to wet submontane forest and cloud forest (COLLAR et al. 1992). Census counts in La Planada, Ricaurte, Nariño, SW Colombia, (01°13'N/77°59'W) by K.-L. S. indicate that the species is a common resident, with 5-6 pairs/ha.

Similar to the closely related genera *Eriocnemis*, *Urosticte*, and *Ocreatus*, the representatives of *Haplophaedia* are relatively territorial, but differ in their foraging habits as they are restricted to the understory and lower levels of dense forests and their edges (SCHUCHMANN 1977). As a characteristic behavioural trait they do not hold up their wings when alighting, as do members of other Andean hummingbird taxa (e.g., *Eriocnemis*, *Boissonneaua*, *Urosticte*, *Ocreatus*, and *Aglaeactis*; see HILTY & BROWN 1986; SCHUCHMANN 1999). Despite this, *Eriocnemis* and *Haplophaedia* share several similarities in mating and territorial behaviour, e.g., the signal presentation of the tibial tufts by males during display flight

(SCHUCHMANN 1979), a feature also known for *Ocreatus* and *Urosticte* (SCHUCHMANN 1987, 1999).

Haplophaedia species are medium-sized trochilids with a total length of 9-10 cm and a mean body mass of 5-6 g. The bill length varies from 19-21 mm in *H. lugens* to 21-24 mm in *H. aureliae russata* and *H. a. floccus*, whereas *H. a. assimilis* is intermediate in this character (20-22 mm; based on males only, see Table 1). In contrast, *H. aureliae* (wings in males: 55.5-63.5 mm, in females: 51-59 mm, r5 in males: 37.5-43 mm, in females: 30-40 mm) and *H. a. assimilis* (wings in males: 57-60 mm, in females: 54-57 mm; r5 in males: 36-41 mm, in females: 33-36.5 mm) have shorter wings and rectrices than *H. lugens* (wings in males: 63-66.5 mm, in females: 60-64 mm; r5 in males: 42-45.5 mm, in females: 37.5-43 mm). In all *Haplophaedia* species the tail is only slightly forked (males: 3-6 mm, females: 1-4 mm) whereas in *Eriocnemis* taxa the tail

Table 1. Biometric characters (bill, wings, rectrices) of *Haplophaedia* ssp. based on data obtained from skins, showing mean value \pm s.d., ranges, and sample sizes (in brackets). Tab. 1. Biometrische Parameter (Schnabel-, Flügel-, Steuerfederlänge) von *Haplophaedia*-Unterarten, basierend auf Balguntersuchungen; angegeben sind Mittelwert \pm Standardabweichung, Wertebereich und Stichprobenumfang (in Klammern).

Taxon	Sex	Bill (mm)	Wing (mm)	Rectrix 1 (mm)	Rectrix 5 (mm)
<i>H. aureliae galindoi</i>	♂	20.6 \pm 0.9 (8) 19.5-22.2	60.4 \pm 1.2 (8) 58.3-62.0	34.9 \pm 1.2 (8) 33.6-37.1	40.1 \pm 0.8 (8) 39.3-41.4
	♀	20.4 \pm 0.2 (4) 20.1-20.6	54.8-56.1 (2)	31.8 \pm 0.9 (3) 31.0-32.8	35.2 \pm 0.8 (3) 34.5-36.0
<i>floccus</i>	♂	22.2 \pm 0.7 (3) 21.5-22.8	60.0-60.2 (2)	33.5 \pm 0.6 (3) 33.0-34.1	37.8 \pm 0.4 (3) 37.5-38.2
	♀	22.2 \pm 1.0 (8) 21.0-23.6	56.3 \pm 0.7 (8) 55.1-57.4	32.3 \pm 0.8 (7) 30.7-33.1	33.9 \pm 2.0 (7) 30.5-36.5
<i>caucensis</i>	♂	21.0 \pm 0.7 (16) 19.4-22.2	60.6 \pm 1.5 (13) 58.2-62.3	34.6 \pm 0.7 (13) 33.8-36.1	38.9 \pm 1.3 (15) 37.4-41.6
	♀	20.6 \pm 0.7 (8) 19.9-21.8	57.2 \pm 1.7 (8) 54.1-58.9	33.8 \pm 0.5 (9) 33.2-34.7	36.2 \pm 1.7 (9) 33.7-38.7
<i>aureliae</i>	♂	20.1 \pm 1.0 (24) 18.4-22.2	60.5 \pm 2.2 (23) 55.6-63.6	34.7 \pm 1.1 (22) 33.1-37.2	40.0 \pm 1.2 (25) 38.4-43.3
	♀	19.8 \pm 0.9 (14) 18.7-21.6	56.5 \pm 2.3 (13) 51.2-58.6	32.7 \pm 0.9 (15) 31.4-34.9	36.2 \pm 1.8 (12) 34.0-40.0
<i>russata</i>	♂	22.5 \pm 1.1 (5) 21.0-23.9	60.7 \pm 0.6 (4) 60.4-61.4	36.0 \pm 0.6 (4) 35.4-36.7	40.4 \pm 1.9 (4) 38.5-42.9
	♀	22.5 \pm 1.2 (4) 21.5-24.2	55.2 \pm 1.5 (4) 54.0-57.2	33.4 \pm 1.4 (4) 31.5-34.7	35.2 \pm 1.5 (4) 33.5-37.0
<i>cutucuensis</i>	♂	21.5 \pm 0.7 (8) 20.5-22.6	60.8 \pm 1.0 (6) 59.8-62.1	35.9 \pm 1.2 (8) 33.8-37.7	40.1 \pm 0.5 (7) 39.4-40.9
	♀	20.9-22.0 (2)	54.6-54.9 (2)	33.0-34.5 (2)	33.2-34.9 (2)
<i>H. lugens</i>	♂	20.0 \pm 0.7 (6) 19.2-20.9	65.1 \pm 1.1 (6) 63.2-66.6	38.6 \pm 0.9 (6) 37.7-40.2	43.4 \pm 1.6 (6) 41.9-45.7
	♀	20.5 \pm 0.7 (8) 19.1-21.2	61.9 \pm 1.4 (8) 60.1-63.8	37.0 \pm 0.4 (8) 36.4-37.8	39.8 \pm 1.8 (7) 37.4-43.0
<i>H. assimilis affinis</i>	♂	21.5 (1)	59.0 (1)	38.2 (1)	39.2 (1)
	♀	22.2 (1)	55.9 (1)	33.9 (1)	38.7 (1)
<i>assimilis</i>	♂	21.1 \pm 0.7 (14) 19.8-22.3	58.8 \pm 0.9 (13) 57.2-60.1	35.4 \pm 1.0 (14) 33.7-37.5	37.9 \pm 1.6 (14) 35.8-40.8
	♀	20.0 \pm 0.5 (3) 19.5-20.5	56.1 \pm 1.5 (3) 54.3-57.0	35.1 \pm 0.5 (3) 34.5-35.5	34.4 \pm 1.7 (3) 33.0-36.3

is deeply forked and shows conspicuously narrowed rectrices.

Typical features in the coloration of *Haplophaedia* are the relatively dull green plumage (almost non-iridescent) combined with

a dark greenish to bluish black tail. Compared to other trochiline hummingbirds, sexual dimorphism is rather slight and sexual differences are chiefly restricted to the extent of greyish or whitish parts in

ventral plumage (e.g., fringes, puffs, abdomen). *Haplophaedia* males usually possess bicoloured thighs (whitish with cinnamon-rufous), a pattern contrasting with that of nearly all *Eriocnemis* species, which have pure white puffs (except *E. derbyi*). Furthermore, both sexes of all *Haplophaedia* taxa lack the characteristic metallic undertail-coverts exhibited by *Eriocnemis*.

