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

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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 Western 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 Western 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.

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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 distinguished 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 sub-species 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 syrmatorphus, 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 σ and ϕ are alike in coloration, sexing specimens proved only a minor problem. Recently collected skins from several institutions include gonad data on their labels. Besides, σ differ from ϕ 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 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

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**FIG. 1.** Linear character measurements taken for this study.
TABLE 1. Linear character measurements of *Phaeornis longirostris*, *P. malariis*, and *P. superciliosus*. For details of measuring see Fig. 1 and text. Specimens with obvious immature plumage or uncertain sex are excluded. Statistical tests Σ — Φ: Mann-Whitney-U test (above), t test (below).

(n = number value; P = probability; Si = significance: ++ = P < 0.01, + = P < 0.05, — = not significant).

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<td>superciliosus</td>
<td>♂</td>
<td>64 (59.48)</td>
<td>1.09</td>
<td>57</td>
<td>62</td>
<td>&lt;0.01++</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>42 (56.79)</td>
<td>1.01</td>
<td>55</td>
<td>58</td>
<td>0</td>
</tr>
</tbody>
</table>

Tail measurement used in this study (TL) [mm]

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Sex</th>
<th>mean (s. d.)</th>
<th>Min</th>
<th>Max</th>
<th>P</th>
<th>Si.</th>
</tr>
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<tbody>
<tr>
<td>griseoventer</td>
<td>♂</td>
<td>13 (56.08)</td>
<td>1.66</td>
<td>54</td>
<td>59</td>
<td>0.772—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>4 (56.25)</td>
<td>2.06</td>
<td>54</td>
<td>58</td>
<td>0.885—</td>
</tr>
<tr>
<td>mexicanus</td>
<td>♂</td>
<td>14 (57.93)</td>
<td>2.37</td>
<td>56</td>
<td>61</td>
<td>0.956—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>19 (57.08)</td>
<td>4.45</td>
<td>47</td>
<td>62</td>
<td>0.96—</td>
</tr>
<tr>
<td>longirostris</td>
<td>♂</td>
<td>81 (44.78)</td>
<td>2.42</td>
<td>40</td>
<td>57</td>
<td>0.199—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>45 (45.36)</td>
<td>2.81</td>
<td>38</td>
<td>52</td>
<td>0.255—</td>
</tr>
<tr>
<td>cephalus</td>
<td>♂</td>
<td>68 (42.16)</td>
<td>2.66</td>
<td>38</td>
<td>49</td>
<td>0.101—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>59 (42.86)</td>
<td>2.73</td>
<td>37</td>
<td>49</td>
<td>0.150—</td>
</tr>
<tr>
<td>susurrus</td>
<td>♂</td>
<td>45 (47.84)</td>
<td>2.15</td>
<td>44</td>
<td>53</td>
<td>0.425—</td>
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<tr>
<td></td>
<td>♀</td>
<td>7 (46.57)</td>
<td>3.36</td>
<td>41</td>
<td>50</td>
<td>0.364—</td>
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<tr>
<td>baroni</td>
<td>♂</td>
<td>20 (44.23)</td>
<td>2.53</td>
<td>41</td>
<td>49</td>
<td>0.298—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>10 (45.10)</td>
<td>2.08</td>
<td>41</td>
<td>48</td>
<td>0.324—</td>
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<tr>
<td>malaris</td>
<td>♂</td>
<td>32 (48.23)</td>
<td>2.66</td>
<td>42</td>
<td>52</td>
<td>0.010+</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>16 (51.13)</td>
<td>3.16</td>
<td>45</td>
<td>56</td>
<td>0.004++</td>
</tr>
<tr>
<td>insolitus</td>
<td>♂</td>
<td>10 (43.10)</td>
<td>1.79</td>
<td>40</td>
<td>46</td>
<td>1.000—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>4 (43.00)</td>
<td>2.94</td>
<td>41</td>
<td>46</td>
<td>0.953—</td>
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<td>moorei</td>
<td>♂</td>
<td>72 (40.28)</td>
<td>2.33</td>
<td>35</td>
<td>46</td>
<td>0.663—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>42 (40.52)</td>
<td>2.68</td>
<td>35</td>
<td>47</td>
<td>0.621—</td>
</tr>
<tr>
<td>Peruvian zone of character introgression</td>
<td>♂</td>
<td>41 (41.50)</td>
<td>2.07</td>
<td>38</td>
<td>46</td>
<td>0.341—</td>
</tr>
<tr>
<td>bolivianus</td>
<td>♂</td>
<td>37 (40.14)</td>
<td>2.56</td>
<td>36</td>
<td>46</td>
<td>&lt;0.01++</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>28 (42.25)</td>
<td>2.65</td>
<td>36</td>
<td>48</td>
<td>0.002++</td>
</tr>
<tr>
<td>margarettae</td>
<td>♂</td>
<td>1 (42)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>1 (46)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>ochraceiventris</td>
<td>♂</td>
<td>16 (42.25)</td>
<td>2.11</td>
<td>39</td>
<td>47</td>
<td>0.122—</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>9 (43.50)</td>
<td>1.62</td>
<td>41</td>
<td>46.5</td>
<td>0.113—</td>
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<tr>
<td>muelleri</td>
<td>♂</td>
<td>24 (41.58)</td>
<td>3.35</td>
<td>34</td>
<td>48</td>
<td>0.030+</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>24 (44.63)</td>
<td>3.19</td>
<td>37</td>
<td>51</td>
<td>0.002++</td>
</tr>
<tr>
<td>superciliosus</td>
<td>♂</td>
<td>60 (42.68)</td>
<td>2.21</td>
<td>37.5</td>
<td>47</td>
<td>&lt;0.01++</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>40 (44.20)</td>
<td>2.14</td>
<td>39</td>
<td>48</td>
<td>0.001++</td>
</tr>
</tbody>
</table>

