SYSTEMATICS AND GEOGRAPHIC VARIATION IN LONG-TAILED HERMIT HUMMINGBIRDS, THE *PHAETHORNIS SUPERCILIOSUS-MALARIS-LONGIROSTRIS* SPECIES GROUP (TROCHILIDAE), WITH NOTES ON THEIR BIOGEOGRAPHY

Christoph Hinkelmann*

Alexander Koenig Zoological Research Institute and Zoological Museum, Ornithology,
Group: Biology and Phylogeny of Tropical Birds, Adenauerallee 160, D-53113 Bonn 1, Germany.

Resumen. El grupo de *Phaethornis superciliosus* y especies relacionadas se compone de tres especies de orígen probablemente monofilético: *P. superciliosus*, *P. malaris* y *P. longirostris*. *P. longirostris* está limitado a América Central y Sudamérica al oeste de los Andes. Existen 6 subespecies válidas; una de estas, *P. l. baroni*, posiblemente ya ha alcanzado aislamiento reproductivo. Las poblaciones distribuidas entre Guatemala y Costa Rica representan una zona extensa de introgresión de caracteres morfológicos entre dos subespecies, *P. l. cephalus* y *P. l. longirostris*. En Sudamérica al este de los Andes, similitudes y introgresión de caracteres morfológicos indican que 6 subespecies válidas pueden ser asignados a *P. malaris* mientras que *P. superciliosus* incluye dos subespecies válidas en los dos margenes del Río Amazonas en su curso inferior. En el Perú, caracteres de coloración de *P. malaris moorei* y *P. m. bolivianus* se mezclan en una zona de introgresión aparentemente en correlación con la distribución altitudinal. Sin embargo, no se puede definir con certeza la posición taxonómica de *P. malaris ochraceiventris*; posiblemente, este taxon ya ha alcanzado el estado de especies. Mientras *P. longirostris* está completamente aislado geograficámente de *P. malaris* y *P. superciliosus*, las subespecies de estas dos actuan como paraespecies o alloespecies en varias partes de sus áreas de distribución. Solamente *P. m. malaris* occurre en simpatría con un otro taxon de este grupo de especies relacionadas, con *P. s. superciliosus*, en la entera área de distribución de *P. m. malaris*. Las dos especies habitan el mismo espacio vital. Probablemente, evitan competencia directa utilizando diferentes recursos de alimentación cual es indicado por diferencias en sus masas corporales y longitudes del pico. La validez de ambas especies está corroborada por el descubrimiento de sólo un especimen híbrido. Areas de distribución de estas tres especies de colibríes ermitaños indican que los procesos de especiación probablemente fueron facilitados por eventos paleoclimáticos y vegetacionales como postulados del modelo biológico de diversificación (teoría de refugios).

Abstract. Long-tailed Hermit hummingbirds can be assigned to three closely related, probably monophyletic species: *Phaethornis superciliosus*, *P. malaris*, and *P. longirostris*. *P. longirostris* is limited to Central America and W Andean South America. There are 6 valid subspecies; one of these, *P. l. baroni*, may already have achieved reproductive isolation. Populations occurring between Guatemala and Costa Rica represent an extensive zone of character introgression between two subspecies, *P. l. longirostris* and *P. l. cephalus*. In E Andean South America, morphological similarity and character introgression indicate that 6 valid subspecies can be assigned to *P. malaris*, whereas *P. superciliosus* is composed of 2 valid subspecies, one on each side of the lower Amazon river. In Peru, coloration characters of *P. malaris moorei* and *P. m. bolivianus* intergrade along an apparently altitude-based introgression zone. However, the taxonomic position of *P. malaris ochraceiventris* cannot be defined with certainty yet; this taxon may have achieved species status. Whereas *P. longirostris* is completely isolated from *P. malaris* and *P. superciliosus*, subspecies of both cis-Andean species behave like para- or allospecies in several parts of their distribution ranges. Only *P. m. malaris* occurs sympatrically with another taxon of this species group, *P. s. superciliosus*, over its whole distribution range. Both species inhabit the same habitat, and probably avoid direct competition by depending on different food niches as indicated by differences in their body masses and bill lengths. The validity of both species is corroborated by the discovery of only one hybrid specimen. Recent distribution patterns within Long-tailed Hermit hummingbirds indicate that speciation processes may have been facilitated by paleoclimatic-vegetational events that are postulated by the biological model of diversification (refuge theory). *Accepted 17 July 1996.*

Key words: Systematics, geographic variation, Phaethornis, hermit hummingbirds, biogeography.

Present address: Timelostr. 38, D-21407 Deutsch Evern, Germany.

INTRODUCTION

Long-tailed Hermit hummingbirds (*Phaethornis superciliosus-malaris-longirostris* species group) inhabit lowland rain forest of the terra firme, humid secondary growth, lower montane forests, and may be found even in gallery forests, plantations, wooded pastures, and mangroves, from S Mexico to N Argentina. They are non-territorial trap-liners, the males gather at leks during certain periods of the year where they utter a simple song to attract females. Nesting, display, and general behavior do not differ significantly from other members of the Phaethornithinae or hermit subfamily (Nicholson 1931, Davis 1958, Snow 1973, Stiles & Wolf 1979). Long-tailed Hermit hummingbirds belong to one of the largest hummingbird genera, *Phaethornis*. Species of this genus may be distiguished by their body masses, and can thus be united in two body mass categories: 2—4 and 4—8 g. Of all *Phaethornis*, only two members of the *superciliosus-malaris-longirostris* species group regularly exceed 8 g. These are birds occurring in SW Mexico (states of Michoacán, Guerrero, Oaxaca) and Surinam, French Guiana as well as in the Brazilian state of Amapá, respectively. In general, Long-tailed Hermit hummingbirds can be assigned to the body mass category of 4—8 g (Hinkelmann 1988a).

For many decades, the taxonomic treatment of the *Phaethornis superciliosus-malaris-longirostris* species group was a topic of intensive discussion. Taxa were assigned to two species by Salvin & Elliot (1873) and Simon (1897), whereas later the same author (Simon 1921), as well as Boucard (1895) and Hartert (1900) considered them to belong to 6 species; others accepted 3 (e.g., Cory 1918) and 5 species (e.g., Gould 1861), respectively. The discussion was almost finished by Peters (1945) who grouped the taxa into 2 species, *P. malaris* and *P. superciliosus*. Zimmer (1950) prepared the most recent taxonomic analysis and accomplished a general shift of subspecies from *P. superciliosus* to *P. malaris* but continued to recognize only 2 species. Peters' (1945) treatment was generally followed in subsequent studies on the behavior (e.g., Davis 1958, Skutch 1964, Snow 1973, Stiles & Wolf 1979), general biology (e.g., Skutch 1964, Young 1971), or ecology (e.g., Stiles 1975, 1980, Stiles & Wolf

1979, Snow 1981) of Long-tailed Hermit hummingbirds, and also in regional lists. Within the genus *Phaethornis*, Long-tailed Hermit hummingbirds form a monophyletic unit. They are most closely related to *Phaethornis syrmatophorus*, *P. koepckeae*, *P. philippii*, and *P. bourcieri*.

Recent taxonomic studies in the *P. superciliosus-malaris-longirostris* species group in Amazonian Peru (Capparella 1987), Brazil (Grantsau 1988) and Central America (Banks, unpubl. ms.) have cast doubt on the validity of Peters' (1945) classification. Therefore, the objective of this paper is to clarify the relationships between the taxa within the *Phaethornis superciliosus-malaris-longirostris* species group which I arrange in three species.

MATERIALS AND METHODS

This study is based on the examination of 1.065 museum skins representing all taxa of Long-tailed Hermit hummingbirds, and probably including the majority of study skins of this group preserved in scientific collections. A list of the institutions providing specimens is given in Appendix I. I examined 13 type specimens of 19 preserved.

For almost all specimens I measured 3 linear characters to the nearest 0.5 mm with a conventional scale (Fig. 1): bill length including the operculum (BL), chord length of the unflattened wing (wing length, WL), and the shortest distance between tips of the outermost (V) and central (I), i.e., longest feathers of the rectrices ("tail length" as used in this study, TL; in case of differences between left and right half, the left side [dorsal] was taken for calculations). I did not measure immature birds (indicated by light feather margins on hind-crown, nape, and back) as well as those with obviously molting rectrices. Differences in linear measurements between respective groups (sexes, taxa, geographical units) were examined by t-test and Mann-Whitney-U test. Significance levels were fixed at $P < 0.05$ and $P < 0.01$, respectively.

Though ♂ and ♀ are alike in coloration, sexing specimens proved only a minor problem. Recently collected skins from several institutions include gonad data on their labels. Besides, ♂ differ from ♀ by significantly longer wings and usually less curved bills (Table 1). Only a very

limited number of specimens (n = 11) could not be sexed with certainty and was thus excluded from calculations.

At the Zoological Research Institute and Zoological Museum Alexander Koenig (ZFMK), Bonn, I united 302 study skins belonging to the scientific collection of the ZFMK and to several of the museums listed in Appendix I, sent on loan to Bonn. These birds originated from almost all regions in which Long-tailed Hermit hummingbirds are distributed. This total of 302 members of the *Phaethornis superciliosus-malaris-longirostris* species group enabled a careful examination of character variation depending on age, sex, and geographical distribution by direct comparisons of all specimens, providing a general survey of variability. With this experience, and many color slides portraying series of birds from the same locality (or limited area), I examined the collections of almost all institutions listed in Appendix I. There I investigated all specimens of the species group, took measurements and noticed plumage variation, and could extend the data basis to 1.065 specimens from which the analysis of character variation was drawn.

For the determination of distribution ranges, locality data from the specimens' labels were plotted with the aid of ornithological gazetteers (Paynter 1982, Paynter & Traylor 1977, 1981, Paynter *et al.* 1975, Stephens & Traylor 1983, 1985), regional ornithological monographs including gazetteers (e.g., Griscom 1932b, Slud 1964, Monroe 1968, Haffer 1974, Novaes 1974, Binford 1989) and atlases (e.g., Scobel 1912, Bartholomew *et al.* 1985). I follow Haffer (1974) in the use of terms "cis-Andean" (= South American E of the Andes) and "trans-Andean" (= Central American and South American W of the Andes).

Pooling of geographical units (population groups, PG) for the analysis of geographic variation was facilitated by physical borders and concentrations of collecting localities within certain areas. Before assigning Peruvian specimens to 5 PG (Fig. 7) they were divided into 21 geographical units. However, this treatment revealed subtle differences in measurements merely between distant populations and thus was used only to trace color variation; I will describe this in more
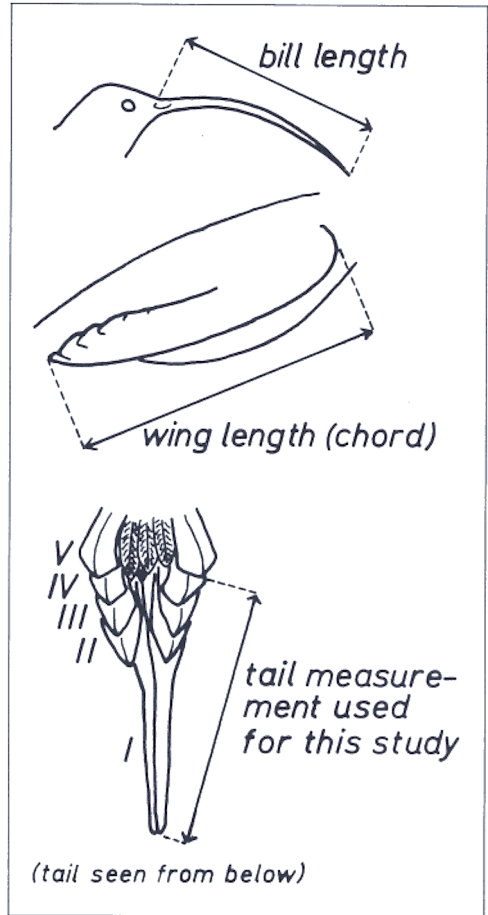

FIG. 1. Linear character measurements taken for this study.

detail while presenting geographical variation and zones of character introgression. In case of small numbers of measurements within a certain sample (n<4), neighbouring PG were united to permit statistical comparisons. In the presentation of results, this treatment is indicated by a "+", e.g.: 4+5>6, $P<0.05$. A comma, ",", means that the calculated significance is of equal value for more than one PG, e.g.: 3, 4, 5>2, $P<0.01$ equals 3>2, $P<0.01$, and 4>2, $P<0.01$, and 5>2, $P<0.01$.

Differences in measurements did not necessarily coincide with color variation. Taxonomically significant variation in plumage coloration

TABLE 1. Linear character measurements of *Phaethornis longirostris*, *P. malaris*, and *P. superciliosus*. For details of measuring see Fig. 1 and text. Specimens with obvious immature plumage or uncertain sex are excluded. Statistical tests ♂ — ♀: Mann-Whitney-U test (above), t test (below).
(n=number value; *P* = probability; Si.= significance: ++ = *P* < 0.01, + = *P* < 0.05, —— = not significant).

Subspecies	Sex	n	mean	s. d.	Min	Max	P	Si.
Bill Length (BL) [mm]								
griseoventer	♂	15	44.20	1.33	42	48	0.092	——
	♀	4	42.00	2.16	40	45	0.131	——
mexicanus	♂	13	46.62	1.21	44	48.5	<0.01	++
	♀	17	42.65	1.47	39	45	0	++
longirostris	♂	82	40.87	1.53	38	46	<0.01	++
	♀	46	38.76	1.21	36	42	0	++
cephalus	♂	74	39.28	1.45	37	43	<0.01	++
	♀	70	37.20	1.21	35	40	0	++
susurrus	♂	44	42.24	0.93	40	44	<0.01	++
	♀	6	40.08	0.97	39	43.5	<0.01	++
baroni	♂	23	41.46	1.39	39	43.5	<0.01	++
	♀	8	39.06	1.50	37	41.5	0	++
	♂	29	47.21	1.01	44	49	<0.01	++
	♀	17	44.08	1.15	42	46	0	++
insolitus	♂	13	41.88	2.25	38	45.5	<0.01	++
	♀	5	38.10	1.14	37	39.5	0	++
	♂	80	41.78	1.94	37	46	<0.01	++
	♀	53	38.44	1.52	35	41	0	++
Peruvian zone of character introgression	♂	48	41.26	1.45	38	44		
	♀	44	38.69	1.59	35	42	0	
bolivianus	♂	62	37.98	1.36	35.5	41	<0.01	
	♀	60	35.88	0.98	34	38	0	
margarettae	♂		(37)		—	—	—	
	♀		(35.5)		—	—	—	—
ochraceiventris	♂	16	43.97	1.47	41.5	46	<0.01	++
	♀	9	41.39	0.65	40.5	42.5	0	++
muelleri	♂	25	37.64	0.84	36	39	<0.01	++
	♀	29	35.97	1.11	34.5	38	0	++
superciliosus	♂	60	38.50	1.43	35	42	<0.01	++
	♀	38	36.03	1.40	33	39	0	++
Wing length (WL) [mm]								
griseoventer	♂	15	66.87	0.67	66	68	<0.01	++
	♀	4	63.50	0.58	63	64	0	++
mexicanus	♂	14	68.64	1.08	67	70	<0.01	++
	♀	19	66.11	1.24	64	68	0	++
longirostris	♂	86	63.98	1.05	61.5	66	0	++
	♀	48	60.94	1.28	59	64	0	++
cephalus	♂	79	62.24	1.55	59	68	0	++
	♀	74	59.26	1.54	55	63	0	++
susurrus	♂	48	65.73	1.25	64	69	<0.01	++
	♀	7	61.71	1.60	59	64	0	++
baroni	♂	24	61.67	1.63	59	65	<0.01	++
	♀	10	58.50	1.65	56	61	0	++
malaris	♂	32	67.61	1.42	64	70	<0.01	++
	♀	16	64.53	1.39	62	66.5	0	++
insolitus	♂	14	63.96	1.08	62.5	66	<0.01	++
	♀	5	60.40	1.14	59	62	0	++
moorei	♂	83	62.57	1.42	59	66	0	++
	♀	54	58.97	1.48	56	63	^	
Peruvian zone of character introgression	♂	49	62.07	1.62	58	65		
	♀	45	58.58	1.56	56	62	0	
bolivianus	♂	65	60.06	1.08	58	63	0	
	♀	69	56.77	1.13	54	59	0	