3.2 Taxonomy and distribution

In former classifications, *Haplophaedia* species were often placed in *Eriocnemis* (e.g., GOULD 1861, ELLIOT 1878, HARTERT 1900). SIMON (1919) separated the former genus from the latter under the present name by morphological differences (bill and tail morphology). However, based on a revision by RICHMOND (1902), the generic appellation *Vestipedes* was used for a long time for both *Eriocnemis* and *Haplophaedia* species (e.g., CHAPMAN 1917, 1926; CARRIKER 1933).

Traditionally, the genus has been regarded by most taxonomists as comprising two species, *H. aureliae* (Bourcier & Mulsant, 1846) and *H. lugens* (Gould, 1851). According to previous taxonomic treatments *H. aureliae* represents a polytypic taxon with several subspecies distributed in montane regions from Panama to Bolivia. Due to insufficient information on range and geographical variation, as well as nomenclatural confusion, well-marked taxa were sometimes cited in synonymy. This was the case in *H. (aureliae) affinis*, which was listed under *H. (aureliae) assimilis* (e.g., Simon 1921). On the other hand, several races were described based on minor morphological differences (e.g., *H. a. floccus*, Nelson, 1912; *H. a. galindoi*, Wetmore, 1967; *H. a. bernali*, Romero-Zambrano & Hernández-Camacho, 1979).

A major attempt to classify this critical group of trochilines was made by ZIMMER

(1951). Among the Andean subpopulations, he distinguished the taxa *assimilis* and *affinis* as races of *H. aureliae*, in which he also included *H. lugens*. However, all subsequent classifications maintained the specific validity of the latter form (e.g., WETMORE 1968, WOLTERS 1982, SIBLEY & MONROE 1990). One interesting fact worth mentioning is that Gould described this taxon twice. The first description was apparently based on a female (*Eriopus lugens*, 1851) and the second one on a male (*Eriocnemis squamata*, 1860), most probably due to actually existing sexual differences in colour and morphometry.

The following taxonomic overview summarizes the distributional ranges of all currently valid species and subspecies (listed from north to south; sequence of numbers maintained throughout the section "Species of *Haplophaedia*"):

- (1) *Haplophaedia aureliae* (Bourcier & Mulsant, 1846)
 - a) *H. a. galindoi* (Wetmore, 1967) – Cerros Malí and Tacarcuna in extreme E Panama (Darién) and extreme NW Colombia (Chocó)
 - b) *H. a. floccus* (Nelson, 1912) – Cerro Pirre, E Panama (Darién).
 - c) *H. a. aureliae* (Bourcier & Mulsant, 1846) – northern part and eastern slope of Cordillera Central and western slope of Cordillera Oriental, Colombia.
 - d) *H. a. caucensis* (Simon, 1911) – Cauca valley to western slope of Cordillera Occidental, Colombia.
 - e) *H. a. bernali* (Romero-Zambrano & Hernández-Camacho, 1979) – western slope of Cordillera Oriental in Santander, Colombia.
 - f) *H. a. russata* (Gould, 1871) – NW Central Andes and E Andean slope, Ecuador.
 - g) *H. a. affinis* (Taczanowski, 1882) – E Andean slope, N Peru.

h) *H. a. assimilis* (Elliot, 1876) – E Andean slope from SE Peru to NW Bolivia.

(2) *Haplophaedia lugens* (Gould, 1851) – W Andean slope from Nariño, SE Colombia, to NW Ecuador and eastern slope in Napo (two records).

3.3 Species of *Haplophaedia*

3.3.1 *Haplophaedia aureliae*

3.3.1.1 Characteristics

The Greenish Puffleg *H. aureliae* is characterized by a golden to bronze-green basic plumage with relatively dull upperparts and dark green (*aureliae*, *assimilis*) to brighter green, more glittering coloration in the underparts, especially on throat and belly (particularly *caucensis*). Crown and dorsal parts such as neck, rump, and uppertail-coverts, are often stronger golden bronzy (e.g., in *aureliae*, *caucensis*) to coppery (*russata*) than the back (shining Emerald Green, 163, to golden green). The tail is dark bronze-green (only inner rectrices) to bronzy black in nominate birds, but usually more bluish black in other races. In contrast, the undertail-coverts have a similar coloration to the belly, but are fringed Cinnamon (39, northern taxa in Panama and Colombia; paler in females) to greyish or greyish brown (*russata*, *assimilis*, *affinis*). In general, geographical variation as well as sexual dimorphism in coloration mainly occur in the greenish dorsal parts and the extent of whitish or greyish areas on the throat, belly (including fringes), and puffs. Males of the southern complex (*affinis*, *assimilis*), and most individuals of nominotypical *aureliae*, are entirely dark golden green below, although a few of the latter form have the abdomen pale greyish brown (Drab, 27, to Drab-Grey, 119D; e.g., ZFMK # 9629). In general, southern birds of *affinis*

and *assimilis* become darker and less shining green than *aureliae*. Likewise, the borders of underpart feathers are rather inconspicuous and narrow in *affinis* (Horn Color mixed with greyish, between Colors 91-92) and *assimilis* (Drab, 27) but broader and hence more pronounced in *aureliae* (Drab-Grey, 119D, to greyish white) and *russata* (119D). Whereas only females of *aureliae* and *russata* have prominent whitish centres to the lower belly, this feature is found in both sexes of *caucensis* and adjacent subpopulations of *galindoi* and *floccus* (extending to the breast, and broader in females).

As with other plumage patterns, two taxa complexes can be distinguished concerning the coloration of the puffs, both at a sexual and subspecific level. In the northern races, males have bicoloured tibial tufts (white with a True Cinnamon patch, 139), a character less pronounced in immature males (with greyish dots in *caucensis*, SCHUCHMANN 1979). As a common pattern, immatures and females of all subspecies show Dark Greyish Brown (20) subterminal parts of puff feathers. In contrast to males, females possess almost whitish terminal parts; those of the nominate race sometimes have a very pale buff tinge (e.g., ZFMK # 8921). In males of the northwestern *H. aureliae* subpopulations (*galindoi*, *floccus*, *caucensis*), the position of the colour patch is on the inner side of the tibial tufts, in *aureliae*/*russata* on the outer side (see also HARTERT 1900, SCHUCHMANN 1979). As an exception, within the southern Andean taxa complex both sexes exhibit uniformly coloured puffs, varying from Pale Pinkish Buff in *assimilis* (121D) to dark cinnamon in *affinis* (between Tawny, 38, and Cinnamon, 39), with greyish subterminal parts in females.

3.3.1.2 Geographical distribution and variation in plumage characters of northern races

The highly scattered range of *H. aureliae* extends over almost all parts of the northern Andes except for Venezuela, including adjacent mountain ridges along the Panamanian-Colombian border. Two subspecies from these northwestern distributional limits were described based on colour differences from the Andean taxa *H. a. caucensis* and *H. a. aureliae: floccus* (Nelson, 1912) and *galindoi* (Wetmore, 1967). Both forms are apparently restricted to one (*floccus*) or two (*galindoi*) adjacent mountain ranges located in eastern Darién and northern Chocó (WETMORE 1968).

As already noted by WETMORE (1968: 362), race *floccus* mainly differs from *caucensis* in the lighter green coloration of the underparts and a less bronzy crown. More obviously, females of the northwestern subspecies can be easily distinguished by their ventral plumage. Compared with female birds of *aureliae* and *galindoi*, those of *caucensis* and particularly *floccus* have broader whitish to greyish white fringes on the lower throat. Additionally, females of *floccus* exhibit more whitish fringes on fore-neck and breast, giving the underparts a rather spotted appearance.