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 Scheffé test with significance level fixed at $P<0.05$. A subsequent discriminant
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 phylogenetical species concept because the latter decreases the information value by “lumping of two categorial levels” (Fjeldsa 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. veraebrucus)
4. cephalus (incl. cassini, panamensis)
5. susurrus
6. baroni
7. malaris
8. insolitus
9. moorei (incl. consobrinus, var. nigella, ucaialii in part)
10. bolivianus (incl. insignis, ucaialii in part)
11. margarettae (incl. camargoi)
12. ochraceiventris
13. superciliosus (incl. fraterculus, guianensis, saturator)
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, malari, insolitits, 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, supercilius, 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 margaretiae; 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 malari and supercilius 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), malari 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 malari and supercilius to occur sympatrically. I will discuss this aspect later in more detail.

Synapomorphic characters as presented above link supercilius and muelleri on the one hand, and malari, insolitits, moorei, bolivianus, and ochraceiventris on the other hand, and I recommend the treatment as two species, Phaethornis superciliius and P. malari. 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 margaretiae as a subspecies of P. malari.

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). |

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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
FIG. 2. a) Bill lengths (BL) of $\sigma$; b) Bill lengths (BL) of $\varphi$; c) Wing lengths (WL) of $\sigma$; d) Wing lengths (WL) of $\varphi$. 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).
LONG-TAILED HERMIT HUMMINGBIRDS

male

female

N = 15 14 86 79 48 24 32 14 83 49 65 1 15 25 64

N = 4 19 48 74 7 10 16 5 54 45 69 1 10 30 42

wing length (WL) [mm]
the majority of specimens was grouped to the "correct" species: $\sigma = 69.5\ %$, $\varphi = 63.5\ %$. 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

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**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.

<table>
<thead>
<tr>
<th>Grouping to</th>
<th>longirostris</th>
<th>superciliosus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. longirostris</em></td>
<td>227 (66.1%)</td>
<td>46 (20.3%)</td>
</tr>
<tr>
<td><em>P. malaris</em></td>
<td>193 (15.0%)</td>
<td>129 (66.8%)</td>
</tr>
<tr>
<td><em>P. superciliosus</em></td>
<td>78 (6.4%)</td>
<td>6 (7.7%)</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. longirostris</em></td>
<td>133 (61.7%)</td>
<td>33 (24.8%)</td>
</tr>
<tr>
<td><em>P. malaris</em></td>
<td>127 (19.7%)</td>
<td>73 (57.5%)</td>
</tr>
<tr>
<td><em>P. superciliosus</em></td>
<td>58 (3.4%)</td>
<td>9 (15.5%)</td>
</tr>
</tbody>
</table>

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 ♀,
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), *insolitus*...
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;