TABLE 1. (continued)

Subspecies	Sex		mean	s. d.	Min	Max	P	Si.
Wing length (WL) [mm]								
margarettae	♂	1	(60)	—	—	—	—	—
	♀	1	(58)	—	—	—	—	—
ochraceiventris	♂	15	64.50	1.24	62.5	67	<0.01	+ +
	♀	10	61.05	1.38	59	63	0	+ +
muelleri	♂	25	60.52	0.95	59	62	<0.01	+ +
	♀	30	57.90	0.96	56	60	0	+ +
superciliosus	♂	64	59.48	1.09	57	62	<0.01	+ +
	♀	42	56.79	1.01	55	58	0	+ +
Tail measurement used in this study (TL) [mm]								
griseoventer	♂	13	56.08	1.66	54	59	0.772	— —
	♀	4	56.25	2.06	54	58	0.885	— —
mexicanus	♂	14	57.93	2.37	56	61	0.956	— —
	♀	19	57.08	4.45	47	62	0.485	— —
longirostris	♂	81	44.78	2.42	40	57	0.189	— —
	♀	45	45.36	2.81	38	52	0.255	— —
cephalus	♂	68	42.16	2.66	38	49	0.101	— —
	♀	59	42.86	2.73	37	49	0.150	— —
susurrus	♂	45	47.84	2.15	44	53	0.425	— —
	♀	7	46.57	3.36	41	50	0.364	— —
baroni	♂	20	44.23	2.53	41	49	0.298	— —
	♀	10	45.10	2.08	41	48	0.324	— —
malaris	♂	32	48.23	2.66	42	52	0.010	+
	♀	16	51.13	3.16	45	56	0.004	+ +
insolitus	♂	10	43.10	1.79	40	46	1.000	— —
	♀	4	43.00	2.94	41	46	0.953	— —
moorei	♂	72	40.28	2.33	34	46	0.663	— —
	♀	42	40.52	2.68	35	47	0.621	— —
Peruvian zone of	♂	41	41.50	2.07	38	46		
character introgression	♀	36	42.03	2.75	32	47	0.341	— —
bolivianus	♂	37	40.14	2.56	36	46	<0.01	+ +
	♀	28	42.25	2.65	36	48	0.002	+ +
margarettae	♂	1	(42)	—	—	—	—	—
	♀	1	(46)	—	—	—	—	—
ochraceiventris	♂	16	42.25	2.11	39	47	0.122	— —
	♀	9	43.50	1.62	41	46.5	0.113	— —
muelleri	♂	24	41.58	3.35	34	48	0.030	+
	♀	24	44.63	3.19	37	51	0.002	+ +
superciliosus	♂	60	42.68	2.21	37.5	47	<0.01	+ +
	♀	40	44.20	2.14	39	48	0.001	+ +

occur on throat, breast, belly, under tail-coverts, and rectrical margins; coloration of crown, nape, upperparts, wings, and primary coloration of the rectrices varied individually, if at all. Geographical variation in plumage coloration, however, proved to be limited to clearly definable geographical areas in most cases; exceptions are discussed in detail in the text. Thus, I took these PG of distinctly reduced color variation as the basic taxonomic entities that were later united to subspecies and species. Detailed descriptions of the subspecies' morphological characters and differential diagnostic aids to distinguish them from another are given in Appendix II.

After having grouped specimens of all populations, the linear measurements BL, WL, and TL were tested in the resulting subspecies and the populations of the Peruvian zone of character introgression by a one-way analysis of variance, ANOVA. Significances found by ANOVA were confirmed by the Scheffe test with significance level fixed at $P<0.05$. A subsequent discriminant

123

analysis was performed on the species level using the three variables BL, WL, and TL in common.

Species as applied in this study are considered as biological species (*sensu* Mayr 1963, 1969, 1982). Geographically representative taxa whose close relationship is indicated by either zones of character introgression or limited, though obligate morphological distinctness are considered as subspecies of a biological species. The latter are ·separated by at least one apomorphy from other such units (i.e., other biological species). Intraspecific entities regarded as valid taxa in this study represent morphologically well-characterized subspecies that could be considered full species under a phylogenetical species concept (sensu Cracraft 1983, McKitrick & Zink 1988). Several levels of differentiation, obviously representing different periods in the evolutionary history of the Long-tailed Hermit hummingbirds, are easier to portray applying the hierarchy of species and subspecies provided by the biological species concept than by the phylogenetic species concept because the latter decreases the information value by "lumping of two categorial levels" (Fjeldså 1985).

RESULTS

Specimens pertaining to the *Phaethornis superciliosus-malaris-longirostris* species group can be assigned to 14 different taxonomic entities, or valid subspecies, based on morphological differences (for details of their plumage colorations, measurements and geographic distributions, see Appendix II and Table 1):

1. *griseoventer*
2. *mexicanus*
3. *longirostris* (incl. *veraecrucis*)
4. *cephalus* (incl. *cassinii*, *panamensis*)
5. *susurrus*
6. *baroni*
7. *malaris*
8. *insolitus*
9. *moorei* (incl. *consobrinus*, var. *nigella*, *ucayalii* in part)
10. *bolivianus* (incl. *insignis*, *ucayalii* in part)
11. *margarettae* (incl. *camargoi*)
12. *ochraceiventris*
13. *superciliosus* (incl. *fraterculus*, *guianensis*, *saturatior*)
14. *muelleri*

Linear measurements, BL, WL, and TL (as used in this study), of all subspecies are presented in Table 1. Comparisons between the sexes revealed that ♂ have longer bills and wings than ♀, confirmed by both statistical tests. To the contrary, the shortest distance between the tips of rectrices I and V (TL) do either not exhibit significal differences, or, in 4 taxa, these are larger in females. Fig. 2 demonstrates BL and WL measurements for both sexes.

Performance of ANOVA resulted in the indication of several significant differences in all 3 linear measurements between the taxa, and in both sexes. These were examined in detail by the Scheffe test, and are presented in Table 2.

Species limits within the Long-tailed Hermit hummingbird group. Distributed in Central America and South America W of the Andes (= trans-Andean) (Figs. 3, 4), *griseoventer, mexicanus, longirostris, cephalus, susurrus,* and *baroni* all agree in having three light ochraceous bands separated by two blackish bands on the outermost, longest feathers of the upper tail-coverts, different from that of their cis-Andean relatives, and I consider them to represent a distinct species, *P. longirostris.* All remaining taxa (Nos. 7—14 in the above list) have two light ochraceous and two blackish bands. Whereas the apomorphic band pattern confirms the monophyly of *P. longirostris,* only some of them, *griseoventer, mexicanus, baroni* and *longirostris* (with the exception of some ochraceous at the inner edges of rectrices IV and V), exhibit white rectrical margins; *susurrus* and *cephalus,* however, bear ochraceous margins (with the exception of whitish tips of rectrix II) similar to their cis-Andean relatives; the central pair is completely white-tipped in all Long-tailed Hermit hummingbirds.

Most cis-Andean members of the *P. superciliosus-malaris-longirostris* species group have relatively broad ochraceous rectrical margins of varying (color) tone. Only *superciliosus* and *muelleri* have narrow and pale ochraceous, rather light brownish rectrical margins. A synapomorphy of these taxa is provided by their whitish under tail-coverts with dark rachises. Both *superciliosus* and *muelleri* bear distinct midthroat streakings in both sexes similar to

those of the trans-Andean Long-tailed Hermit hummingbirds.

The remaining cis-Andean taxa, *malaris, insolitus, moorei, bolivianus,* and *ochraceiventris,* however, all agree in a sexual difference in the development of the midthroat streaking. Whereas females bear it as distinct as *muelleri, superciliosus* and the trans-Andean taxa, it is distinctly less pronounced or even lacking in males. (Due to a very limited number of specimens [n = 2], I cannot confirm this character for *margarettae*; color photographs of this taxon [Ruschi 1973, 1986] do not exclude the eventuality that ♂ bear midthroat streakings as clearly marked as ♀.)

Based on geographical grounds, the cis-Andean Long-tailed Hermit hummingbirds may almost be considered a single, polytypic species. Most of the morphologically well-characterized taxa occur in clearly definable distribution ranges that are separated from another by major rivers' courses but interbreed freely where there is no physical barrier. However, the sympatric occurrence of *malaris* and *superciliosus* in E Surinam, French Guiana, and adjacent N Brazil (Amapá) indicates that there are at least two biological species involved in this complex. Whereas all remaining cis-Andean taxa of the species group are of equal body mass (ranging from 4 to 8 g), *malaris* is larger in body mass (7.5—10 g) and size (see Table 1) as well. These differences probably provide somewhat differing food niches, enabling *malaris* and *superciliosus* to occur sympatrically. I will discuss this aspect later in more detail.

Synapomorphic characters as presented above link *superciliosus* and *muelleri* on the one hand, and *malaris, insolitus, moorei, bolivianus,* and *ochraceiventris* on the other hand, and I recommend the treatment as two species, *Phaethornis superciliosus* and *P. malaris.* In the following paragraphs, I will present details on the relationships between the taxa composed to both species, and besides explain why I consider the geographically isolated *margarettae* as a subspecies of *P. malaris.*

The variation of linear measurements of most of the taxa is similar, and there is broad overlap between those of several subspecies. However, a discriminant analysis between the three species, based merely on BL, WL, and TL, revealed that

TABLE 2. Results of a one-way ANOVA, Scheffe tests ($P<0.05$). a) Bill lengths (BL). b) Wing lengths (WL). c) Tail measurements used in this study (TL). + = significant, — = not significant. Peruvian means specimens from the zone of character introgression in Peru (Fig. 8).

a) Bill lengths (BL)

male \ female	griseoventer	mexicanus	longirostris	cephalus	susurrus	baroni	malaris	insolitus	moorei	PERUVIAN	bolivianus	ochraceiventris	muelleri	superciliosus
griseoventer		—	+	+	—	—	—	+	+	+	+	—	+	+
mexicanus	—		+	+	—	+	+	+	+	—	+	+	+	+
longirostris	+	+		+	—	—	+	—	—	—	+	+	+	+
cephalus	+	+	+		+	—	—	+	+	+	—	—	+	+
susurrus	—	+	+	+		—	—	+	—	—	—	+	+	+
baroni	+	+	—	+	—		+	—	—	—	+	+	+	+
malaris	+	—	+	+	+	+		+	+	+	+	+	+	+
insolitus	+	+	—	+	—	—			—	—	—	+	+	+
moorei	+	+	—	+	—	—		—		+	+	+	+
PERUVIAN	+	+	—	+	—	—		—	—		+	+	+	+
bolivianus	+	+	+	+	+	+	+	—	+			+	—	+	+
ochraceiventris	—	+	+	+	—	+	+	—	+	+			+	+
muelleri	+	+	+	+	+	+	+	+	+	—	+	—			+
superciliosus	+	+	+	—	+	+	+	+	+	—	—	+	—	

b) Wing lengths (WL)

male \ female	griseoventer	mexicanus	longirostris	cephalus	susurrus	baroni	malaris	insolitus	moorei	PERUVIAN	bolivianus	ochraceiventris	muelleri	superciliosus
griseoventer		—					+		—	+	+		—	+
mexicanus	—		+	+	+	—	+	—	+	+	+	—	+	+
longirostris	+	+		+	—	+	—	—	+	—	+	+
cephalus	+	+	+		—	—	—	—	+	—	—	+	+
susurrus	—	+	+	+		+	—	—	+	—	—	+	+
baroni	+	+	+	—	+		—	—	—	—	—	—	—
malaris	—	—	+	+	+	—		+	+	+	+	+	+
insolitus	+	+	—	—	—	+	+		—	+	—	—	+	+
moorei	+	+	—	—	+	—	+	—		—	+	—	+
PERUVIAN	+	+	+	—	—	—	+	+	—		+	+	+
bolivianus	+	+	+	+	—	—	+	—	+	+		+	—
ochraceiventris	+	+	—	+	—	+	+	—	—	+	+		+	+
muelleri	+	+	+	+	+	—	+	+	+	—	+	—		+
superciliosus	+	+	+	+	+	—	+	+	+	—	+	—

c) Tail measurements (TL)

male \ female	griseoventer	mexicanus	longirostris	cephalus	susurrus	baroni	malaris	insolitus	moorei	PERUVIAN	bolivianus	ochraceiventris	muelleri	superciliosus
griseoventer		—	+	+	+	+	+	—	+	+	+	+	+	+
mexicanus	—		+	+	+	+	+	+	+	+	+	+	—	+
longirostris	+	+		—	—	—	+	—	+	—	+	—	—	—
cephalus	+	+	—		—	—	+	—	—	—	—	—	—	—
susurrus	+	+	+	+		—	+	—	—	—	—	—	+	+
baroni	+	+	—	—	+		+	—	—	—	—	+	+	+
malaris	+	+	+	+	—	+		+	+	+	+	+	+	+
insolitus	+	+	—	—	—	+	+		—	—	—	—	+	+
moorei	+	+	—	—	+	+	+	—		—	—	—	+	+
PERUVIAN	+	+	—	+	—	—	+	—	—		+	+	—
bolivianus	+	+	—	+	+	+	+	—	—	—		+	+
ochraceiventris	+	+	—	+	—	+	+	—	—	+	+		+	+
muelleri	+	+	+	—	+	+	+	—	+	—	—	+	+		—
superciliosus	+	+	+	—	+	—	+	—	+	—	+	+	—