Although males of the Panamanian races and *caucensis* are more similar to each other than the females, *floccus* and *galindoi* have on average more greenish backs and less bronzy crowns. However, there is also individual variation in many plumage characters, particularly in males, throughout the range of *caucensis*. As an example, in our representative series from Cauca valley ($n = 24$), no less than nine individuals (5 males, 4 females) have the coppery to bronzy head coloration either less intensive or reduced to the hindneck only, or even lack it almost entirely (ZFMK #

8926). Likewise, the green of the underparts (throat) is highly variable, from shining Emerald Green (163) to dark golden green. Moreover, the extent of the whitish area in the ventral plumage in specimens of both sexes from Cauca valley reveals differences. The uppertail-coverts vary in both male and female *caucensis* from weak golden green to strong coppery, thus not showing the bright cinnamon of some *floccus* specimens (compare WETMORE 1968) which may be encountered on immature plumage or freshly moulted individuals.

Nominate *aureliae* inhabits disjunct areas of the central and eastern Andes. The range includes not only the northern parts of Cauca valley (western slope of Cordillera Central in Cundinamarca) but seems to extend southward as far as Risaralda (ROMERO-ZAMBRANO & HERNÁNDEZ-CAMACHO 1979), situated adjacent to the northeastern distributional limits of *caucensis*. As we could not examine the specimens concerned, it remains unclear to which degree intergradation occurs, if at all. In ventral plumage, we found that individuals from the Cordillera Central (e.g., Cañon del Mt. Tolima, ZFMK # 9634, 9635; specimens from Medellín) show on average more greyish belly feathers than those from the Cordillera Oriental.

Although *aureliae* seems to be restricted to the western slope of the eastern Andes there are a few records from the eastern slope, mostly from Medina (e.g., three specimens in NHM collection). Meyer de Schauensee (1949) also mentions "Llanos of Rio Meta," in the vicinity of Villavicencio and Medina, as a collection site of *H. a. aureliae*. Disregarding the fact that the region around Medina (04°30'N/73°21'W) is situated in the lower submontane zone (with altitudes of ca. 250-460 m), and thus represents an inappropriate habitat for *Haplophaedia*, PAYNTER (1997) doubts it as the source of many specimens, considering it as one of

the dubious Bogotá collections. As the origin of the individuals in question appears doubtful, we excluded them from the present biogeographical analysis.

With respect to variation in the dorsal plumage, the nominate race is comparable to *caucensis*, although the latter is generally less bronze-coloured. More obviously, individual differences in *aureliae* exist in the underparts. For instance, the basic plumage varies in males from shining grass-green or golden green to dark bronze-green; females are usually lighter green than male birds. Independently of subpopulations, the latter exhibit more or less pronounced greyish centres to the belly and abdomen. Another sexual difference is that the narrow fringes of the central lower throat and breast feathers are greyish in males and whitish grey in females, but buff to cinnamon on the upper throat in both sexes. Immature birds have the centre of belly and abdomen pale cinnamon (similar to True Cinnamon, 139; ZFMK # 9636, 9637). Unfortunately for biogeographical analysis, many specimens found in the collections proved to be Bogotá trade skins. One adult nominate male from Cañon del Mt. Tolima (ZFMK # 9634) is somehow aberrant in the throat plumage as it has the gorget dark bronzy green with pale cinnamon fringes.

Apart from individual variation, geographical colour shifts in the ventral plumage of *H. aureliae* were also recognized by FJELDSÅ & KRABBE (1990), who noted that several subpopulations throughout the Andean range differ in extent and coloration of throat feather fringes. With regard to the scaling pattern, FJELDSÅ & KRABBE (1986) mentioned affinities of a subpopulation from the Cutucú Mts. to *caucensis*, although some similarities to *russata* seem to exist (e.g., puff colour). Furthermore, according to R. Bleiweiss (pers. comm.) they postulate “an undescribed form” in

southern Ecuador “with very heavy greyish white scaling below” (1986: 119). After comparison of specimens from the Cutucú Mts. with further skin material from the adjacent southern mountain range of Cordillera del Condor, we believe that these subpopulations are diagnostically distinct from both *caucensis* and *russata*. As this form has apparently remained unnamed (FJELDSÅ & KRABBE 1998; FjeldsÅ, pers. comm.), we suggest ranking it subspecifically as

Haplophaedia aureliae cutucuensis,
subspec. nov.

Diagnosis. Differs from subspecies *russata*, *caucensis*, and *floccus* in having the back on average darker, more bronze-green; underparts including chin broadly scaled greyish white in both sexes, extending to chin, instead of gorget feathers narrowly fringed greyish brown as in *russata*, and broadly fringed buff to greyish brown as in *caucensis* and *aureliae*. Compared with *caucensis*, *galindoi*, and *floccus*, males almost lack the whitish centres of belly and abdomen, whereas in females this coloration only extends to lower belly; throat less metallic green; compared with *aureliae*, throat brighter green.

Holotype. Adult male, 20.11.1984.101, Zoologisk Museum, København (ZMK); collected on 20 April 1984 at crest of central Cutucú Mts., 2100 m, Morona-Santiago, SE Ecuador, by Niels Krabbe.

Description of holotype. Bill almost straight, blackish; crown, neck bronze-green; upper back, wing-coverts, flanks shining golden emerald-green, more bronzy towards rump; uppertail-coverts coppery; gorget grass-green with faint golden sheen, becoming golden green towards belly; fringes pronounced, pale greyish brown on chin (Light Drab, 119C), and greyish white on gorget, centre of belly,

and abdomen; undertail-coverts shining Emerald Green (163), bordered greyish white to Light Drab; tail almost entirely bluish black, innermost two pairs of rectrices basally blackish bronze-green; tibial tufts pure white, with rufous patch (Kingfisher Rufous, 240) on outer side.

Female. Similar to male, but centre of belly more whitish; puffs terminally almost entirely whitish, basally Dark Greyish Brown (20); wings and outer rectrices shortened.

Distribution. Only known from the Cordillera de Cutucú, Morona-Santiago, and the Cordillera del Condor, Zamora-Chinche, southern Ecuador.

Etymology. This race is named after the mountain range where the type locality is situated.

Variation. Occurs among individuals, but is not related to range. The plumage on crown and hindneck is mostly bronzy to dark bronze, but in some individuals can be dark golden green with only slight traces of bronze (e.g., ZMK, Ecuador, 16 Sept. 1990). Similarly, the upper back coloration varies from golden emerald-green to bronze-green, except for one male which has the upper gorget feathers more cinnamon-greyish (ZMK # 20.11.1984.100) resembling those of *russata* on throat, all others are fringed greyish-whitish. Moreover, in males the puffs are cinnamon (True Cinnamon, 139) or rufous-coloured (Kingfisher Rufous, 240). Contrary to the holotype, some individuals have the undertail-coverts entirely bordered greyish white (e.g., ZMK # 20.11.1984.99).

3.3.1.3 Variation in mensural characters of northern races

Generally, morphometric variation is weak among all subspecies (Table 1), evident in the extensive overlap in most measured characters. Males and females of all races

are dimorphic, the latter on average having shortened wings and rectrices and a less bifurcated tail (Table 1). For *H. a. caucensis*, these findings contradict the data obtained for a small series ($n = 10$) from Cauca valley (SCHUCHMANN 1979).

Similar to colour differences among the northwestern subpopulations of *H. aureliae*, *H. a. floccus* shows relatively strong differences in biometric characters towards the adjacent taxa. *Floccus* females have significantly longer bills than those of *galindoi* and *caucensis* ($p < 0.01$, all *t*-test) but shorter rectrices than the latter ($r1: p < 0.001$, $r5: p < 0.05$; see Table 1). This trend is also observed in males ($n = 3$). In comparison, *galindoi* and *caucensis* are less distinct in morphometry and solely differ in tail length of males ($r5: galindoi > caucensis$, $p < 0.05$).

Within race *caucensis*, comparison of two male pools (1, 2) from Cordillera Central yielded no proof of clinal variation between northern and southern subpopulations (Fig. 3). Vice versa, strong geographical variation is found in wing length between male pools of *aureliae* (Fig. 3b: pools 3, 4; $p < 0.05$, *t*-test) from the Cordillera Central and Oriental (see Fig. 1 for location of pools). From the latter part of the range, subspecies *bernali* was described based on minor differences in exposed culmen length (measured differently in this study, see Methods) from nominate birds (ROMERO-ZAMBRANO & HERNÁNDEZ-CAMACHO 1979), but the type series from Virolín, Santander (deposited in ICN-MHN, Bogotá), comprises only 3 individuals (1 male, 2 females). Three additional specimens taken at the same locality (NMNH) yielded similar measurements, ranging between 21.2–22.2 mm (2 adult males) and 21.6 mm (adult female). Although lacking statistical significance, these data are close to the mean values of other studied pools or even suggest overlap in bill length with other sub-

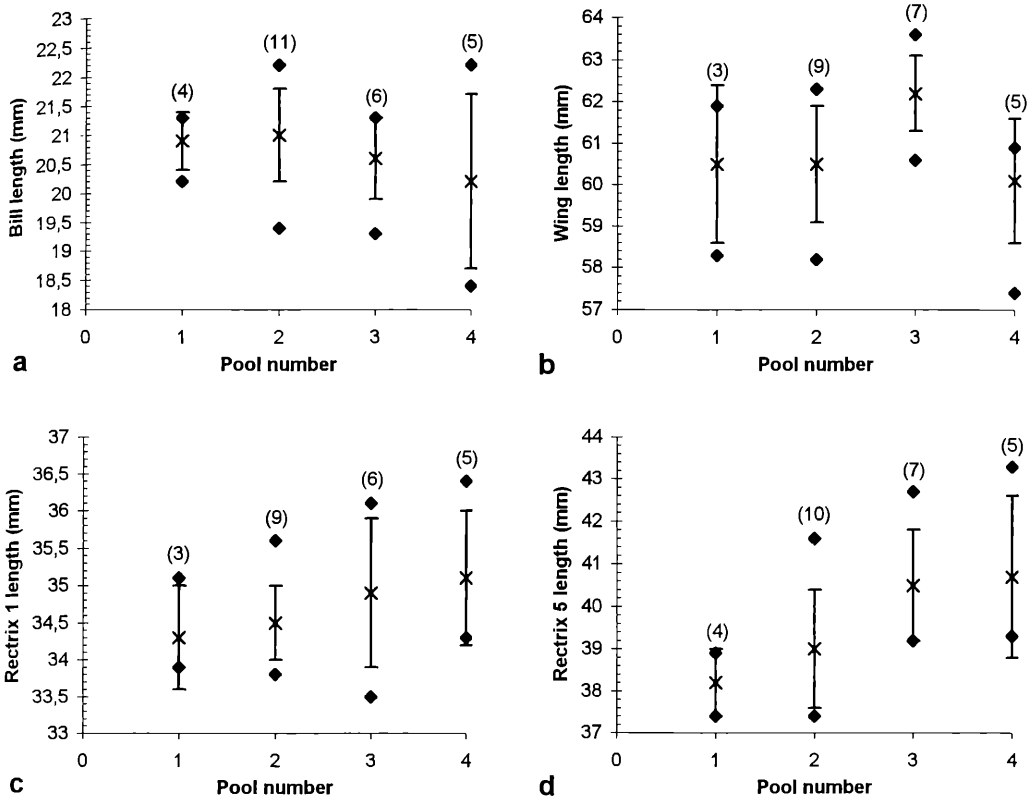


Fig. 3: Mean \pm s.d., minimum and maximum values of biometric characters (bill, wings, rectrices) in male pools of *Haplophaedia aureliae caucensis* (pools 1, 2) and *H. a. aureliae* (pools 3, 4); in brackets, sample sizes. Localities (from N to S): pool 1: Hacienda Potreros, Urrao; pool 2: San Antonio, Alto de las Cruces; pool 3: Medellín, Cañon del Mt. Tolima; pool 4: Vírolin, Fusagasuga, Paramós de Bogotá; for coordinates and altitudes, see Appendix. Abb. 3: Mittelwerte, Standardabweichungen und Extremwerte biometrischer Merkmale (Schnabel-, Flügel-, Steuerfederlänge) in Männchen-Pools von *Haplophaedia aureliae caucensis* (Pools 1, 2) und *H. a. aureliae* (Pools 3, 4); in Klammern: Stichprobenumfang. Lokalitäten s. oben, Koordinaten und Höhenangaben s. Appendix.

populations (e.g., pool 3, males: 19.3–21.3 mm, mean 20.6 mm, $n = 6$; cf. Fig. 3b).

3.3.1.4 Geographical distribution and variation in plumage characters of southern races

In contrast to the biogeography of other races, the taxa *affinis* and *assimilis* are exclusively confined to the east Andean slope of northern Peru (*affinis*) and southeastern Peru to northwestern Bolivia (*assimilis*).

Their distributional patterns are similar as both taxa apparently seem to occupy a disjunct range (e.g., BRACK EGG 1969, FJELD-SÅ & KRABBE 1990; Fig. 1) although this could be due to collecting gaps. Contrary to ZIMMER (1951) who found no distinctions in plumage morphology between nominate birds from Peru and Bolivia, one male from the latter part of range (Chulumani, 16°24'S/67°31'W; NHM # 1902.3.13.2053) has the head, wing-coverts, and uppertail-coverts more bronzy than the

northern individuals. There is no indication for significant variation in *affinis* (BOND & MEYER DE SCHAUNSEE 1943, ZIMMER 1951), although we were able to examine only two specimens. Interestingly, a female from Sira Pico (AMNH # 820941) has the centre of the belly unusually cinnamon (True Cinnamon, 139). Some colour variation in the puffs is related rather to sexual dimorphism (with whitish traces basally in females) than to geographical patterns (ZIMMER 1951). In comparison with the nearest northern representatives of *H. aureliae*, *russata* and *cutucuensis*, the body plumage is duller green and the thighs are almost uniformly coloured in both sexes (varying from Buff, 121D, in *assimilis*, to Dark Cinnamon, 38-39, in *affinis*) and lack the conspicuous whitish parts typical of the former taxa.

3.3.1.5 Variation in mensural characters of southern races

In the northern subspecies *affinis*, variation along a geographical gradient was not detectable because of the lack of additional skin material ($n = 2$). However, the available data on both *assimilis* and *affinis* indicate strong affinities with the northern races of *H. aureliae* (Table 1). Since we failed to group *assimilis* individuals in pools due to the scattered localities of study specimens, biometric characters of subpopulations could not be statistically compared. As in the northern complex, sexes differ chiefly in length of wings and rectrix 5 (Table 1).