125

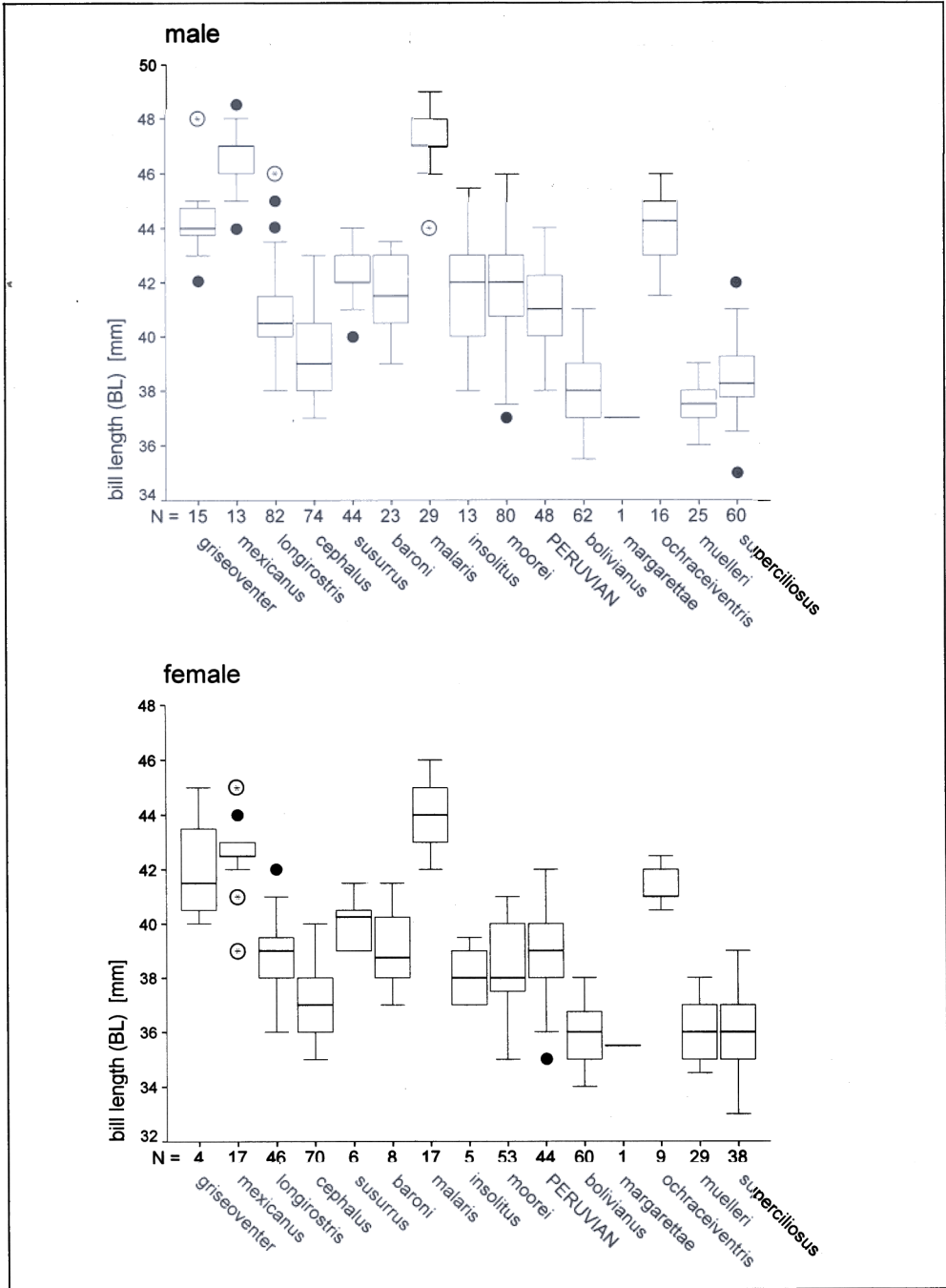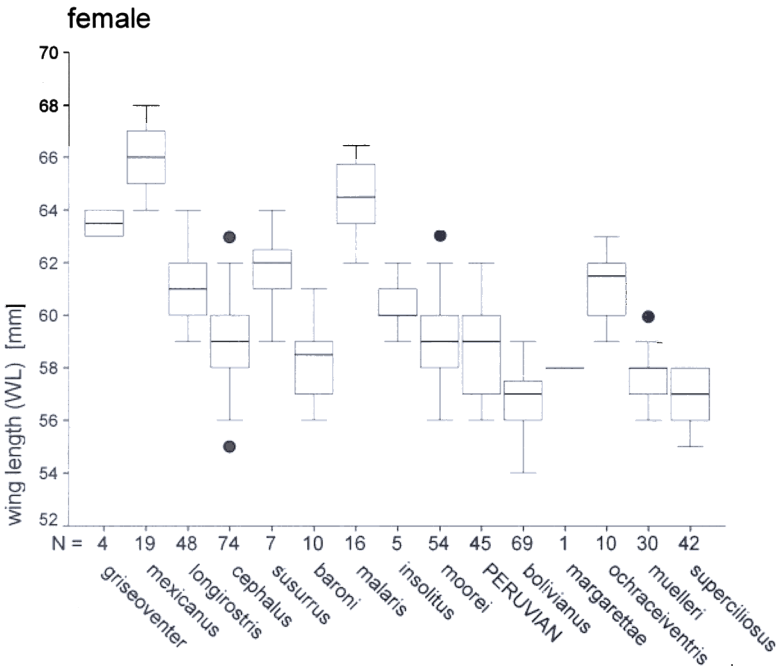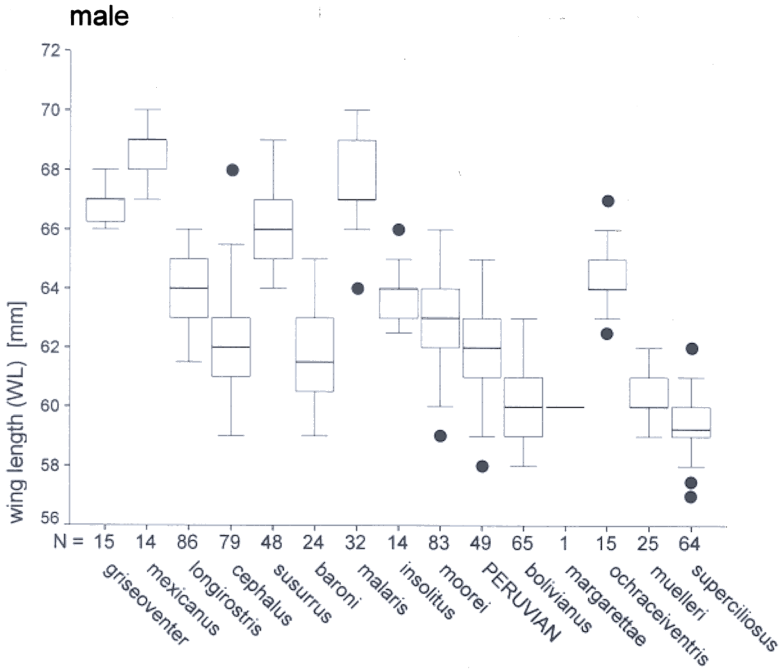FIG. 2. a) Bill lengths (BL) of ♂; b) Bill lengths (BL) of ♀; c) Wing lengths (WL) of ♂; d) Wing lengths (WL) of ♀. Dots and circles including asterisks indicate measurements outside the regular range. PERUVIAN means specimens from the zone of character introgression in Peru (c.f. Fig. 8).

the majority of specimens was grouped to the "correct" species: $\male$ = 69.5 %, $\female$ = 63.5 %. Details of the discriminant analysis' classification are presented in Table 3.

Geographic variation and zones of character introgression in Phaethornis longirostris. Four subspecies, *griseoventer, mexicanus, susurrus,* and *baroni* inhabit relatively small areas (Fig. 4). These populations appear to be quite uniform in both coloration and linear measurements. Exceptions are observable only in those areas where their respective ranges are close to each other or to those of the remaining subspecies, *longirostris* and *cephalus. P. l. griseoventer* and *P. l. mexicanus* approach each other in S Michoacán, Mexico, and apparently hybridize. A specimen from 22 km S Arteaga (DMNH 18892) exhibits intermediate coloration and size. *P. l. mexicanus* and *P. l. longirostris* meet each other in the state of Oaxaca, Mexico. There are only few specimens collected along the SE margins of the Sierra Madre mountains where the subspecies could get in contact with each other, and some of them (e.g., USNM 477532, DMNH 18657, AMNH 778267) link both taxa by intermediate coloration and linear measurements.

P. l. baroni represents a well-distinguished form isolated in the trans-Andean lowlands of Ecuador and NW Peru. There is only very limited, and no geographical, variation in coloration and linear measurements (Fig. 5).

The populations distributed between S Mexico and N Colombia, considered here as subspecies *longirostris* (NW) and *cephalus* (SE), exhibit an extensive zone of character introgression between Guatemala and Costa Rica. Several morphological characters exhibit gradual change, and differences in some cases can be separated clearly only if specimens from the northern- or southernmost distribution limits are compared. These characters are:

(1) barred throat markings: regularly developed in Colombia and Panama, less regularly in Costa Rica and Nicaragua, seldom in Honduras and Guatemala, and lacking in S Mexico.

(2) under tail-coverts: increasing intensity of ochraceous coloration from N to S; *cephalus* have these more ochraceous than *longirostris*.

(3) rectrical margins: increasing amounts of ochraceous coloration from N to S. In S Mexican populations almost completely white, only the outermost rectrices (IV and V) usually have some
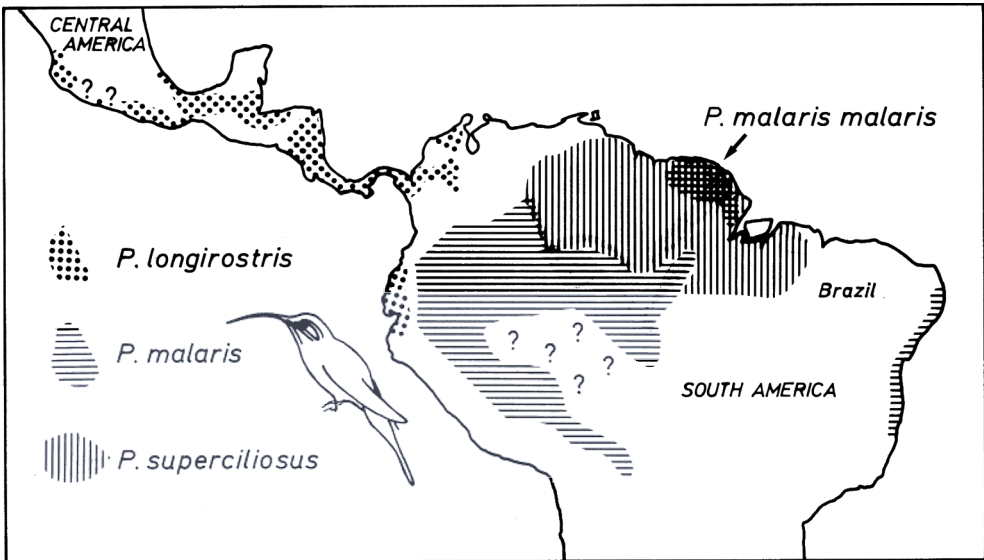

FIG. 3. Distribution and geographical replacement of the species of the *Phaethornis superciliosus-malaris-longirostris* species group.

TABLE 3. Classification results of a discriminant analysis. Only data from specimens with indications for all three linear measurements were processed.

| | | Grouping to | | |
		longirostris		superciliosus
Males				
P. longirostris	227	150 (66.1 %)	46 (20.3 %)	31 (13.7 %)
P. malaris	193	29 (15.0 %)	129 (66.8 %)	35 (18.1 %)
P. superciliosus	78	5 (6.4 %)	6 (7.7 %)	67 (85.9 %)
Females				
P. longirostris	133	82 (61.7 %)	33 (24.8 %)	18 (13.5 %)
P. malaris	127	25 (19.7 %)	73 (57.5 %)	29 (22.8 %)
P. superciliosus	58	2 (3.4 %)	9 (15.5 %)	47 (81.0 %)

ochraceous at their inner edges. In populations from Panama and Colombia these are almost completely ochraceous with whitish tips of the rectrices (II) next to the central, i.e., longest pair; (4) underparts: increasing intensity of ochraceous coloration from N to S corresponding to that of the under tail-coverts; (5) whisker/malar streakings: slightly increasing intensity of ochraceous coloration from N to S. Birds occurring between Nicaragua and Panama exhibit either weak or intensive ochraceous colorations apparently side-by-side. (6) bill curvature: slightly increasing curvature from S to N. This trend is observable in both sexes regardless of the fact that ♀, in general, have stronger curved bills than ♂.

However, these characters appear not to vary continuously between Guatemala and Costa Rica; there is a noticeable interruption corresponding to the obvious distributional break between NW Honduras and the border with Nicaragua (see Fig. 4). In this area, Knapp (1965) specifies a disjunction of lowland rain forest, the species' preferred habitat in Honduras (Monroe 1968), in favor of other forest types that may easily have been interrupted in the past. Comparing linear measurements by testing adjacent PG against each other the interruption of morphological characters is even more distinct (Fig. 5). Significant differences proved to exist in BL (♀: 3>4+5, $P<0.01$), WL (♀: 3>4+5, $P<0.01$), and TL (♂: 3>4, $P<0.05$) (differences

in ♂ BL and WL as well as in ♀ TL are distinct, but not significant; Fig. 5), whereas all remaining PG exhibit merely slight differences (unique exception: ♀ WL: 6>4+5, $P<0.05$). Thus, the obvious distribution gap in Honduras provides the best opportunity to define the range limits of the adjacent subspecies longirostris and cephalus. However, linear measurements displayed in Fig. 5 do not exhibit clearly defined variation as do the other morphological characters but show distinct minima between Costa Rica and E Panama (the female TL minimum in N Colombia may be due to the limited number of examined specimens).

Restricted to the Sierra Nevada de Santa Marta area of N Colombia (Fig. 4), P. l. susurrus appears to be merely a larger version of adjacent cephalus. There is no coloration difference between susurrus and the cephalus populations from E Panama and N Colombia; however, P. l. susurrus is significantly larger ($P<0.01$) in all linear measurements and in both sexes. It is unlikely that susurrus and N Colombian cephalus are (or very recently were) in permanent genetic contact due to the distinct size difference, and an obvious, though small distribution gap.

Geographic variation and zones of character introgression in Phaethornis malaris. The distribution of the nominate subspecies malaris, is limited to a relatively small area (Fig. 6). No character variation was observed. However, a unique specimen examined from Amapá, Brazil (adult ♀,

129

Serra do Navio, ZFMK 89.031) has the shortest bill of all malaris investigated in this study.

Due to little collecting within its distribution range, *P. m. insolitus* is known from only few localities and specimens (Fig. 6). This limited number, however, exhibits a certain color variation: birds from the type locality and its vicinity closely approach the dark brownish coloration of nominate *malaris* and in some cases are ·merely distinguishable by their smaller size. On the contrary, specimens from E Colombia are lighter, more greyish and resemble *P. m. moorei*. Thus, *insolitus* "links" the geographically clearly separated subspecies *malaris* and moorei by coloration. This connection is corroborated only to a certain degree by linear measurements. BL, WL, and TL variations of *insolitus* specimens are ranked within the upper levels of those within

moorei, but are clearly separated from the variation found within *malaris*. This, however, may be explained by the geographic proximity to *moorei*, whereas there is a distinct separation from *malaris*. Most probably, *insolitus* merely represents populations of *P. malaris* (secondarily) intergrading between *moorei* and the nominate subspecies but the probably once existing, extensive zone of character introgression was recently interrupted by the advance of the closely related *P. superciliosus* (Figs. 3, 6, 9). Both *P. m. insolitus* and *P. s. superciliosus* replace each other at the opposite banks of the lower Negro river and meet each other, obviously to a certain degree parapatrically, at the upper Negro in the Colombian/Venezuelan border area. In spite of intensive field work (summarized in Phelps & Phelps 1958, Meyer de Schauensee & Phelps 1978), *inso-*
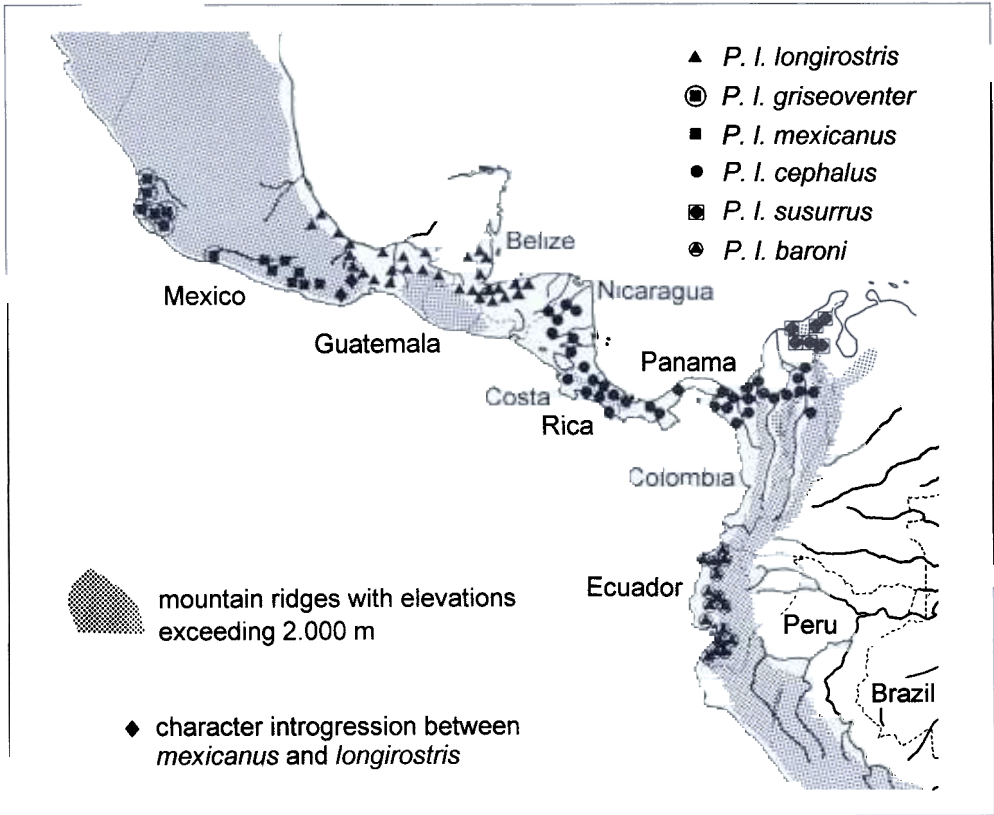