3.3.2 *Haplophaedia lugens*

3.3.2.1 Characteristics

The Hoary Puffleg *H. lugens* mainly differs from *H. aureliae* in the underparts coloration, which is generally blackish grey (Blackish Neutral Grey, 82) in the gorget, becoming paler greyish (Dark Neutral Grey, 83) in the centre of the belly and abdomen;

The flanks exhibit a shining golden green tone. The broadly whitish fringed gorget feathers (particularly pronounced in females) give the ventral side a scaled appearance. On the upperparts, back and rump are usually not as greenish as in most northern races of *aureliae*, reflecting more bronzy to coppery (see HILTY & BROWN 1986). The tail is almost blackish, with broader rectrices than in the sister taxon, and the undertail-coverts often have a Dark Neutral Grey tinge (83) and reduced green discs. As in the northern *aureliae* complex, the tibial tufts of males are bicoloured (whitish with a Rufous patch, c. 240-340), those of females pure white with Blackish Grey (82) bases.

3.3.2.2 Geographical distribution and variation in plumage characters

This monotypic taxon is relatively continuously distributed along the western Andean slope from Nariño, Colombia, to western Ecuador in the provinces of Carchi, Imbabura, and Pichincha, where it can be regarded as locally fairly common to very common in appropriate habitats (K.-L. S., pers. obs.). Additional records come from the eastern slope in Napo (Papallacta, Baeza). Because of the small number of specimens examined from both Colombia and Ecuador, we could not distinguish a clinal variation. Hence, differences in plumage characters are based on individual dimorphism (age-related?). As an example, the hindneck and back feathers vary from golden green to dark bronze-green or even coppery.

3.3.2.3 Variation in mensural characters

With respect to the length of wings and rectrices, *H. lugens* is larger than all other congeneric taxa (Table 1). The bill is on average shorter than in the geographically closer taxa *russata*/*cutucuensis* and possi-

bly *affinis*, but similar to the more distant races *aureliae/ caucensis* and *assimilis*. Females show strong variation in tail bifurcation from 0.3 to 6.0 mm, caused by partly

elongated outer rectrices (Table 1). Again, the small sample size prevents comparison of subpopulations to detect any progressions in morphometric characters.

4. Discussion

4.1 Taxonomic conclusions and systematic relationships

Knowledge of biogeographical and morphological affinities among closely related species groups (either at conspecific, generic, or intergeneric level) has proved to be a useful tool both for the evaluation of taxonomy and for the reconstruction of the phylogeny of widespread lowland or montane hummingbird clades (e.g., SCHUCHMANN & DUFFNER 1993, SCHUCHMANN &

HEINDL 1997, HEINDL & SCHUCHMANN 1998, WELLER 1998). As in other trochiline species groups, the systematic position and intrageneric relationships of the genus *Haplophaedia* have been widely neglected in biogeographical surveys since PETERS (1945), chiefly due to uncertainties in questions of range and phenotypic patterns (FJELDSÅ & KRABBE 1990).

The historical taxonomy and the results derived from this study are summarized in Table 2. For our taxonomic approach, we

Table 2. Historical and recent taxonomy of the genus *Haplophaedia*. Tab. 2. Historische und aktuelle Taxonomie der Gattung *Haplophaedia*.

First description	Goold (1861)	Hartert (1900)	Simon (1921)	Peters (1945)	this study
<i>Trochilus Aureliae</i>	<i>Eriocnemis Aureliae</i>	<i>E. aureliae</i>	<i>Haplophaedia A. Aureliae</i>	<i>H. a. aureliae</i>	<i>H. a. aureliae</i>
<i>Eriocnemis russata</i>	–	<i>E. russata</i>	<i>H. Aureliae russata</i>	<i>H. aureliae russata</i>	<i>H. aureliae russata</i>
<i>Haplophaedia Aureliae caucensis</i>	–	–	<i>H. Aureliae caucensis</i>	<i>H. aureliae caucensis</i>	<i>H. aureliae caucensis</i>
<i>Eriocnemis floccus</i>	–	–	<i>H. Aureliae caucensis</i>	<i>H. aureliae caucensis</i>	<i>H. aureliae floccus</i>
<i>Haplophaedia a. galindoi</i>	–	–	–	–	<i>H. aureliae galindoi</i>
<i>Haplophaedia a. bernali</i>	–	–	–	–	<i>H. a. aureliae</i>
–	–	–	–	–	<i>H. aureliae cutucuensis</i>
<i>Eriocnemis assimilis</i>	–	<i>Eriocnemis assimilis</i>	<i>H. Aureliae assimilis</i>	<i>H. aureliae assimilis</i>	<i>H. assimilis assimilis</i>
<i>Eriocnemis affinis</i>	–	<i>Eriocnemis assimilis</i>	<i>H. Aureliae assimilis</i>	<i>H. aureliae affinis</i>	<i>H. assimilis affinis</i>
<i>Eriopus lugens</i>	<i>Eriocnemis lugens E. squamata</i>	<i>E. lugens</i>	<i>H. lugens</i>	<i>H. lugens</i>	<i>H. lugens</i>

used the concept of morphospecies (implying the biological species concept *sensu* MAYR 1942) being aware that some of the taxa concerned are highly allopatric (e.g., there are no contact zones between northern and southern Andean populations).

At the northwestern distributional limits of *H. aureliae*, the taxa *floccus* and *galindoi* should be maintained as subspecies, mainly based on differentiation within females and from *caucensis*. Within the Andean range, the disjunct distribution of both *caucensis* and *aureliae* on opposite sides of valleys or in rather isolated mountain ranges apparently strengthens the occurrence of character shifts, as can be recognized in, for example, the variation of the belly colour in nominate birds.

Given the very small sample size ($n = 3$), and the marginal shift in average bill length towards other subpopulations of *H. a. aureliae* (see Fig. 2), we suggest that race *bernali* simply represents character progression within the the nominate race. A similar north-south trend in bill length decrease can be observed within the southern subpopulations of *H. aureliae* as race *russata* has on average longer bills than *cutucuensis*.

In agreement with more recent taxonomic works (WETMORE 1968, SIBLEY & MONROE 1990), we confirm the species status of *H. lugens*. ZIMMER (1951) doubted the specific validity of the taxon, not only for morphological reasons but also because of assumed allopatry with *H. a. russata*, and questioned specimens from the eastern slope (Papallacta) in Ecuador. However, our results not only support this record and another adjacent collecting site (Baeza), but give further evidence for the sympatry of these taxa (for several *russata* specimens from northern central Ecuador, see Appendix). The high plateau of Porculla (below 3000 m) probably serves as a pathway for cis- and trans-Andean invading

species from both slopes of the Andes. Similar range extensions across the Andes are known from the Amazilia Hummingbird *Amazilia amazilia* in Loja, southern Ecuador (WELLER 2000).

In plumage morphology, *H. lugens* appears more derived than *H. aureliae*, although similarities exist with the southern complex of the sister taxon, namely *cutucuensis*, in the scaled throat pattern and bronzy sheen on the upperparts. On the other hand, bill length places *H. lugens* closer to *caucensis* and *aureliae* (Table 1).

The taxa *assimilis* and *affinis*, currently placed in the complex *H. aureliae*, should be distinguished as subspecies of a distinct allospecies, *H. assimilis*. This treatment is justified not only by their complete geographical isolation from *H. aureliae* and *H. lugens* but also by the distinct, relatively apomorphic coloration pattern (puff colour, very dull green plumage). Nevertheless, we think that further field studies are needed to verify whether *H. assimilis* can also be ethologically distinguished from its sister taxa (e.g., song structure, display).

Following the guidelines of HAFFER (1986) and AMADON & SHORT (1992), we apply the superspecies concept to *Haplophaedia aureliae* and *H. assimilis* (first order superspecies), as well as to *H. assimilis* and *H. lugens* (second order superspecies), since the taxa of both groups replace each other geographically and ecologically.

Concerning systematic relationships, we suggest considering *Eriocnemis* and *Urosticte* as sister groups of *Haplophaedia* based on synapomorphic characters in morphology and behaviour (SCHUCHMANN 1987).

4.2 Biogeography and speciation model

Recent studies on biogeography, systematics, and phylogeny of Neotropical bird taxa (among them many representatives of Trochilidae) have focused either on bio-

chemical (e.g., SIBLEY & MONROE 1990; BLEIWEISS ET AL. 1994, 1997; GARCIA-MORENO & FJELDSÅ in press) or biogeographical-morphological aspects (e.g., WALTERS 1980, HOWELL & WEBB 1995, STILES 1996, HEINDL & SCHUCHMANN 1998), often coinciding with the application of different species concepts (for review, see HAFFER 1997). In each case, the frequent lack of substantial distribution data and information on geographical variation represents the most critical point for the evaluation of taxa limits, often leading to misinterpretation of data derived from non-selective comparative analysis. Likewise, we believe that such data are necessary prerequisites for a biogeographical and phylogenetic analysis, i.e., for the localization of zoogeographical centres and the establishment of the sequence of speciation processes within a defined group.

In the case of *Haplophaedia*, morphological and morphometric patterns suggest that northern representatives (*H. aureliae* complex) possess relatively plesiomorphic characters compared with the southern members of the genus (*H. lugens*, *H. assimilis*). In addition, geographical variation is relatively high in the northern but low in the southern part of the range, especially in Peru and Bolivia, where only two taxa (*H. a. assimilis*, *H. a. affinis*) occur along the eastern Andean slope. This pattern contradicts assumptions made for the majority of the high montane tropical avifauna of the cordilleras (VUILLEUMIER 1986), as well as for other widely distributed Andean trochilid genera such as *Chalcostigma* (SCHUCHMANN & HEINDL 1997) and *Metallura* (Heindl & Schuchmann 1998). For the latter taxa the authors suggested that precursors evolved in the Andes south of the equator, either originating in the Amazonian lowlands or lower montane regions (cf. HAFFER 1970), and subsequently invaded the northern parts of the Andes. Regarding the

biogeography of *Haplophaedia*, we conclude that the genus evolved in the northern rather than in the central Andes.

The most characteristic plumage features of *Haplophaedia* are the greenish plumage combined with a contrasting, slightly forked tail, and the enlarged puffs. If we postulate a north Andean centre of evolution (cf. Fig. 4: 1) the question arises if any conclusions on relationships to other trochiline groups can be drawn from morphological aspects. Interestingly, the premontane zone northwest of the present Andes in Colombia has been shown to be one likely major distributional centre of the phenotypically similar taxon *Saucerottia* (WELLER 1998, WELLER in press). This genus, particularly the type species *Saucerottia saucerrottei*, is marked by a more glittering golden green plumage, a slightly forked, bluish to purplish tail, and white tibial tufts (also found in other trochiline species groups) combined with a sexual dimorphism (throat more whitish in females) similar to that in *Haplophaedia*. With regard to habitat choice, *Saucerottia* species are characteristic forest-edge residents, chiefly occurring between 500 m and 2000 m. Due to the slightly different vertical and ecological niches inhabited by *Saucerottia* and *Haplophaedia*, we presume that the latter evolved from descendants of the former by altitudinal and habitat segregation, probably in the humid forests of the upper submontane to lower montane zone. The initial separation of a proto-*Haplophaedia* population was probably complete before the Pleistocene but after the final rise of the high Andean crests, which seems to follow from the present distributional patterns (possible barrier effect of high mountain ridges).

The following hypothetical radiation and speciation processes (Fig. 4) may be initiated by glacial events (changes in humid or arid climatic conditions). First, the ances-

tor population of *H. aureliae* expanded its range across several parts of the northern Andes (Fig. 4: 2a-b). The *caucensis* precursor possibly evolved in the western cordillera, whereas that of the nominate form was isolated in humid forest refuges of the central and/or eastern cordilleras. Colour transition in the ventral plumage may indicate that more recently both taxa have come into secondary contact in the central cordillera east of the Cauca valley (Risaralda).

The strong morphological affinities of the Panamanian representatives *H. a. floccus* and *H. a. galindoi* to the Andean subpopulation of *caucensis* suggest a rather recent invasion from the western cordilleras (Fig. 4: 2c), with the Cuchillo mountains (NW Colombia) possibly serving as "stepping-stones" across the Atrato valley. We assume that both evolved independently of each other in very local refuges. Regarding *floccus*, the avifaunistic diversity of Cerro Pirre (ROBBINS et al. 1985) indi-

cates that this mountain range represents an important centre of endemism, with even one hummingbird genus (*Goethalsia*) exclusively restricted to that mountain range.

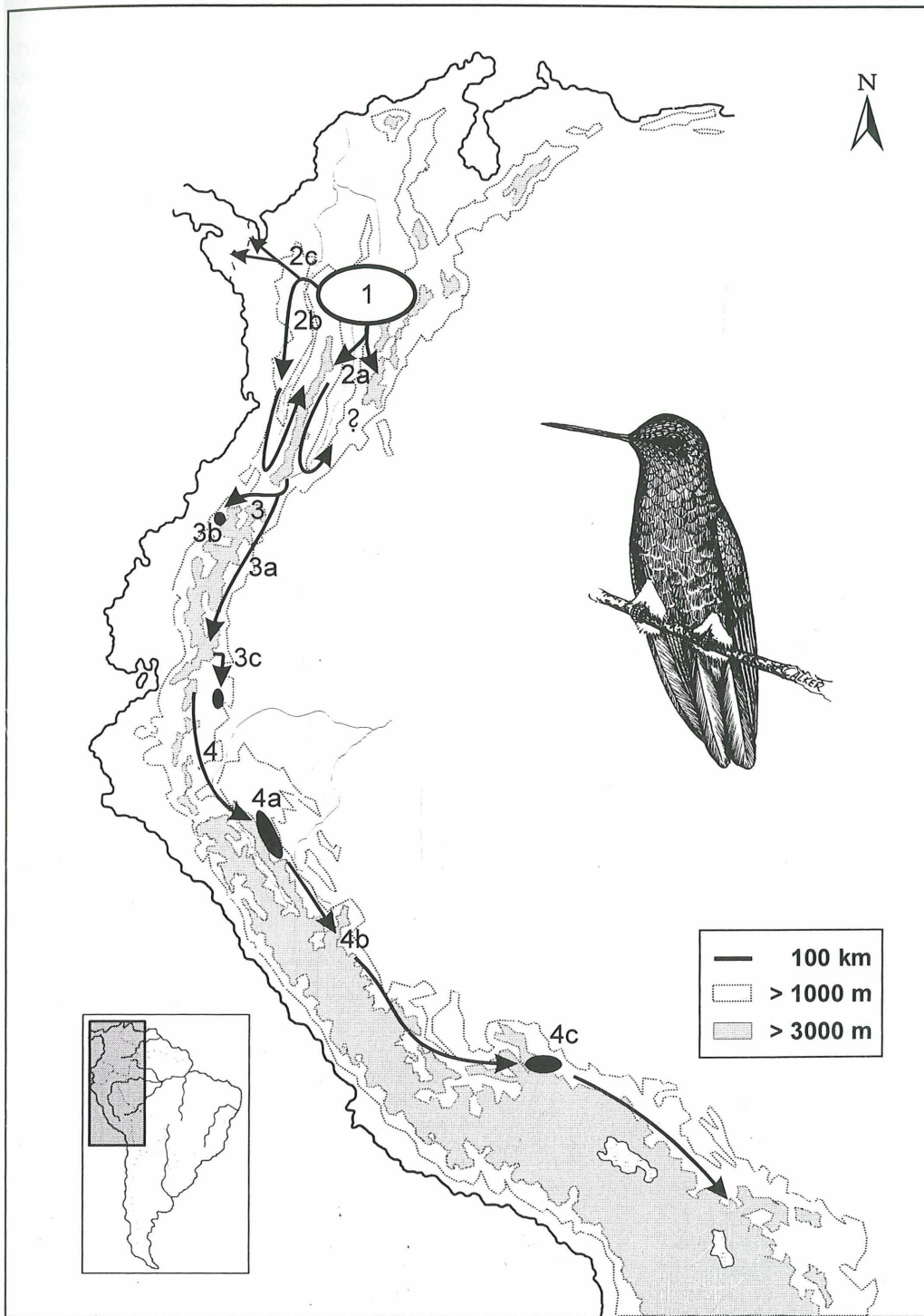
Based on similar morphological patterns, *H. lugens* most likely derived from a common ancestor with *H. a. russata* (Fig. 4: 3). Final isolation from the east Andean lineage could have taken place in a montane refuge either located in Nariño (cf. WELLER & SCHUCHMANN 1999) or northern Ecuador (Fig. 4: 3a). Currently, the range overlap of *H. lugens* with *H. aureliae* (ssp. *russata*) in northeastern Ecuador highlights the specific distinctness of both taxa. To our knowledge, hybrids between both forms are unknown.