FIG. 4. Distribution range of *Phaethornis longirostris.*

Subsp.	longirostris			cephalus					baroni	
PG	1	2	3	4	5	6	7	8	9	10
n ♂♀	23 18	15 7	42 20	5 2	41 24	9 18	7 20	12 6	5 1	16 7

BL [mm] 45 — 40 — 35 —

| n ♂♀ | 23 19 | 16 8 | 45 20 | 7 2 | 42 22 | 9 20 | 8 23 | 13 7 | 6 2 | 16 8 |

WL [mm] 65 — 60 — 55 —

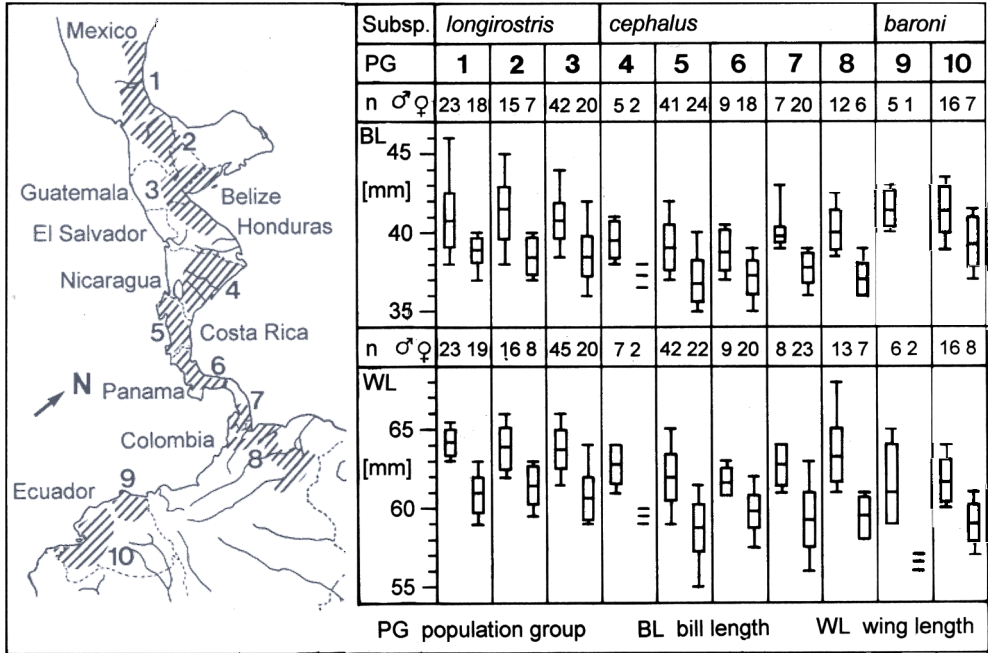PG population group   BL bill length   WL wing length

FIG. 5. Geographic variation of linear measurements in *Phaethornis longirostris longirostris*, *P. l. cephalus*, and *P. l. baroni*. Presented are mean, standard deviation, minimal and maximal values of bill length (BL) and wing length (WL).

litus was never found in inner Venezuela where it is (ecologically) replaced by *P. superciliosus* as well. Thus, only a recent interruption of a N Amazonian zone of character introgression between *malaris* and *moorei* by *P. superciliosus* justifies the maintenance of *P. m. insolitus*, which is darker than *moorei*.

Except for variation in the color (light brownish, whitish, or light ochraceous in variable amounts) of the rectrical margins (I found no correlations to geographic distribution, age or sex) *P. m. moorei* is rather uniform in plumage. In contrast, some linear measurements vary geographically. Northernmost populations of *moorei* (PG 1 in Fig. 7) exhibit significantly shorter bills than the remaining ones (♂: 2, 3, 5>1, $P<0.01$; ♀: 3, 4, 5>1, $P<0.01$, 2>1, $P<0.05$). Whereas WL in ♂ are more or less equal, those in ♀ vary to a certain degree (♀: 1>3, $P<0.01$, 5>3, $P<0.05$) (Fig. 7).

South of the Marañon river *moorei* characters intergrade with those of *bolivianus* (Fig. 8). At least in central Peru, color introgression seems to be influenced by topography. Whereas the greyish, less ochraceous *moorei* plumage is mainly confined to the Andean foothills and adjacent lowlands S to the dept. of Pando, Bolivia (12 km S Cobija, 1109S/6851W; LSUMNS specimens) and the Shintuya area, Peru (around 1250S/7116W; FMNH specimens), the darker, intensely ochraceous *bolivianus* plumage prevails in forested areas along the E Andes slopes north to Pomará (Dept. of Amazonas, 7823W/0523S; AMNH 185593). Between the areas inhabited only by individuals of *moorei* or *bolivianus* colorations, there is a character introgression zone of more than 1000 km length observable. Specimen series from various localities exhibit variable amounts of general *moorei* or general *bolivianus* colorations of the underparts but are not unequivocally referable to either subspecies (Fig. 8): 1. Carretera Corral Quemado to Nazareth (275 m); NE Chiriaco (320 m) — LSUMNS; 2. NE Tarapoto (750–1050 m) — LSUMNS;
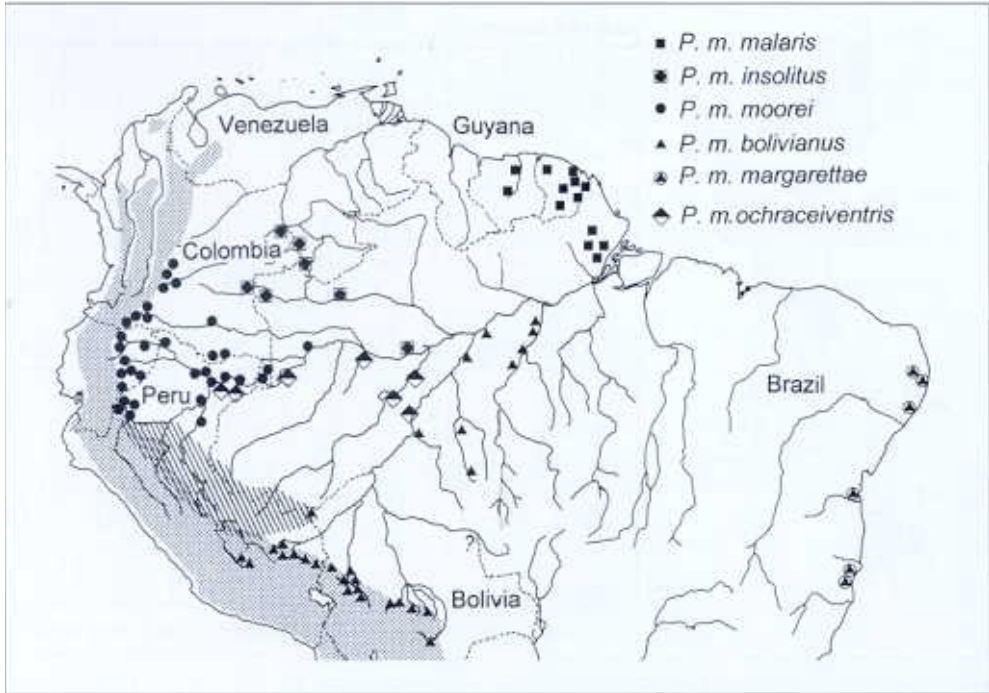
FIG. 6. Distribution range of *Phaethornis malaris*. The question-mark represents the Parque Nacional "Prof. Noel Kempff Mercado" (LSUMNS, unpubl. list). Locality data from the hatched area in E Andean Peru are explained in detail in Fig. 8.

3. 59 km W Pucallpa — AMNH; 4. Hacienda Flor, Puerto Victoria (350 m) — ZFMK; 5. Lagarto (type locality of *P. m. ucayalii* Zimmer, 1950); Santa Rosa, Boca Río Urubamba — AMNH; 6. Balta (300 m) — LSUMNS; 7. Río Mapitunuari (930 m) and E Luisiana (890 m), Cordillera Vilcabamba — AMNH; 8. Cerro de Pantiacolla (460—1350 m); Pantiacolla (430 m); Hacienda Amazonia, Shintuya (500—830 m); Río Palotoa (490 m) — FMNH; Cosñipata (700 m) — AMNH; S Cobija (325 m) — LSUMNS. However, note that some bird specimens collected by the Olallas along the upper Ucayali river (Lagarto, Santa Rosa) may in fact originate from the lower Ucayali river (Haffer 1978, p. 43).

There is also some variability in the color of the rectrical margins and under tail-coverts. These areas are always orange-ochraceously in *bolivianus*, but variable in *moorei* (rectrical margins: whitish, light brownish, or ochraceous in variable amounts; under tail-coverts: whitish

or ochraceous); this variation does not correlate with that of the underparts' coloration. In general, whitish or light brownish rectrical margins as well as whitish under tail-coverts prevail in N Peru whereas ochraceous rectrical margins and under tail-coverts are predominantly found in S Peru.

Almost continuous variation is observed in some linear measurements. BL and WL in both sexes decrease slightly from N to S independent of the apparently altitude-related variability in coloration. Careful comparison of all measurements within 21 geographical units (adjoining localities) revealed that variation is limited to larger areas, and populations could be grouped to 5 PG (Nos. 3—7 in Fig. 7). Some BL and WL display significant differences (Fig. 7 and Table 4). Some PG, however, do not reflect the slight southward decrease of the WL but have larger wings than the neighbouring ones in the N (wing: $\male$: 6>3, 5, $P<0.05$; $\female$: 6, 7>3, $P<0.05$).

TABLE 4. Significant differences in bill (BL) and wing lengths (WL) between various poulation groups in the *Phaethornis malaris moorei* / *P. m. bolivianus* zone of character introgression (numbers of population groups, PG, correspond with those in Fig. 7).

BL: ♂: 3, 5, 6 > 7, P < 0.01; 6, 7 > 8, 9, P < 0.01;
     ♀: 6 > 7, 8, 9, P < 0.01; 7 > 8, 9, P < 0.01;

WL: ♂: 5 > 7, P < 0.01; 6 > 7, 8, 9, P < 0.01; 7 > 8, P < 0.05; 7 > 9, P < 0.01;
     ♀: 5, 6 > 7, P < 0.05; 6, 7 > 8, 9, P < 0.01.

Populations of *P. m. bolivianus* from extreme SE Peru and Bolivia do not show any appreciable variation in either coloration or linear measurements. This seems to be the same over the entire range of the subspecies, although present information indicates an interruption of about 850 km between the Bolivian and the Brazilian populations (Fig. 6). This "distribution gap" is more likely due to the lack of ornithological exploration than to the absence of suitable habitat. There is only one, still unpublished note indicating the occurrence of *"Phaethornis superciliosus"* in the Parque Nacional Noel Kempff Mercado, Bolivia (? in Fig. 6; LSUMNS, unpubl. list) that can be referred to *P. malaris bolivianus*. Formerly separated as *"insignis"*, populations occurring between the lower rivers Madeira and Tapajós show almost no differences in either coloration or linear measurements from Andean-based *bolivianus*. Possibly, Brazilian birds have slightly more intensely colored rectrical margins. However, due to the small number of specimens examined, this character as well as the possibility that males more regularly show a well-marked midthroat streaking than males of "true" *bolivianus* cannot be confirmed. Linear measurements of the two are similar (exception: TL in ♂: 8>10, P<0.05; Fig. 7). I do not consider the slight character variation sufficient to maintain a valid subspecies *"insignis"*.

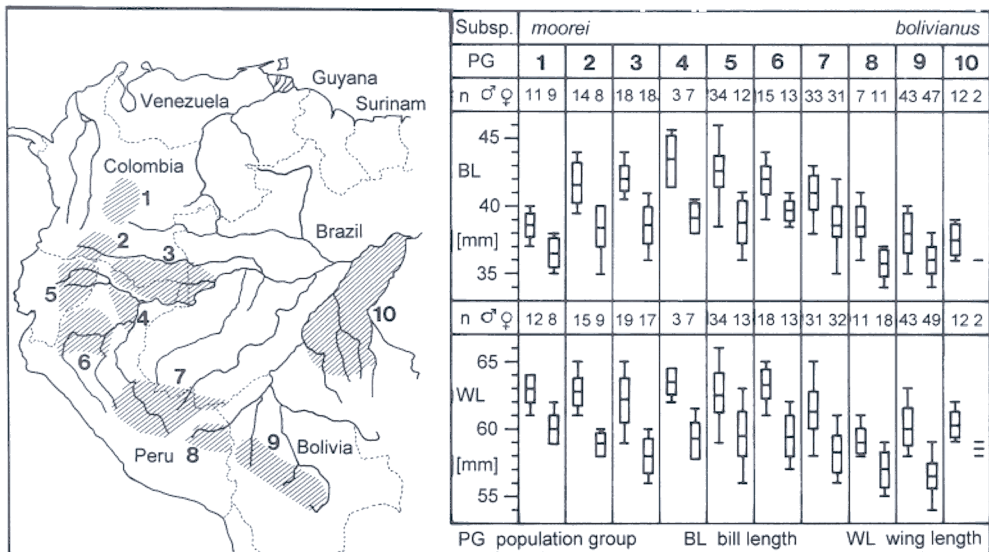Geographically well separated from its Amazonian relatives, *margarettae* inhabits some

FIG. 7. Geographic variation of linear measurements in *Phaethornis malaris moorei* and *P. m. bolivianus*. Presented are mean, standard deviation, minimal and maximal values of bill length (BL) and wing length (WL).
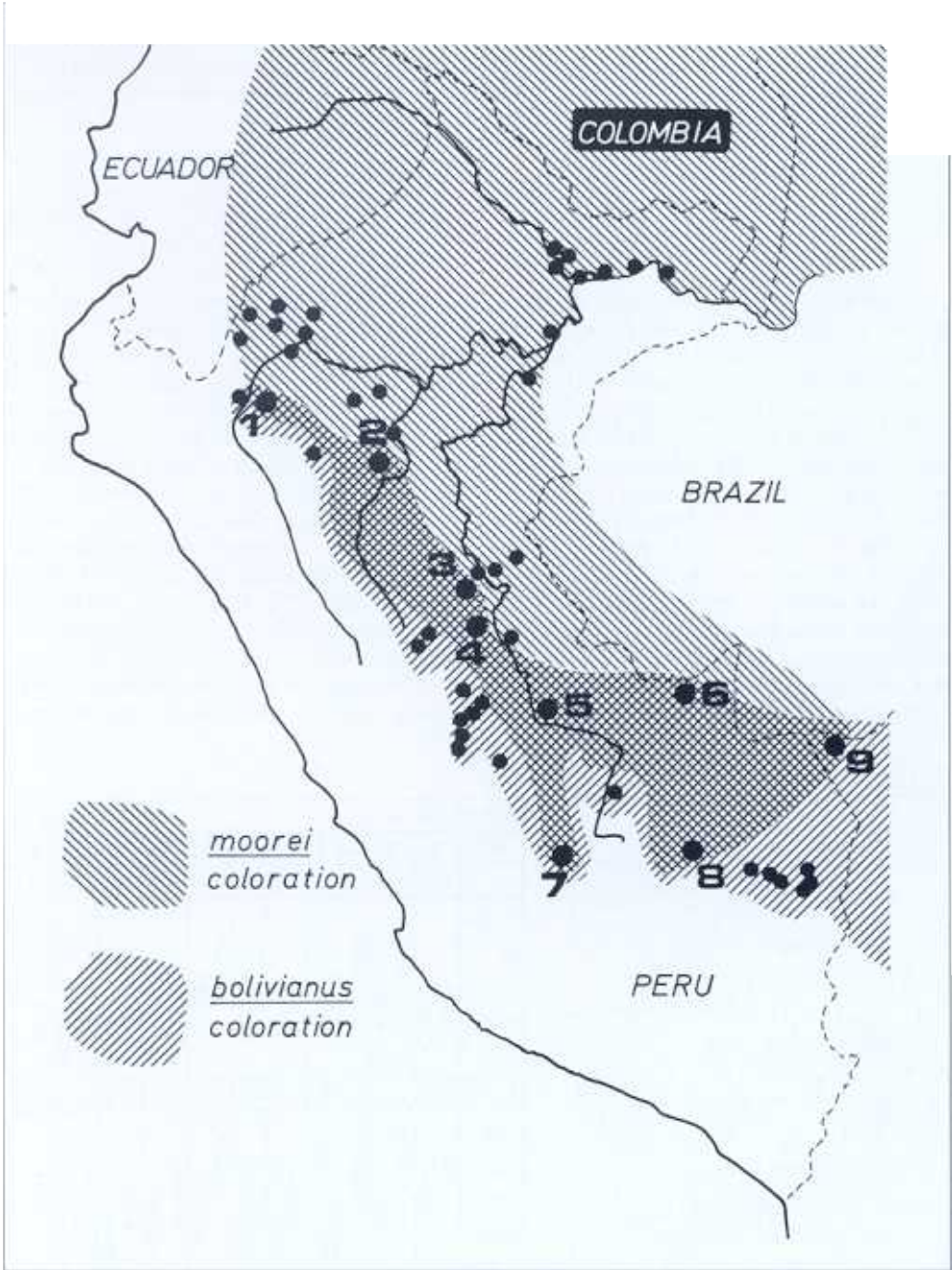
FIG. 8. Approximate distributions of colorations typical for *Phaethornis malaris moorei* and *P. m. bolivianus* in the Peruvian area of contact. Large dots indicate collecting localities where series of specimens exhibit variable amounts of *moorei* and *bolivianus* colorations; their numbers correspond to localities listed in the text. Small dots (without numbers) indicate collecting localities of birds with pure *moorei* and pure *bolivianus* colorations in Peru.

remnants of the highly endangered Atlantic forests of SE Brazil (Fig. 6). According to Hueck & Seibert (1972), the intervening area is covered by unsuitable habitat for at least 2000 km distance. However, *bolivianus* and *margarettae* are surprisingly similar in all morphological characters. Perhaps *margarettae* has paler underparts, and males may have more regularly distinct midthroat streakings than those of *bolivianus* (due to a very limited number of specimens examined this has still to be confirmed). In contrast, there are several morphological differences (underparts, under tail-coverts, rectrical margins, and bill curvature) between *margarettae* and *P. s. muelleri*, the geographically closest member of the species group, and I thus consider *margarettae* a subspecies of *P. malaris*. The very narrow linear distribution theoretically facilitates the development of clinally varying characters, in particular because the distribution strip crosses the valley of the São Francisco river. Due to the lack of material, however, this possibility cannot be confirmed today.

Although geographically separated by distribution gaps in various regions, all hitherto treated subspecies of *P. malaris* appear to be closely related to each other based on morphological similarity or character introgression. Only *P. m. ochraceiventris* does not fit easily into this assemblage. Its distribution range is clearly separated from that of *bolivianus* by the course of the lower Madeira, and from those of *insolitus* and *moorei* by the Amazon (Solimões) (Fig. 6). Although the distribution ranges of *ochraceiventris* and *moorei* may closely approach each other in the lower Ucayali river region (Figs. 3, 6), there is no indication of character introgression. Unfortunately, little or no collecting has been done in the E and SE of this area, along the Peruvian-Brazilian border where these subspecies probably are in contact. It is possible that they do not hybridize where they meet. Specimens available in museum collections are from the S bank of the Amazon (Solimões) and from a relatively small area between the lower rivers Purús and Madeira, and represent only a small portion of its probable large range. I found no color differences among these PG. Linear measurements as well exhibited little variation (compared to other *malaris* subspecies); however, the limited number (n = 21 and 5, respectively) prohibited any test of significance.

Geographic variation in Phaethornis superciliosus. The nominate subspecies, *superciliosus*, occupies the largest area of all subspecific taxa treated in this paper (Fig. 9). However, I found no appreciable geographic variation in coloration. Differences in the amount of ochraceous coloration in the rectrical margins are apparently age-related; juveniles always have these areas white, while various amounts of ochraceous coloration are found only in adults. While there is no color variation, tests between several PG revealed some significant differences in linear measurements (Fig. 10 and Table 5).

Well separated by the lower Amazon, *superciliosus* and *muelleri* do not exhibit any character introgression. Although the *muelleri* specimens examined represent only the westernmost and easternmost populations (Figs. 9, 10), I found no geographic variation in either coloration or linear measurements between them.

Sympatry and hybridization in the Phaethornis superciliosus-malaris-longirostris *species group.* The distribution of *Phaethornis longirostris* is completely limited to trans-Andean, i.e., Central American and west-Andean South American lowlands and lower mountain ridges (Figs. 3, 4). At present, the members of this species cannot come in contact with *P. superciliosus* or *P. malaris*

TABLE 5. Significant differences in linear measurements (bill length, BL, and shortest distance between tips of rectrices I and V, TL) among population groups (PG) in *Phaethornis superciliosus superciliosus* (numbers for PG correspond with those in Fig. 10).

BL: ♂: 3, 6 > 4, $P < 0.05$; 5 > 3, 4, 6, $P < 0.01$; 5 > 7+8, $P < 0.05$;
♀: 6 > 3, $P < 0.05$; 6 > 7+8, $P < 0.01$.
TL: ♀: 4+5 > 3, 7+8, $P < 0.05$; 3 > 6, $P < 0.05$; 4+5 > 6, $P < 0.01$

due to topographical barriers. Narrow lowlands with gallery forests, plantations, wooded pastures and similar habitats all along and around the base of the N Andes are inhabited by *P. anthophilus*, a species of similar body mass and apparently better adapted to drier, more open habitats than Long-tailed Hermit hummingbirds.

P. superciliosus and *P. malaris*, however, behave like paraspecies in most areas and replace each other on the opposite banks of some major rivers (Figs. 3, 6, 9); thus, ecologically the species behave towards each other like several subspecies (within both *P. superciliosus* and *P. malaris*) which are separated by rivers. They replace each other geographically where they meet. This is the case along the upper Negro river, the Casiquiare junction, and the upper Orinoco river where *P. s. superciliosus* and *P. m. insolitus* meet each other. Because there is no indication either of character introgression or of broader sympatry, these taxa probably replace each other parapatrically to avoid direct competition. Only one exception is presented by *P. m. malaris* and *P. s. superciliosus* which occur sympatrically in E

Surinam, French Guiana, and adjacent Brazil (Novaes 1974, Mees 1977). Data on the habitat requirements of both *P. m. malaris* (Mees 1977, Dick *et al.* 1984) and *P. s. superciliosus* (Snethlage 1913, Nicholson 1931, Davis 1958, Snyder 1966, Haverschmidt 1968, Snow 1973, Willis 1977, Dick *et al.* 1984) indicate that they occupy the same altitudinal and habitat niche. Thus, they apparently avoid direct competition by, at least, depending on different food resources, as indicated by their body masses (*P. m. malaris*: 7.5—10 grams; *P. s. superciliosus*: 4—6.5). This situation is similar to the one found regularly in the Caribbean islands (Lack 1973, Schuchmann 1980).

Extensive sympatry can occur only in taxa which are genetically and reproductively isolated. This does not necessarily exclude occasional hybridizations; however, until today only one example could be found. A ♀ collected by S.M. Klages at Pied Saut, French Guiana, is perfectly intermediate in coloration, linear measurements, and even in bill curvature (Hinkelmann 1996). Both *malaris* and *superciliosus* were recorded from Pied Saut (Zimmer 1950).
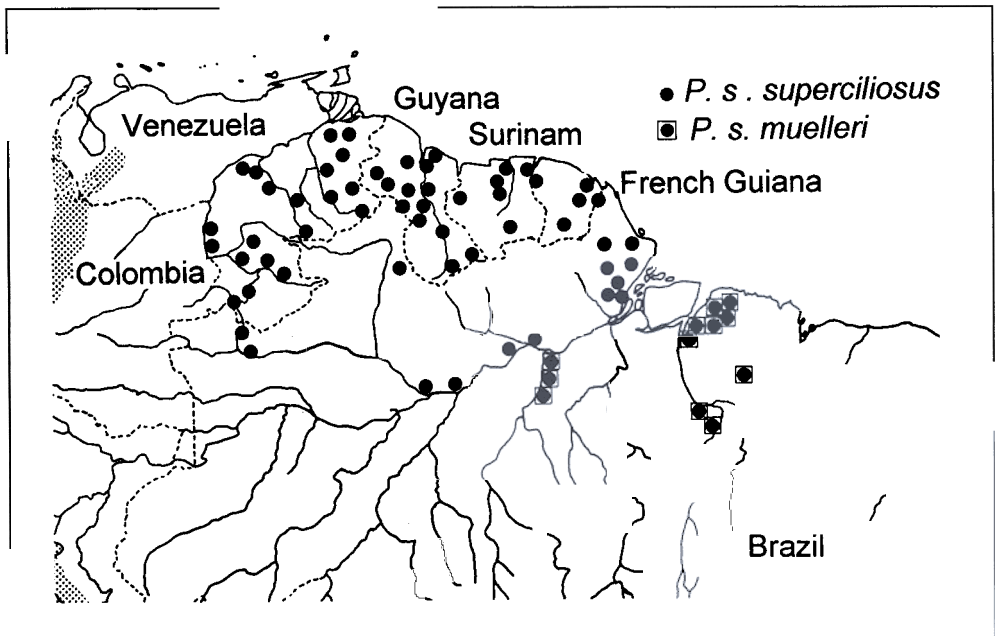

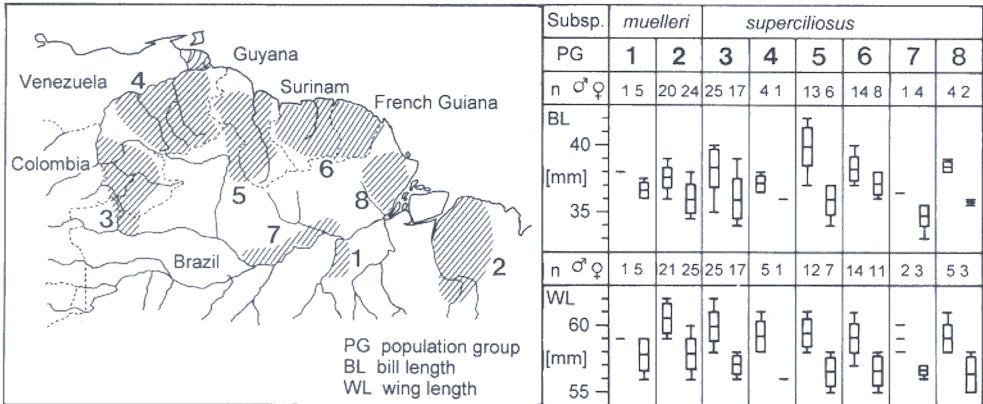FIG. 9. Distribution range of *Phaethornis superciliosus*.

FIG. 10. Geographic variation of linear measurements in *Phaethornis superciliosus*. Presented are mean, standard deviation, minimal and maximal values of bill length (BL) and wing length (WL).

Biogeographical remarks. Phaethornis superciliosus/P. malaris and *P. longirostris* represent a cis-/trans-Andean relationship as it is known from several bird species, superspecies and species groups (e.g., Haffer 1967, 1975). It is obvious that lowland biota of both W and E Andean areas were once in contact. Warm, humid conditions probably permitted the predecessors of *P. longirostris* to cross the northern Andean ridges that act as an almost insuperable barrier to species adapted to humid lowland forests today. The crossing may have occurred at lower elevations of the Coastal Cordillera along the Colombian/Venezuelan border and between the extreme northern foothills of the East Cordillera and the isolated massif of the Sierra Nevada de Santa Marta in N Colombia. In trans-Andean South America and Central America, the ancestors of *P. longirostris* probably spread out and colonized all suitable habitats. Subsequent climatological and geological events temporarily interrupted the probably once continuous distribution range. According to Haffer's (1967, 1969, 1975, 1982) model of biological diversification (refuge theory), several populations may have survived geographically and genetically isolated from one another resulting in the evolution of several morphologically differentiated populations. Zones of character introgression between the most of the adjoining PG and subspecies indicate that the isolation period was not sufficient to obtain reproductive isolation.

Data on the habitat requirements of *P. longirostris griseoventer* (Phillips 1962, Schaldach 1963), *P. l. mexicanus* (Binford 1968, 1989), and *P. l. baroni* (Oberholser 1902, Wiedenfeld et al. 1985) indicate that these subspecies at the northern- and southernmost limits of the species' distribution are adapted to less humid forest types than are the remaining subspecies. This may, at least in part, explain why there is a distribution gap between the ranges of *P. l. cephalus* and *P. l. baroni*: *Phaethornis yaruqui*, a congeneric species of similar body mass, appears to be better adapted to extremely humid conditions and replaces *P. longirostris* in the lowland forests of trans-Andean Colombia and Ecuador. Haffer (1975) already presumed that the lack of seasonal forests in W Colombia may be responsible for the absence of Long-tailed Hermit hummingbirds in this area. However, F. Gary Stiles observed *P. longirostris* in Bahia Solano, north-central dept. Chocó, Colombia, and expects its occurrence even farther to the S in adequate habitats (Stiles, in litt.).

Within the cis-Andean South American taxa, the history of distribution ranges still provides some problems. Subspecies of *P. malaris* in most cases inhabit areas that are in accordance with the location of forest refuges postulated by Haffer (1969, 1974, 1978) for drier periods in the past. (Only the distribution of *P. m. ochraceiventris* does not include any forest refuge.) In some cases, subspecies' distributions are separated from

137

another by major rivers (Amazon [Solimões], lower Madeira and lower Tapajós) that probably facilitated the morphological differentiation of several taxa. *P. superciliosus muelleri* and *P. malaris bolivianus*, which are separated by the lower Tapajós river, may be in parapatric contact in southern Pará, Brazil, but no specimens are available from this area. Separation of the subspecies' distribution ranges by major rivers is especially important in *P. malaris* because this species is limited to the forests of the terra firme whereas the várzea and other river-created forest types in W Amazonia are inhabited by *Phaethornis hispidus*, another closely-related species of similar body mass (Remsen & Parker 1983). Thus, the riverine barriers between the respective ranges are not only represented by the width of the rivers but, along their lower courses, also enlarged by a river-created vegetation of variable extension.

The subspecies of *Phaethornis superciliosus* "interrupt" the distribution ranges of closely related subspecies of *P. malaris* by inhabiting the intervening areas. As already mentioned earlier, *P. s. superciliosus* occurs between the areas inhabited by *P. m. insolitus* and *P. m. malaris*, whereas *P. s. muelleri* occupies the only region where *P. m. bolivianus* and *P. m. margarettae* might come in contact with each other during a warmer, more humid period than today. This assumption would reproduce the probable situation that enabled the ancestors of *P. m. margarettae* to colonize the Atlantic forests of SE Brazil. The most likely connection between the lowland rain forests of Amazonia and SE Brazil would be established along the southern bank of the Amazon and north of the Brazilian highlands in the states of Maranhão, Piauí, Ceará, Rio Grande do Norte, and Paraiba (T. A. Parker, pers. comm.). Another alternative, a forest contact via the Brazilian states of São Paulo and Paraná, and across Paraguay to Bolivia, however, is unlikely due to the presence of *Phaethornis eurynome*, an endemic species of similar body mass replacing *P. malaris margarettae* in the S and SW. In the southern parts of its range, *P. m. margarettae* inhabits the lowland forests whereas *P. eurynome* is limited to mountain forests (Hinkelmann 1988b).