Southern expansion of *russata* descendants led to the invasion of Cordillera del Condor and Cordillera de Cutucú, where *H. a. cutucuensis* could evolve under conditions of isolation (Fig. 4: 3c). Both mountain ranges are more or less semi-isolated

Fig. 4: Speciation model of *Haplophaedia*. Numbers refer to proposed speciation events (as listed in the following), arrows indicate directions of radiations: 1 – evolution of proto-*Haplophaedia* in cloud forest zone of northern Andes (prior to Pleistocene); 2 – radiation: along Cordillera Central and Cordillera Oriental of northern Andes (*H. a. aureliae*, 2a); around Cauca valley (*H. a. caucensis*, 2b); northwestward to Serrania del Darién, Cerro Pirre (*H. a. galindoi*, *H. a. floccus*, 2c); 3 – separation of precursors of *H. lugens* and *H. a. russata/cutucuensis*: isolation of *H. lugens* on western Andean slope (3a, Nariño refuge?); evolution of *H. a. russata* on eastern slope (3b) and of *H. a. cutucuensis* in present southern Ecuador (3c, Cordillera de Cutucú?); 4 – invasion of Central Andes after crossing the North Peruvian Low: isolation of *H. assimilis* precursor (*affinis*) east of Marañón valley due to increasing aridity (4a, late Pleistocene?); radiation along eastern slope, separation of *H. a. assimilis* in Andes of present southeastern Peru.

Abb. 4: Speziationsmodell von *Haplophaedia*. Zahlen bezeichnen hypothetische Speziationsereignisse (s. folgende Auflistung), Pfeile geben Radiationsrichtungen an:

1 – Entstehung eines proto-*Haplophaedia* in der Nebelwaldzone der Nordanden (präpleistozän); 2 – Ausbreitung: entlang der Zentral- und Ostkordillere der Nordanden (*H. a. aureliae*, 2a); entlang des Caucales (*H. a. caucensis*, 2b); nordwestwärts bis Serrania del Darién, Cerro Pirre (*H. a. galindoi*, *H. a. floccus*, 2c); 3 – Trennung der Vorläufer von *H. lugens* und *H. a. russata/cutucuensis*: Isolation von *H. lugens* an der Westandenseite (3a, Nariño-Refugium?); Entstehung von *H. a. russata* an der Ostandenseite (3b) und von *H. a. cutucuensis* in Südecuador (3c, Cordillera de Cutucú?); 4 – Besiedlung der Zentralanden nach Überschreitung der Nordperuanischen Senke: Isolation der *H. assimilis*-Vorläuferpopulation (*affinis*) östlich des Marañontales aufgrund zunehmender Aridität (4a, spätes Pleistozän?); Ausbreitung entlang der Ostandenseite, Abspaltung von *H. a. assimilis* in den südostperuanischen Anden.



from the main chain of the Andes (Chinguela Mts.) by altitudinal, edaphic, and vegetational factors (ROBBINS et al. 1987). Actually, they share a similar submontane avifauna, indicating a common evolutionary centre and similar invading pathways of the associated bird taxa. Concerning the distribution of *H. aureliae*, the southern distributional limits of *russata*, as well as the current southwestward range extension of *cutucuensis*, remain unclear. ROBBINS et al. (1987) failed to record the species in Cordillera del Condor, perhaps due to a lack of wet floral elements (FITZPATRICK et al. 1977), as well as in Chinguela. However, recent studies by KRABBE et al. (1998), based on habitat availability, and single specimen records (two individuals from Chinapanza, Condor; ZMK # 160990, 220990) supply evidence for a wider distribution than previously assumed, pointing out the need for reliable specimen data

from the regions involved.

Diversification in the central Andes started after the invasion of that area across the North Peruvian Low by a proto-*assimilis* (Fig. 4: 4). Presumably, race *affinis* first evolved east of the Río Marañon (Fig. 4: 4a), because of increasing aridity and hence the barrier effect of the Marañon valley during a late glacial phase (PARKER et al. 1985). With regard to the phenotypic differentiation of *H. assimilis* from *H. aureliae* and *H. lugens*, we postulate the influence of strong selection factors along the eastern slope of the central Andes from Peru to Bolivia (Fig. 4: 4b-c). In general, the (north)-eastern Peruvian Andes are presumed to comprise several important evolutionary centres for many high-Andean genera including trochilids (e.g., *Metallura*, HEINDL & SCHUCHMANN 1998; *Coeligena*, SCHUCHMANN & ZÜCHNER 1998).

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Summary

This study analyses the biogeography and taxonomy of the hummingbird taxon *Haplophaedia*, based on the examination of biometric and plumage characters, and summarizes various life history traits. Currently, the genus *Haplophaedia* comprises two species, *H. aureliae* (ssp. *aureliae*, *caucensis*, *floccus*, *galindoi*, *russata*, *assimilis*, *affinis*) and *H. lugens*. Based on biogeographical and morphological aspects, we suggest that *H. assimilis* (ssp. *assimilis*, *affinis*) is

distinct at species level. Due to significant geographical variation within the range of *H. aureliae*, we give subspecific recognition to the southernmost, allopatric subpopulation in Ecuador, named as *H. aureliae cutucuensis* subsp. nov. It is postulated that *Haplophaedia* evolved prior to the Pleistocene in the “cloud forests” of the northern Andes, subsequently invading similar habitats in the western and central Andes during glacial phases.