Previous attempts at classifying the Phaethornis superciliosus-malaris-longirostris *species group.* The classification of the Long-tailed Hermit hummingbirds in three species, *P. superciliosus, P. malaris,* and *P. longirostris* was already presented by Cabanis & Heine (1860) and Cory (1918). All remaining authors accepted a larger number of species (e. g., Gould 1861, Boucard 1895, Hartert 1900, Simon 1921) or limited their number to two. Salvin & Elliot (1873) accepted *P. superciliosus* and *P. longirostris,* Simon (1897) *P. superciliosus* and *P. bolivianus,* whereas Peters (1945) and Zimmer (1950) assigned the taxa to *P. superciliosus* and *P. malaris.*

In *P. longirostris,* several taxa were regarded as separate species by some authors (Boucard 1895, Hartert 1900, Simon 1921), whereas they were treated as subspecies of *P. longirostris* by Cory (1918) and Todd (1942), as subspecies of *P. superciliosus* by Peters (1945) and as those of *P. malaris* by Zimmer (1950). Heretofore, specimens belonging to the Central American populations linked by an almost clinal relationship (considered here as *P. l. longirostris* and *P. l. cephalus*) were assigned to four subspecies (from NW to SE): *veraecrucis, longirostris, cephalus,* and *cassinii* (Griscom 1932a, Peters 1945, Zimmer 1950, Wetmore 1968). Their respective morphological differences and distribution limits were repeatedly discussed:
"veraecrucis" — *longirostris*: Austin 1929, Peters 1945, Brodkorb 1943, Friedmann *et al.* 1950, Paynter 1957;
longirostris — *cephalus*: Hartert 1897a, Peters 1929, Griscom 1932a, Todd 1942, Monroe 1968;
cephalus — *"cassinii"*: Bangs & Barbour 1922, Griscom 1932a, Zimmer 1950, Wetmore 1968.

However, these studies did not reveal the gradual character introgressions among the trans-Andean populations.

P. l. baroni was described as a separate species (Hartert 1897a) with closer affinities to "*P. superciliosus moorei*" than to *P. longirostris.* Isolated in trans-Andean lowlands, it may have achieved reproductive isolation and, if so, may thus be considered a separate species, as the only taxon within the trans-Andean Long-tailed Hermit Hummingbirds. However, this possibility cannot be verified on morphological characters alone.

Relationships of the cis-Andean South American taxa have always provided some taxonomical difficulties. First, there has been confusion regarding the identity of *Trochilus superciliosus* Linnaeus, 1766. Gould (1861) applied it to the larger and darker species from "Cayenne and the adjacent countries" (*Trochilus malaris* Nordmann, 1835) and was followed by Boucard (1895) and Hellmayr (1906). As a consequence, the misnaming resulted in the descriptions of two synonyms: *Phaethornis fraterculus* Gould, 1861, and *Phaethornis guianensis* Boucard, 1891 to separate the smaller and lighter species. Others, e.g., Hartert 1897a, Salvin & Elliot 1873, Salvin 1892, Penard & Penard 1910, treated both species occurring in French Guiana as synonyms. Finally, Pelzeln (1871), Berlepsch (1887, 1888, 1908), Hartert (1897b, 1900) and Hellmayr (1912) presented the correct taxonomical treatment of both nominate subspecies.

Another problem has been how to assign the various cis-Andean subspecies to either *P. superciliosus* or *P. malaris*. Several taxa were regarded as separate species, e.g., *P. m. moorei* (as "*Phaethornis consobrinus*" [Reichenbach, 1854, nomen nudum] by Gould 1861, Eudes-Deslongchamps 1881, and Boucard 1895) and *P. m. bolivianus* (Gould 1861; Boucard 1895; Simon 1897, 1921; and Hartert 1900). Todd (1942), however, considered all cis-Andean taxa known at that time as valid species. Peters (1945) assigned all subspecies to *Phaethornis superciliosus* in contrast to a monotypical *P. malaris*. This treatment was accepted by Eisenmann (in Meyer de Schauensee 1966), whereas Zimmer (1950) assigned all subspecies with the exception of *saturatior* to *P. malaris*. Recently, Grantsau (1988) separated the Brazilian taxa occurring S of the Amazon river as a distinct species, *P. ochraceiventris*, assigning to it *muelleri, insignis, camargoi, margarettae,* and *ochraceiventris*. *P. ochraceiventris* is said to be distinguishable from *P. superciliosus* (*sensu* Peters 1945) of N Amazonian Brazil by mandible color, song, and nest structure, but, unfortunately, Grantsau (1988) neither specifies these differences nor discusses the relationships to *bolivianus* and its character introgression with *moorei*.

Zimmer (1950) was the first to examine the relationships within the cis-Andean taxa and stated: "It appeared even that it might be possible to consider *malaris* and *superciliosus* as terminal forms of a 'ring species'...". Consequently, he emphasized some intermediate morphological characters in populations geographically linking the ranges of morphologically well-differentiated subspecies. He pointed to the intermediate coloration and size of some populations from the Venezuelan/Colombian border area (that he described as *P. malaris insolitus*) between nominate *malaris* and *moorei*, later confirmed by Blake (1962). Zimmer (1950) also recognized that Peruvian birds inhabiting the area between the S bank of the Amazon and the Chanchamayo Valley (Dpto. Junín) differed from *moorei, ochraceiventris,* and *bolivianus*. Thus, he described these as a new subspecies, *P. malaris ucayalii* which he considered to be intermediate between *ochraceiventris* and *bolivianus*. Zimmer (1950) determined SE Peruvian birds as intermediate between *ucayalii* and *bolivianus* but did not discover the introgression of characters between *bolivianus* and *moorei* along the E Andean slopes in Central Peru leaving "*ucayalii*" as an intergrade, or invalid taxon. Interestingly, a "transitional" relationship between *moorei* and *bolivianus* was already emphasized by Seilern (1934) who investigated SE Peruvian birds.

Due to its morphological similarity to *P. longirostris*, typical *bolivianus* was considered to be of mislabeled origin by Salvin & Elliot (1873); later authors regarded it as a subspecies of *P. longirostris* (Oberholser 1902, Cory 1918) or preferred to treat it as a separate species"... unless future explorations show that it occurs in the long stretch of intervening countries ..." (Hartert 1897a). Populations occurring S of the Amazon between the lower rivers Madeira and Tapajós, formerly separated as "*insignis*", hitherto were not carefully compared with *bolivianus* from Bolivia, but considered as a valid subspecies of *P. superciliosus* (Todd 1937) or even a species (Todd 1942). Peters (1945) and Pinto (1978) again regarded them as subspecies of *P. superciliosus*.

The occurrence of *Phaethornis malaris* in SE Brazil has been known for a relatively short time (reviewed by Hinkelmann 1988b, 1989b). Ruschi (1972) described birds of a population inhabiting remnant forest in Espirito Santo as *Phaethornis margarettae* after having compared these with all subspecies of *P. malaris* (*sensu* Zimmer 1950). Unfortunately, he did not provide sufficient diagnostical characters to separate this "species"

from *P. malaris* (*P. superciliosus sensu* Peters 1945);
thus, the species was considered doubtful (Mayr
& Vuilleumier 1983, Collar 1987) or even invalid
(Grantsau [in Vuilleumier & Mayr 1987], 1988,
Teixeira *et al.* 1987, Hinkelmann 1988b). Sick
(1985) considered *margarettae* as the sister species
of the Amazonian *superciliosus* (*sensu* Peters
1945). Recently, Grantsau (1988) separated birds
from Pernambuco as "*Phaethornis ochraceiven-
·tris camargoi*", considering these as geographical-
ly well-isolated from "*P. o. margarettae*". How-
ever, he neither provided definite morphological
characters not due to individual variation nor did
he discuss the probably uninterrupted distribu-
tion range of *margarettae* before the Europeans
arrived in SE Brazil. According to Hueck &
Seibert (1972), a homogeneous kind of rain forest
covered the coastal lowlands between the states
of Paraiba and Espirito Santo. A summary of
locality data for *P. m. margarettae* is provided by
Hinkelmann (1989b).

   P. m. ochraceiventris was considered a sub-
species of "*P. boliviana*" (Simon 1921, Hartert
1922), of *P. malaris* (Zimmer 1950), of *P. super-
ciliosus* (Hellmayr 1912, Peters 1945, Pinto 1978),
and a separate, monotypic species *P. ochraceiven-
tris* (Hellmayr 1907b, Todd 1942, Gyldenstolpe
1950). Zimmer (1950) detected some morpholo-
gical approaches to neighbouring "*insignis*" and
"*ucayalii*" which he concluded to be "... inter-
mediate between *P. m. moorei* ... and *P. m. ochra-
ceiventris* ...". Probably, *ochraceiventris* does not
have regular contact with the taxa occupying the
opposite banks of the rivers Amazon and Madei-
ra. It has perhaps achieved reproductive isolation
and may thus be regarded as a distinct species,
but its affinities to *moorei* are still obscure.

   Several authors tried to assign different popu-
lations within *Phaethornis superciliosus supercilio-
sus* to separate additional subspecies, in particu-
lar, those of S Venezuela (e.g., Hartert 1900,
Simon 1921, Zimmer 1950, Phelps & Phelps
1958, Grantsau 1988). Peters (1945), however,
considered *Phaethornis superciliosa saturatior*
Simon, 1921, as "doubtfully distinct from *P. s.
superciliosus*" and Todd (1942) found "no
grounds for the distinction" of "*saturatior*". The
affinities between *superciliosus* and *muelleri*,
resulting in the assignment of *muelleri* as the
only valid subspecies of *P. superciliosus* in this
paper, have not been discovered previously.

DISCUSSION

Unfortunately, the continuously increasing for-
est destruction in Central and South America
has devastated many localities treated as in-
habited by Long-tailed Hermit hummingbirds in
this paper. Thus, distribution ranges given
should be considered as referring to the situation
prior to the large-scale habitat alteration of this
century.

   Long-tailed Hermit hummingbirds form a
species group. At first sight, they seem to repre-
sent a situation similar to those of many other
tropical American superspecies distributed in
both cis- and trans-Andean lowlands, e.g., *Pio-
nopsitta caica* (6 species), *Pipra erythrocephala* (5
species), *P. serena* (6 species) (Haffer 1970), *Cotin-
ga maynana* (6 species), *Psarocolius bifasciatus* (4
species), *Ramphastos dicolorus* (4 species) or *Sele-
nidera maculirostris* (6 species) (Haffer 1974).
Many taxa of the *Phaethornis superciliosus- mala-
ris-longirostris* species group are parapatric or
even allopatric and most of them probably
occupy a single ecological niche. However, the
sympatric occurrence of *P. malaris malaris* and *P.
superciliosus superciliosus* in French Guiana, E
Surinam and adjacent Brazil indicates that at
least two taxa successfully established sympatry
which is probably supported by significant diffe-
rences in body mass and bill size. There are 3 bio-
logical species united in the Long-tailed Hermit
hummingbird species group: *P. malaris*, *P. super-
ciliosus* and *P. longirostris*. Two taxa, *P. m. ochra-
ceiventris* and *P. l. baroni*, may also turn out to
be separate species.

   Plumage coloration in Long-tailed Hermit
hummingbirds appears to be very conservative.
As a consequence, this overall similarity caused
many authors to treat the birds as belonging to
no more than two species. Unfortunately, there
are no studies on the systematics of the *P. superci-
liosus-malaris-longirostris* species group based on
non-morphological methods that treat a number
of taxa. Based on electrophoretic analyses of en-
zymes, Capparella (1987) investigated the genetic
differentiation of Long-tailed Hermit humming-
birds from opposite river banks in Amazonian
Peru and concluded that "*Phaethornis supercilio-
sus moorei*" (N of the Amazon) and "*Phaethornis
superciliosus ucayalii*" (= *P. malaris ochraceiven-
tris*; S of the Amazon) "are different species if
one compares those levels to allozyme analyses

of temperate zone birds" (Capparella, in litt.). Gill & Gerwin (1989) examined the protein relationship of 12 *Phaethornis* species including Long-tailed Hermit hummingbirds from the Peruvian departments of Pasco, Loreto, and San Martín (*P. malaris bolivianus*, *P. m. moorei*) but did not investigate possible intraspecific differences.

There are also few studies on behavioral characters in members of the *P. superciliosus-malaris-longirostris* species group that may contribute to the systematic relationship among the taxa. Snow (1973) reported a *P. s. superciliosus* ♂ to intrude into the lek territory of another ♂ (of *P. s. superciliosus*): "the owning ♂ opened his beak and displayed his orange-red gape. The visitor then touched the inside of the displayed gape either with its tongue or the tip of its beak." A very similar, probably homologous behavior was reported for *P. s. muelleri* (Hellmayr 1912) and may support the affiliation to the same species. Stiles & Wolf (1979), however, indicate that they could never observe a corresponding behavior in *P. longirostris cephalus*, a taxon still regarded as conspecific. Unfortunately, there are no similar descriptions or detailed informations of lek behavior in any subspecies of *P. malaris* published.

Zones of character introgression between the core areas of the ranges of several taxa point to the lack of genetical barriers. In *P. longirostris*, these are barely evident (few collecting localities) between *griseoventer* and *mexicanus* as well as between *mexicanus* and *longirostris*. As a consequence, Banks (MS) prefers to treat *griseoventer* and *mexicanus* as separate species, and Howell & Webb (1995) recently included both taxa in a distinct species, *P. mexicanus*. There is probably no zone of character introgression between *cephalus* and *susurrus* today, and *baroni* is geographically clearly separated from the remaining subspecies. However, there is an extensive hybridization zone between *longirostris* and *cephalus*. Due to the relatively narrow distributions of both subspecies in Central America, their secondary contact area (Guatemala — Costa Rica) exhibits a situation very similar to a phenocline. In contrast to clinal variation, however, character variation in Central American Long-tailed Hermit hummingbirds is highest in the (N)W and in the (S)E of Honduras where both subspecies may approach each other, and

several plumage characters differ simultaneously between Guatemala and NW Honduras as well as between SE Honduras and Costa Rica. Similar to *longirostris* and *cephalus*, there is an obvious distributional break in Honduras between two closely related *Ortalis* species, *O. vetula* (NW) and *O. garrula* (SE). Whereas these differ in their habitat preferences (Vaurie 1968), however, there is apparently no such separation between *P. l. longirostris* and *P. l. cephalus* (according to habitat data from Russell 1964, Skutch 1964, Slud 1964, Monroe 1968, Wetmore 1968, Stiles & Wolf 1979, Binford 1989). Stiles (in litt.) pointed to clearly geographical-based differences in *P. l. cephalus* from Costa Rica; birds from the SW are significantly larger than those of the Caribbean slope.

In cis-Andean South America, contacts of several Long-tailed Hermit hummingbird subspecies are inhibited by the courses of large rivers. Consequently, there are no zones of character introgression along the rivers even when taxa of opposite banks are considered to belong to the same species and might interbreed freely where they get in contact without physical barriers. Zimmer (1950) discovered character introgression and intermediate plumage characters between most Amazonian taxa and regarded *P. m. malaris* and *P. s. superciliosus* as the terminal forms of a "ring species". There is a remarkable plumage similarity between *malaris* and *insolitus*, an obvious zone of character introgression (though few collecting localities) between *insolitus* and *moorei*, and an extensive zone of character introgression between *moorei* and *bolivianus*. Regarding the distributions of these taxa, there is an almost continuous area — N of the Amazon from French Guiana (interrupted in Venezuela and Guyana) to Colombia, Ecuador, Peru, and Bolivia, and S of the Amazon to the W bank of the Tapajós river — inhabited by a single species. In contrast to a "ring species", however, there is no indication of a continuing genetical relationship between *bolivianus* and the remaining E Amazonian taxa, *muelleri* and *superciliosus*. If *P. superciliosus muelleri* and *P. malaris bolivianus* should get in contact in the headwater region, most likely they would remain in parapatry or one taxon would replace the other on a long-term basis; they are of equal body mass (4—7 g).

Haffer (1970, 1974) provided examples for species crossing the Tapajós S of its lower course (*Pipra nattereri*, *Pteroglossus beauharnaesii*) that obviously remain in parapatry with their congeners of the opposite bank. *Xipholena punicea* of N and W Amazonia also crosses the Tapajós in the headwater region whereas the SE Amazonian *X. lamellipennis* was able to colonize the W bank of the lower Tapajós (Haffer 1970).

The close relationship between *superciliosus* and *muelleri* indicates that even broad rivers need not represent an important barrier for the range expansion of terra firme birds. There are several species of Amazonian birds limited to the lower Amazon region but inhabiting both the N and S banks of the Amazon, e.g., *Ortalis motmot* (Vaurie 1968), *Phoenicircus carnifex*, *Euphonia cayennensis* (Haffer 1970), *Pteroglossus aracari*, or *Brachygalba lugubris* (Haffer 1974). Besides, the closely related *Phaethornis bourcieri* was able to cross the lower Amazon as well, and like *P. superciliosus*, different subspecies inhabit the opposite banks (Hinkelmann 1989a). Major rivers are able to prevent an extensive gene flow and may support the differentiation of taxa. However, it is still unproven that riverine barriers cause speciation as emphasized by, e.g., Sick 1976, Connor 1986, Salo *et al.* 1986, and Capparella 1987. It is unlikely in Long-tailed Hermit hummingbirds because some taxa occur on both banks of major rivers (Purús, Juruá: *ochraceiventris*; Xingú, Tocantins: *muelleri*; Marañon, Napo: *moorei*), although other rivers (Amazon, Negro, Madeira, Tapajós) delimit the range of taxa.

ACKNOWLEDGEMENTS

REFERENCES

Austin, O.L., Jr. 1929. Birds of the Cayo District, British Honduras. Bull. Mus. Comp. Zool. 69: 361—394.

Bangs, O., & T. Barbour. 1922. Birds from Darien. Bull. Mus. Comp. Zool. 65: 191—229.

Banks, R. C. (Unpubl. MS). Comments on the systematics of some Central American hermit hummingbirds.

Bartholomew, J. C., Christie, J. H., Ewington, A., Geelan, P. J. M., Lewis, H. A. G., Middleton, P., & B. Winkleman. 1985. The Times atlas of the world. 7th ed., London.

Berlepsch, H. von. 1887. Kritische Übersicht der in den sogenannten Bogota-Collectionen (S. O. Colombia) vorkommenden Colibri-Arten. J. Orn. 35: 313—336.

Berlepsch, H. von. 1888. Notes on some Neotropical birds belonging to the United States National Museum. Proc. U. S. Nat. Mus. 11: 559—566.

Berlepsch, H. von. 1908. On the birds of Cayenne. Novit. Zool. 15: 261—324.

Binford, L. C. 1968. A preliminary survey of the avifauna of the Mexican state of Oaxaca. Ph. D. diss. Louisiana State University, Baton Rouge.

Binford, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. Orn. Monogr., No. 43.

Blake, E. R. 1962. Birds of the Sierra Macarena, eastern Colombia. Fieldiana (Zool.) 44: 69—112.

Boucard, A. 1891. Notes on rare species of Humming Birds and descriptions of several supposed new species in Boucard's Museum. Humming Bird 1: 17—18.

Boucard, A. 1892. A complete list up to date of the Humming birds found in Colombia, with descriptions of several supposed new species. Humming Bird 2: 73—87.

Boucard, A. 1895. Genera of Humming Birds. Humming Bird 5: 1—402.

Brisson, M. J. 1760. Ornithologia sive synopsis methodica ... Paris.

Brodkorb, P. 1943. Birds of the gulf lowlands of southern Mexico. Misc. Publ. Mus. Zool. Univ. Mich., No. 55.

Cabanis, J., & F. Heine. 1860. Museum Heineanum. Verzeichnis der ornithologischen Sammlung des Oberamtmanns Ferdinand Heine auf Gut St. Burchard vor Halberstadt., Volume 3. Halberstadt.

Capparella, A. P. 1987. Effects of riverine barriers on genetic differentiation of Amazonian forest undergrowth birds. Ph. D. diss. Louisiana State University, Baton Rouge.

Collar, N. J. 1987. Red data bird Hook-billed Hermit. World Birdwatch, 9/1, p. 5.

Connor, E. F. 1986. The role of Pleistocene forest refugia in the evolution and biogeography of tropical biotas. Tree 1: 165—168.

Cory, C. B. 1918. Catalogue of the birds of the Americas, Volume 2. Field Mus. Nat. Hist. Publ., No. 197.

Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159—187 in Johnston, R. F. (ed.). Current Ornithology, Volume 1. New York.

Davis, T. A. W. 1958. The displays and nests of three forest hummingbirds of British Guiana. Ibis 100: 31—39.

Dick, J. A., McGillivray, W. B., & D. J. Brooks. 1984. A list of birds and their weights from Saül, French Guiana. Wilson Bull. 96: 347—365.

Dickerman, R. W. 1987. Type localities of birds described from Guatemala. Proc. West. Found. Vert. Zool. 3: 51—107.

Eudes-Deslongchamps, E. 1881. Catalogue descriptif des Trochilidés ou Oiseaux-mouches aujourd'hui connus. Caen.

Fjeldså, J. 1985. Subspecies recognition in ornithology: history and the current rationale. Fauna norv. Ser. C, Cinclus 8: 57—63.

Friedmann, H., Griscom, L., & R. T. Moore. 1950. Distributional check-list of the birds of Mexico, Volume 1. Berkeley.

Gill, F. B., & J. A. Gerwin. 1989. Protein relationships among hermit hummingbirds. Proc. Acad. Nat. Sci. Philadelphia 141: 409— 421.

Gould, J. 1861. An introduction to the Trochilidae or family of Humming-birds. London.

Grantsau, R. 1988. Os beija-flores do Brasil. Rio de Janeiro.

Griscom, L. 1932a. The ornithology of the Caribbean coast of extreme eastern Panama. Bull. Mus. Comp. Zool. 72: 303—372.

Griscom, L. 1932b. The distribution of bird-life in Guatemala. A contribution to the study of the origin of Central American bird-life. Bull. Amer. Mus. Nat. Hist. 64: 1—439.

Gyldenstolpe, N. 1950. The ornithology of the Rio Purús region in western Brazil. Arkiv för Zool., 2nd ser. 2: 1—320.

Haffer, J. 1967. Speciation in Colombian forest birds west of the Andes. Amer. Mus. Novit., No. 2294.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165: 131—137.

Haffer, J. 1970. Art-Entstehung bei einigen Waldvögeln Amazoniens. J. Orn. 111: 285—331.

Haffer, J. 1974. Avian speciation in tropical South America. With a systematic survey of the Toucans (Rhamphastidae) and Jacamars (Galbulidae). Publ. Nuttall Orn. Club, No. 14.

Haffer, J. 1975. Avifauna of northwestern Colombia, South America. Bonn. zool. Monogr., No. 7.

Haffer, J. 1978. Distribution of Amazon forest birds. Bonn. zool. Beitr. 29: 38—78.

Haffer, J. 1982. General aspects of the refuge theory. Pp. 6—24 in Prance, G. T. (ed.)., Biological diversification in the tropics. New York.

Hartert, E. 1897a. Various notes on Humming-Birds. Ibis 7, 3rd ser., pp. 423—435.

Hartert, E. 1897b. Various notes on Humming-birds. Novit. Zool. 4: 529—533.

Hartert, E. 1900. Trochilidae. Das Tierreich, Volume 9. Berlin.

Hartert, E. 1922. Types of birds in the Tring museum. B. Types in the general collection. Novit. Zool. 24: 365—412.

Haverschmidt, F. 1968. Birds of Surinam. Edinburgh and London.

Hellmayr, C. E. 1906. Notes on a second collection of birds from the district of Pará, Brazil. Novit. Zool. 13: 353—385.

Hellmayr, C.E. 1907a. Phoethornis (sic) affinis ochraceiventris, subsp. n. Bull. Brit. Orn. Club 19: 54—55.

Hellmayr, C. E. 1907b. On a collection of birds made by Mr. W. Hoffmanns on the Rio Madeira, Brazil. Novit. Zool. 14: 343—412.

Hellmayr, C. E. 1911. Descriptions of two new races of Humming-birds. Bull. Brit. Orn. Club 27: 92—93.

Hellmayr, C. E. 1912. II. Vögel. Pp. 1—142 in Müller, L. (ed.). Zoologische Ergebnisse einer Reise in das Mündungsgebiet des Amazonas. Abh. Math. Physik. Cl. Kgl. Bayr. Akad. Wiss. 26.

Hinkelmann, C. 1988a. Taxonomie, geographische Variation und Biogeographie der Gattung Phaethornis (Aves, Trochilidae). Unpubl. Diss. Univ. Bonn.

Hinkelmann, C. 1988b. Comments on recently described new species of hermit hummingbirds. Bull. Brit. Orn. Club 108: 159—169.

Hinkelmann, C. 1989a. Notes on the taxonomy and geographic variation of Phaethornis bourcieri (Aves: Trochilidae) with the description of a new subspecies. Bonn. zool. Beitr. 40: 99—107.

Hinkelmann, C. 1989b. Anmerkungen zu „Phaethornis margarettae" und anderen nicht validen neu beschriebenen Kolibriarten. Trochilus 10: 64—70.

Hinkelmann, C. 1996. Evidence for natural hybridisation in hermit hummingbirds (Phaethornis spp.). Bull. Brit. Orn. Club 116: 5—14.

Howell, S. N. G., & S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford, New York, Tokyo.

Hueck, K., & P. Seibert. 1972. Vegetationskarte von Südamerika. Stuttgart.

Jouanin, C. 1950. Catalogue systématique des types des Trochilidés du Muséum National d'Histoire Naturelle de Paris. Bull. Mus. Nat. Hist. Nat., 2nd ser., 23, suppl. 2: 1—27.

Knapp, R. 1965. Die Vegetation von Nord- und Mittelamerika und der Hawaii-Inseln. Stuttgart.

Lack, D. 1973. The number of species of hummingbirds in the West Indies. Evolution 27: 326—337.

Lawrence, G. N. 1858. Descriptions of seven new species of Humming-Birds. Ann. Lyc. Nat. Hist. New York 6: 258—264.

Lawrence, G. N. 1866. Characters of seven new species of birds from Central and South America, with a note on *Thaumatias chionurus*, Gould. Ann. Lyc. Nat. Hist. New York 8: 344—350.

LSUMNS (unpubl. list). Lista preliminar de las aves del Parque Nacional "Prof. Noel Kempff Mercado", Santa Cruz, Bolivia. Louisiana State University, Museum of Natural Sciences.

Mayr, E. 1963. Animal species and evolution. Cambridge.

Mayr, E. 1969. Principles of systematic zoology. New York.

Mayr, E. 1982. The growth of biological thought. Diversity, evolution and inheritance. Cambridge.

Mayr, E., & F. Vuilleumier. 1983. New species of birds described from 1966 to 1975. J. Orn. 124: 217—232.

McKitrick, M. C., & R. M. Zink. 1988. Species concepts in ornithology. Condor 90: 1—14.

Mees, G. F. 1977. Zur Verbreitung von *Phaethornis malaris* (Nordmann) (Aves, Trochilidae). Zool. Meded. 52: 209—212.

Meyer de Schauensee, R. 1966. The species of birds of South America and their distribution. Narberth.

Meyer de Schauensee, R., & W. H. Phelps, Jr. 1978. A guide to the birds of Venezuela. Princeton.

Monroe, B. L., Jr. 1968. A distributional survey of the birds of Honduras. Orn. Monogr., No. 7.

Nicholson, E. M. 1931. Communal display in Humming-birds. Ibis 13.1: 74—83.

Nordmann, A. von. 1935. I. Vögel. *In* Erman, A. (ed.). Reise um die Erde durch Nord-Asien und die beiden Oceane in den Jahren 1828, 1829 und 1830. Naturhistorischer Atlas. Verzeichnis von Thieren und Pflanzen, welche auf einer Reise um die Erde gesammelt wurden. Berlin.

Novaes, F. C. Ornitologia do Território do Amapá. I. Publ. Avuls. Mus. Goeldi, No. 25.

Oberholser, H. C. 1902. Catalogue of a collection of hummingbirds from Ecuador and Colombia. Proc. U. S. Nat. Mus. 24: 309—342.

Paynter, R. A., Jr. 1957. Birds of Laguna Ocotal. Pp. 249—285 *in* Paynter, R. A. (ed.). Biological investigations in the Selva Lacandona, Chiapas, Mexico. Bull. Mus. Comp. Zool. 116.

Paynter, R. A., Jr. 1982. Ornithological gazetteer of Venezuela. Cambridge.

Paynter, R. A., Jr., & M. A. Traylor, Jr. 1977. Ornithological gazetteer of Ecuador. Cambridge.

Paynter, R. A., Jr., & M. A. Traylor, Jr. 1981. Ornithological gazetteer of Colombia. Cambridge.

Paynter, R. A., Jr., Traylor, M. A., Jr., & B. Winter. 1975. Ornithological gazetteer of Bolivia. Cambridge.

Pelzeln, A. von. 1871. Zur Ornithologie Brasiliens. Resultate von Johann Natterers Reisen in den Jahren 1817 bis 1835. Wien.

Penard, F. P., & A. P. Penard. 1910. De vogels van Guyana (Suriname, Cayenne en Demerara), Volume 2. Paramaribo.

Peters, J. L. 1929. An ornithological survey in the Caribbean lowlands of Honduras. Bull. Mus. Comp. Zool. 69: 395—478.

Peters, J. L. 1945. Check-list of birds of the world, Volume 5. Cambridge.

Phelps, W. H., & W. H. Phelps, Jr. 1958. Lista de las aves de Venezuela con su distribución, Volume 2, pt. 1, No Passeriformes. Bol. Soc. Venez. Cienc. Nat. 19: 1—317.

Phillips, A. R. 1962. Notas sistemáticas sobre aves mexicanas. I. An. Inst. Biol. Mex. 32: 333—381.

Pinto, O. 1978. Novo catálogo das aves do Brasil. São Paulo.

Reichenbach, L. 1854. Aufzählung der Colibris oder Trochilideen in ihrer wahren natürlichen Verwandtschaft, nebst Schlüssel ihrer Synonymik. J. Orn. 1, Suppl.: 1—24.

Remsen, J. V., Jr., & T. A. Parker, III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15: 223—231.

Ridgway, R. 1910. Diagnoses of new forms of Micropodidae and Trochilidae. Proc. Biol. Soc. Wash. 23: 53—56.

Ruschi, A. 1972. Uma nova espécie de Beija-flor do E. E. Santo. *Phaethornis margarettae* — Ruschi. Bol. Mus. Biol. Prof. Mello-Leitão, Ser. Zool., No. 35.

Ruschi, A. 1973. Beija-flores. Santa Teresa.

Ruschi, A. 1986. Aves do Brasil, Volume 4: Beija-flores. Rio de Janeiro.

Russell, S. M. 1964. A distributional study of the birds of British Honduras. Orn. Monogr., No. 1.

Salo, J., Kalliola, R., Häkkinen, I., Niemelä, P., Puhakka, M., & P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322: 354—358.

Salvin, O. 1892. *In* Salvin, O., & E. Hartert (eds.). Catalogue of the Picariae in the collection of the British Museum. Catalogue of the birds in the British Museum, Volume 16. London.

Salvin, O., & D. G. Elliot. 1873. Notes on the Trochilidae. The genus *Phaethornis*. Ibis, 3rd Ser. 9: 1—14.

Schaldach, W. J. 1963. The avifauna of Colima and adjacent Jalisco, Mexico. Proc. West. Found. Vert. Zool. 1: 1—100.

Schuchmann, K.-L. 1980. Ökologie und Evolution der Trochilidenfauna auf den ozeanischen Inseln der Karibischen See. Bonn. zool. Beitr. 31: 289—309.

Scobel, A. 1912. Andrees Allgemeiner Handatlas. 5th ed. Bielefeld and Leipzig.

Seilern,· J. 1934. Ornithologische Miszellen. Ann. Naturhist. Mus. Wien 47: 33—41.

Sick, H. 1967. Rios e enchentes na Amazônia como obstáculo para a avifauna. In Lent, H. (ed.). Atas do simpósio sôbre a biota amazônic, Volume 5 (Zool.). Rio de Janeiro.

Sick, H. 1985. Ornitologia brasileira. Uma introdução, Volume 1. Brasilia.