Resumen

El presente estudio analiza la biogeografía y taxonomía del género *Haplophaedia* (Trochilidae), basándose en la examinación de caracteres biométricos y de plumaje, y resume a la par varias características ecológicas de los mencionados colibríes. El género *Haplophaedia* comprende actualmente dos especies, *H. aureliae* (ssp. *aureliae*, *caucensis*, *floccus*, *galindoi*, *russata*, *assimilis*, y *affinis*), y *H. lugens*. Basándonos en aspectos biogeográficos y morfológicos, sugerimos la recategorización de *H. assimilis* (ssp. *assimilis*, *affinis*), al nivel específico. Debido a la

variación geográfica significativa a lo largo del rango de distribución de *H. aureliae*, le damos reconocimiento subespecífico en el extremo sur de dicho rango a la subpoblación alopatrica en Ecuador, denominándola *H. aureliae cutucuensis* subsp. nov. Se postula además que la aparición de *Haplophaedia* (es anterior al Pleistoceno) en los “bosques nublados” de los Andes del norte*, invadiendo luego hábitats similares en los Andes centrales y occidentales durante las diferentes épocas de glaciación.

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Appendix

Localities of study specimens and additional records from literature, listed from N to S (compare Fig. 3):

H. aureliae (including data from MEYER DE SCHAUENSEE 1949, ROMERO-ZAMBRANO & HERNÁNDEZ-CAMACHO 1979; coordinates after PAYNTER 1993, 1997):

H. a. galindoi:

Panama: Cerro Tacarcuna, eastern slope, Darién, 1340-1590 m, 08°05'N/77°17'W; Cerro Malí, Darién, 1280-1435 m, 08°00'N/77°32'W.

H. a. floccus:

Panama: Cerro Pirre, near head/mouth of Río Limon, Darién, 1525-1590 m, ca. 07°57'N/77°52'W.

H. a. caucensis:

Colombia: Hacienda Potreros, Antioquia, 1980 m, 06°39'N/76°09'W; Urrao, Antioquia, 1880 m, 06°20'N/76°11'W; Pueblorrico, Risaralda, 1560 m, 05°12'N/76°08'W; Miraflores, Valle del Cauca, 1432 m, 05°12'N/76°12'W; Salento, Quindío, 1895 m, 04°38'N/75°34'W; Dagua, Valle del Cauca, ca. 03°40'N/76°33'W; La Cumbre, Valle del Cauca, 1580 m, 03°39'N/76°33'W; Bitaco, Valle del Cauca, 1350 m, 03°36'N/76°36'W; San Antonio, Valle del Cauca, 1860-2135 m, 03°30'N/76°38'W; Alto de las Cruces, Valle del Cauca, 2200 m, ca. 03°30'N/76°38'W; Río Munchique, Cauca, 900 m, 02°35'N/77°15'W; Gallera, Cauca, 1740 m, 02°35'N/76°55'W; Cerro Munchique, W of Popayan, Cauca, 02°32'N/76°57'W.

H. a. aureliae:

Colombia: Valdivia, Antioquia, 2135-2260 m, 07°05'N/75°27'W; Ventanas, Antioquia, 2000 m, 07°05'N/75°27'W; Medellín, Antioquia, 1538 m, 06°15'N/75°35'W; Barro Blanco, Antioquia, 2200 m, 06°15'N/75°30'W; Santa Elena, Antioquia, 2750 m, 06°13'N/75°30'W; Caldas, Antioquia, not located; Virolín, Santander, 1680-1830 m, 06°05'N/73°12'W; Salamina, Caldas, 1820 m, 05°25'N/75°29'W; Santa Rosa de Cabal, Risaralda, 1500 m, 04°52'N/75°38'W; Cañon del Mt. Tolima, Tolima, 1700 m, 04°40'N/75°19'W; Páramos de Bogotá, Cundinamarca, ca. 04°36'N/74°05'W; "Llanos of Río Meta" (= Llanos de San Martín), not located; Ibagué, Tolima, 1260 m, 04°27'N/75°14'W; El Peñón, Cundinamarca, 3000 m, 04°26'N/74°18'W; La Aguadita, Cundinamarca, 2000 m, 04°25'N/74°20'W; El Roble, Cundinamarca, 2475 m, 04°23'N/74°19'W; Fusagasuga, Cundinamarca, 1830-2135 m, 04°21'N/74°22'W; Belén, Huila, 2135 m, 02°15'N/76°05'W; San Agustín, Huila, 1690 m, 01°53'N/76°16'W; La Candela, Huila, 1525-1675 m, 01°50'N/76°20'W; Buenavista, Huila, 2000 m, 01°50'N/75°57'W.

H. a. russata:

Ecuador: Guala, Pichincha, 1500 m, 00°07'N/78°50'W; Río Oyacachi, below El Chaco, Napo, 1615 m, ca. 00°23'S/77°49'W; Volcán Sumaco, Napo, 00°34'S/77°38'W; Cabaceras de Bobonaza, Pastaza, not located.

H. a. cutucuensis:

Ecuador: Cordillera de Cutucú Oriental, Morona-Santiago, 2000 m, 02°40'S/77°51'W; Cordillera de Cutucú Occidental, Morona-Santiago: at crest E of Logroño, 2100 m (ca. 02°37'S/78°12'W), and Yapitea (Camp 2), 1750 m, not located; Cordillera del Condor, near Chinapinza, Zamora-Chinchipec, 1700 m, ca. 04°00'S/78°27'W.

H. lugens (including data from COLLAR et al. 1992; coordinates after PAYNTER 1993, 1997):

Colombia: Ricaurte, Nariño, 1190 m, 01°13'N/77°59'W; La Planada (near Ricaurte), 1800 m, 01°13'N/77°59'W; Piguale, not located (near Ricaurte), Nariño; San Pablo, Nariño, 1400 m, 01°06'N/78°01'W; Ecuador: Intag, Imbabura, 1200 m, 00°24'N/78°36'W; Cerro Ingapi, Pacto, 1000-1200 m, 00°12'N/78°52'W; Nanegal, Pichincha, 1525 m, 00°07'N/78°46'W; Río Saloya, near Mindo, Pichincha, 00°01'N/78°57'W; Mindo, Pichincha, 1260-2125 m, 00°02'S/78°48'W; (vicinity of) Quito, Pichincha, ca. 2800 m, 00°13'S/78°30'W; Santo Domingo de los Colorados, Pichincha, 00°15'S/79°09'W; Papallacta, Napo, 3150 m, 00°22'S/78°08'W; Baeza, Napo, 1375-1900 m, 00°27'S/77°53'W.

H. assimilis (including data from ZIMMER 1951; coordinates after PAYNTER 1992, PAYNTER & TRAYLOR 1983):

H. a. affinis:

Peru: Ray Urmana, Amazonas, 2290 m, 06°28'S/77°21'W; Chirimoto, Amazonas, 2100 m, 06°31'S/77°24'W; Río Jelashe, San Martín, 1370-1525 m, 06°48'S/77°12'W; Utcubamba, La Libertad, ca. 2000 m, 08°13'S/77°08'W; Sira Pico, Huánuco, 1500-2220 m, 09°21'S/74°43'W.

H. a. assimilis:

Peru: Huaisampillo, Cuzco, 3050 m, 13°14'S/71°26'W; Santo Domingo (= Inca Mine), Puno, 1830 m, 13°51'S/69°41'W; Oconeque, Puno, 2135 m, 14°03'S/69°42'W; Limbani, Puno, 3350 m, 14°08'S/69°42'W; Bolivia: Sandillani, La Paz, 2500 m, 16°12'S/67°54'W; Tilotilo, near Sandillani, La Paz, not located; Cerro Sillutincara, La Paz, 3000 m, 16°17'S/67°54'W; Yungas, La Paz/Cochabamba, 1500 m, 16°20'S/66°45'W; Chaco, La Paz, 16°20'S/67°48'W; Chulumani, La Paz, 2000 m, 16°24'S/67°31'W.

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