Simon, E. 1897. Catalogue des espèces actuellement connues de la famille des Trochilidae. Paris.

Simon, ·E. 1921. Histoire naturelle des Trochilidae (Synopsis et catalogue). Paris.

Skutch, A. F. 1964. Life histories of hermit hummingbirds. Auk 81: 5—25.

Slud, P. 1964. The birds of Costa Rica. Distribution and ecology. Bull. Amer. Mus. Nat. Hist. 128: 1—430.

Snethlage, E. 1913. Über die Verbreitung der Vogelarten in Unteramazonien. J. Orn. 61: 469—539.

Snow, B. K. 1973. The behavior and ecology of hermit hummingbirds in the Kanaku Mountains, Guyana. Wilson Bull. 85: 163—177.

Snow, B. K. 1981. Relationships between hermit hummingbirds and their food plants in eastern Ecuador. Bull. Brit. Orn. Club 101: 387—396.

Snyder, D. E. 1966. The birds of Guyana (formerly British Guiana). Salem.

Stephens, L., & M. A. Traylor, Jr. 1983. Ornithological gazetteer of Peru. Cambridge.

Stephens, L., & M. A. Traylor, Jr. 1985. Ornithological gazetteer of the Guianas. Cambridge.

Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. Ecology 56: 285—301.

Stiles, F. G. 1980. The annual cycle in a tropical wet forest hummingbird community. Ibis 122: 322—343.

Stiles, F. G., & L. L. Wolf. 1979. Ecology and evolution of lek mating behavior in the Long-tailed Hermit Hummingbird. Orn. Monogr., No. 27.·

Teixeira, D. M., Nacinovic, J. B., & F. B. Pontual. 1987. Notes on some birds of northeastern Brazil (2). Bull. Brit. Orn. Club 107: 151—157.

Todd, W. E. C. 1937. New South American birds. Ann. Carn. Mus. 25: 243—255.

Todd, W. E. C. 1942. List of the hummingbirds in the collection of the Carnegie Museum. Ann. Carn. Mus. 29: 271—370.

Vaurie, C. 1968. Taxonomy of the Cracidae (Aves). Bull. Amer. Mus. Nat. Hist. 138: 131—260.

Vuilleumier, F., & E. Mayr. 1987. New species of birds described from 1976 to 1980. J. Orn. 128: 137—150.

Wetmore, A. 1968. The birds of the Republic of Panama, Volume 2. Columbidae (Pigeons) to Picidae (Woodpeckers). Smithson. Misc. Coll. 150, 2.

Wiedenfeld, D. A., Schulenberg, T. S., & M. B. Robbins. 1985. Birds of a tropical deciduous forest in extreme northwestern Peru. Pp. 305—315 in Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, R. S., & F. G. Buckley (eds.). Neotropical ornithology. Orn. Monogr., No. 36: 305—315.

Willis, E. O. 1977. Lista preliminar das aves da parte noroeste e áreas vizinhas da Reserva Ducke, Amazonas, Brasil. Rev. brasil. Biol. 37: 585—601.

Young, M. A. 1971. Foraging for insects by a tropical hummingbird. Condor 73: 36—45.

Zimmer, J. T. 1950. Studies of Peruvian birds No. 55. The hummingbird genera Doryfera, Glaucis, Threnetes, and Phaethornis. Amer. Mus. Novit., No. 1449.

APPENDIX I

Museums, with their aconyms, providing specimens for this study

AMNH	American Museum of Natural History, New York
ANSP	The Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History), Tring
CMNH	Carnegie Museum of Natural History, Pittsburgh
DMNH	Delaware Museum of Natural History, Greenville
FMNH	Field Museum of Natural History, Chicago
IVIC	Instituto Vallecaucano de Investigaciones Científicas, Cali
LACM	Natural History Museum of Los Angeles County, Los Angeles
LSUMNS	Louisiana State University, Museum of Zoology, Baton Rouge
MBPML	Museu de Biologia "Prof. Mello-Leitão", Santa Teresa
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHB	Museum für Naturkunde der Humboldt-Universität zu Berlin
MNHN	Muséum National d'Histoire Naturelle, Paris
MZUSP	Museu de Zoologia da Universidade de São Paulo

NHMW	Naturhistorisches Museum Wien
NMFS	Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt/M.
PMNH	Peabody Museum of Natural History, Yale University, New Haven
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden
ROM	Royal Ontario Museum, Toronto
SMNS	Staatliches Museum für Naturkunde in Stuttgart
SMTD	Staatliches Museum für Tierkunde, Dresden
UCB	Museum of Vertebrate Zoology, University of California, Berkeley
ÜMB	Überseemuseum Bremen
UNCB	Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia Bogotá
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C.
WFLA	Western Foundation of Vertebrate Zoology, Los Angeles
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
ZMUC	Zoologisk Museum Copenhagen
ZMUH	Zoologisches Institut und Zoologisches Museum, Universität Hamburg
ZSM	Zoologische Staatssammlung, München

APPENDIX II

Taxonomy, type localities, distributions and characters of all taxa in the *Phaethornis superciliosus-malaris-longirostris* species group

Phaethornis longirostris
P. longirostris griseoventer
Phaethornis superciliosus griseoventer Phillips, 1962. Type specimen: no type specimen designated; a type series of 9 specimens is preserved in the DMNH. Type locality: "Arroyo de la Cordoncillera, al sur de Puerto Vallarta, Jalisco" (Mexico; Phillips 1962).
Characters: Smaller, underparts more greyish, under tail-coverts and midthroat streaking paler than in *P. l. mexicanus*. Larger than remaining subspecies. Bill curvature less pronounced than in *P. l. longirostris*. Rectrical margins pure white.
Distribution: W Mexico, states of Colima, Jalisco, and Nayarit (Fig. 4).

P. longirostris mexicanus
Phaethornis mexicanus Hartert, 1897. Type specimen: AMNH. Type locality: "Dos Arroyos in Chilpancingo" (Mexico; Hartert 1897a). Characters: Larger than other subspecies. Underparts darker and more brownish than in *P. l. griseoventer* and *P. l. baroni*; the remaining subspecies lack pure white rectrical margins.
Distribution: SW Mexico, states of Michoacán, Guerrero, and Oaxaca (Fig. 4).

P. longirostris longirostris
Ornismya longirostris DeLattre, 1843. Type specimen: "Location of type material unknown" (Dickerman 1987). Type location: "Guatimala" (Hartert 1897a).
Synonym: *Phaethornis longirostris veraecrucis* Ridgway, 1910 (Type specimen: USNM; type locality: "Buena Vista, Veracruz, southeastern Mexico", Ridgway 1910).

Characters: Smaller and more curved-billed than *P. l. griseoventer* and *P. l. mexicanus*. Birds of the northernmost populations tend to have large amounts of white in their rectrical margins while there is an increasing amount of ochraceous coloration from Guatemala southward. Throat on both sides of the midthroat streaking more uniform, less barred than in *P. l. cephalus* and *P. l. susurrus*.
Distribution: S Mexico, states of Veracruz, Oaxaca, Tabasco, and Chiapas; N Guatemala; Belize; NW Honduras (Fig. 4).

P. longirostris cephalus
Trochilus cephalus Bourcier and Mulsant, 1848. Type specimen: location unknown; there are no indications in either Eudes-Deslongchamps 1881 or Jouanin 1950. Type locality: "... 'l'Amerique centrale' = Rio San Juan, Nicaragua" (Bangs and Barbour 1922).
Synonyms: *Phaethornis cassinii* Lawrence, 1866 (Type specimen: USNM; type locality: "New Granada, Carthagena", Colombia, Lawrence 1866)
Phaethornis panamensis Boucard, 1892 (Type specimen: MNHN; type locality: "Panama and Veragua, Columbia", Boucard 1892).
Characters: Similar to *P. l. longirostris*, but larger amounts of ochraceous coloration in the rectrical margins (in particular SE of Costa Rica), less uniform, more barred throat, less distinct bill curvature and more ochraceous coloration of the underparts. Smaller than *P. l. susurrus*.
Distribution: E Honduras; Nicaragua; Costa Rica; Panama; NW Colombia, Depts. of Chocó, Antioquia, Bolívar, and Santander (Fig. 4). Recently, F. Gary Stiles became aware of Colombian specimens distributed S to Caldas (Stiles, in litt.).

146

P. longirostris susurrus
Phaethornis longirostris susurrus Bangs, 1901. Type specimen: MCZ. Type locality: "Chirua, Sierra Nevada de Santa Marta, Colombia" (Bangs 1901).
Characters: Almost completely ochraceous rectrical margins (feather tips and inner webs may be whitish). Larger than *P. l. cephalus*.
Distribution: Sierra Nevada de Santa Marta area, N Colombia; adjacent Venezuela, W Zulia (Fig. 4).

P. longirostris baroni
Phaethornis baroni Hartert, 1897. Type specimen: AMNH. Type locality: "Naranjal, near the Rio Pescado, in Western Ecuador" (Hartert 1897a). Characters: Barred appearance of the throat feathers on both sides of the midthroat streaking similar to *P. l. cephalus* and *P. l. susurrus*; different from these taxa by pure white rectrical margins. Smaller than *P. l. mexicanus* and *P. l. griseoventer*. More greyish underparts than *P. l. longirostris*.
Distribution: W Ecuador; adjacent NW Peru, Dept. of Tumbes (Fig. 4).

Phaethornis malaris
P. malaris malaris
Trochilus malaris Nordmann, 1835. Type specimen: before 1945 in MNHB, now obviously lost. Type locality: "No type locality = Cayenne" (French Guiana; Peters 1945).
Characters: Distinctly larger and with darker brownish underparts than all remaining subspecies. Only *P. m. insolitus* may closely approach the coloration characters which distinguish *malaris* from the other subspecies.
Distribution: Surinam; French Guiana; adjacent Brazil, territory of Amapá (Fig. 6).

P. malaris insolitus
Phaethornis malaris insolitus Zimmer, 1950. Type specimen: AMNH. Type locality: "Río Huaynia, junction with Río Casiquiare, right bank, (...), Venezuela" (Zimmer 1950).
Characters: Smaller than *P. m. malaris*, larger than *P. m. bolivianus* and (probably) *P. m. margarettae*. Distinctly more brownish underparts than *P. m. moorei* and *P. m. ochraceiventris*.
Distribution: E Colombia, intendencias of Vaupés and Guainia; adjacent Venezuela, territory of Amazonas; adjacent Brazil, state of Amazonas (Fig. 6).

P. malaris moorei
Phaethornis moorei Lawrence, 1858. Type specimen. AMNH. Type locality: "Ecuador" (Lawrence 1858), "Napo" (specimen's label).
Synonyms: *Trochilus consobrinus* Bourcier, MS; Reichenbach, 1854 (nomen nudum) (Type specimen: destroyed in 1944; Jouanin, in litt.)
Phaethornis superciliosa moorei var. nigella Simon, 1921

(Type specimen: private collection Simon-Berlioz, Paris; type locality: "Bogota", Colombia, Simon 1921)
Phaethornis malaris ucayalii Zimmer, 1950 (Type specimen: AMNH; type locality: "Lagarto, right bank of the upper Río Ucayali, Peru", Zimmer 1950).
Characters: Distinctly more greyish underparts than all other subspecies: *P. m. malaris* and *P. m. insolitus* have darker, more brownish underparts, *P. m. bolivianus*, *P. m. margarettae*, and *P. m. ochraceiventris* have distinctly more ochraceous-colored bellies.
Distribution: East-Andean Colombia, Depts. (and other political entities) of Meta, Caquetá, Putumayo, and Amazonas; E Ecuador; N Peru, north of rivers Marañon and Amazonas, probably in the lower Ucayali region (Fig. 6). Adjoining populations south of N Peru exhibit characters of *P. m. bolivianus* as well (Fig. 8).

P. malaris bolivianus
Phaethornis boliviana Gould, 1861. Type specimen: BMNH. Type locality: "Bolivia" (Gould 1861).
Synonyms: *Phaethornis superciliosus insignis* Todd, 1937 (Type specimen: CMNH; type locality: "Itaituba, Rio Tapajóz, Brazil", Todd 1937)
Phaethornis malaris ucayalii Zimmer, 1950 (Type specimen: AMNH; type locality: "Lagarto, right bank of the upper Río Ucayali, Peru", Zimmer 1950).
Characters: Smaller than *P. m. malaris*, *P. m. insolitus*, *P. m. ochraceiventris*, and *P. m. moorei*. Darkish brown throat and breast as well as ochraceous belly are additional characters to distinguish *bolivianus* from *ochraceiventris* and *moorei*. *P. m. margarettae* appears to be paler below and might have a distinct midthroat streaking in males as well.
Distribution: SE Peru, Depts. of Cuzco, Puno, and Madre de Dios; Bolivia, Depts. of La Paz, Beni, Cochabamba, Santa Cruz; Brazil, between lower rivers Madeira and Tapajós (Fig. 6). Populations north of Peruvian Depts. of Cuzco and Madre de Dios exhibit characters of *P. m. moorei* as well (Fig. 8).

P. malaris margarettae
Phaethornis margarettae Ruschi, 1972. Type specimen: MBPML. Type locality: "Rio Agua Preta, Fazenda Klabin, Município de Conceição da Barra, Estado do E. Santo, Brasil" (Ruschi 1972).
Synonym: *Phaethornis ochraceiventris camargoi* Grantsau, 1988 (Type specimen: MZUSP; type locality: "Agua Azul, Vicência, Pernambuco, Brasil", Grantsau 1988).
Characters: Very similar to *P. m. bolivianus*, but apparently somewhat paler below. Males may have distinct midthroat streakings, like females.
Distribution: Brazil, close to the Atlantic coast between the states of Pernambuco and Espirito Santo (Fig. 6).

147

P. malaris ochraceiventris

Phoethornis (sic) *affinis ochraceiventris* Hellmayr, 1907. Type spècimen: AMNH. Type locality: "Humaytha, on the left bank of the Rio Madeira, Brazil" (Hellmayr 1907a).

Characters: Differing from all remaining subspecies of *P. malaris* by the orange-ochraceous coloration on breast, belly, and under tail-coverts. Larger than *bolivianus* and *margarettae*.

Distribution: W Brazil, state of Amazonas, S of the Amazon river between the confluence of the rivers Marañon and Napo and the W bank of the lower Madeira (Fig. 6).

Phaethornis superciliosus

P. superciliosus superciliosus

Trochilus superciliosus Linnaeus, 1766. Type specimen: not existent; description is based on a bird named *"Polytmus cayanensis longicaudus"* and portrayed by Brisson (1760). Type locality: "Cayenne" (Peters 1945).

Synonyms: *Phaethornis fraterculus* Gould, 1861 (nom. nov.)

Phaethornis guianensis Boucard, 1891 (Type specimen: MNHN; type locality: "Demerara", Guyana, Boucard 1891)

Phaethornis superciliosa saturatior Simon, 1921 (Type specimen: private collection Simon-Berlioz, Paris; type locality: "Guyane française: Maroni, Vénézuela E.: bassin de l'Orenoque et de la Caura. — ? Brésil nord: sur le haut rio Branco", Simon 1921).

Characters: Like *P. s. muelleri,* *superciliosus* has white under tail-coverts' feathers with dark coloration along the rachis. Throat and breast lighter, more ochraceous, and bill more intensively curved than in *muelleri*.

Distribution: Venezuela, S and E of the Orinoco; N Brazil, N of the rivers Negro and Amazon; Guyana; Surinam; French Guiana (Fig. 9).

P. superciliosus muelleri

Phaethornis superciliosus muelleri Hellmayr, 1911. Type specimen: ZSM. Type locality: "North-eastern Brazil, State of Pará: San Antonio do Prata (...), Peixe-Boi (...), Ipitinga, on the R. Acará (...)" (Hellmayr 1911); "Peixe-Boi, Pará" (specimen's label).

Characters: Throat and breast on both sides of the midthroat streaking darker, more brownish, and bill distinctly less curved than in *P. s. superciliosus.*

Distribution: Brazil, state of Pará S of the Amazon between the lower Tapajós river and the Gurupí river as well as adjacent Maranhão (Fig. 9).