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**FIG. 5.** Geographic variation of linear measurements in *Phaethornis longirostris longirostris*, *P. l. cepalus*, 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;
3. 59 km W Pucallpa — AMNH; 4. Hacienda Flor, Puerto Victoria (350 m) — ZFMK; 5. Lagarto (type locality of P. m. ucyalii 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: ♂: 6>3, 5, P<0.05; ♀: 6, 7>3, P<0.05).
TABLE 4. Significant differences in bill (BL) and wing lengths (WL) between various population 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* < 0.01; |
|     |♀ | 5, 6 > 7, *P* < 0.01; 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. 8. Approximate distributions of colorations typical for *Phaethornis malari* 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 agerelated; 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>
<thead>
<tr>
<th>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).</th>
</tr>
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<tr>
<td><strong>BL:</strong></td>
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<tr>
<td><strong>Q:</strong> 6 &gt; 3, P &lt; 0.05; 6 &gt; 7+8, P &lt; 0.01</td>
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<tr>
<td><strong>TL:</strong></td>
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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. anthophius*, 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*. 136
Biogeographical remarks. Phaethornis superciliosus/F. 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 griseovenust (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. ochraceovenus does not include any forest refuge.) In some cases, subspecies’ distributions are separated from
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 Paraíba (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. m. 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. Sávill & 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): *veraecruci5*, *longirostris*, *cephalus*, and *cassini5* (Griscom 1932a, Peters 1945, Zimmer 1950, Wetmore 1968). Their respective morphological differences and distribution limits were repeatedly discussed:

- *veraecruci5* — *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;

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 taxonomic 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 *R. superciliosus* or *R. malaris*. Several taxa were regarded as separate species, e.g., *R. m. moorei* (as “*Phaethornis consobrinus*” [Reichenbach, 1854, nomen nudum] by Gould 1861, Eudes-Deslongchamps 1881, and Boucard 1895) and *R. 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 monotypic *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 *R. malaris*. Recently, Grantzau (1988) separated the Brazilian taxa occurring S of the Amazon river as a distinct species, *P. ochraceiventris*, assigning to it *muelleri*, *insignis*, *camargoii*, *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, Grantzau (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 diagnostic 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 *margarretae* as the sister species of the Amazonian *superciliosus* (sensu Peters 1945). Recently, Grantsau (1988) separated birds from Pernambuco as “*Phaethornis ochraceiventris camargoi*”, considering these as geographically well-isolated from “*P. o. margarettae*”. However, he neither provided definite morphological characters nor due to individual variation nor did he discuss the probably uninterrupted distribution range of *margarretae* 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 subspecies of “*P. boliviana*” (Simon 1921, Hartert 1922), of *P. malaris* (Zimmer 1950), of *P. superciliosus* (Hellmayr 1912, Peters 1945, Pinto 1978), and a separate, monotypic species *P. ochraceiventris* (Hellmayr 1907b, Todd 1942, Gyldenstolpe 1950). Zimmer (1950) detected some morphological approaches to neighbouring “*insignis*” and “*ucayalii*” which he concluded to be “… intermediate between *P. m. moorei* … and *P. m. ochraceiventris* …”. Probably, *ochraceiventris* does not have regular contact with the taxa occupying the opposite banks of the rivers Amazon and Madeira. 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 populations within *Phaethornis superciliosus superciliosus* to separate additional subspecies, in particular, those of S Venezuela (e.g., Hartert 1900, Simon 1921, Zimmerman 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 forest destruction in Central and South America has devastated many localities treated as inhabited 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 represent a situation similar to those of many other tropical American superspecies distributed in both cis- and trans-Andean lowlands, e.g., *Pionopsitta caica* (6 species), *Pipra erythrocephala* (5 species), *P. serena* (6 species) (Haffer 1970), *Cotinga maynana* (6 species), *Psarocolius bifasciatus* (4 species), *Ramphastos dicolorus* (4 species) or *Seleidoderus maculirostris* (6 species) (Haffer 1974). Many taxa of the *Phaethornis superciliosus-malaris-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 sympathy which is probably supported by significant differences in body mass and bill size. There are 3 biological species united in the Long-tailed Hermit hummingbird species group: *P. malaris*, *P. superciliosus* and *P. longirostris*. Two taxa, *P. m. ochraceiventris* 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. superciliosus-malaris-longirostris* species group based on non-morphological methods that treat a number of taxa. Based on electrophoretic analyses of enzymes, Capparella (1987) investigated the genetic differentiation of Long-tailed Hermit hummingbirds from opposite river banks in Amazonian Peru and concluded that “*Phaethornis superciliosus moorei*” (N of the Amazon) and “*Phaethornis superciliosus ucayalii*” (= *P. malaris ochraceiventris*; 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 (R. 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 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, variation in Central American Long-tailed Hermit hummingbirds is highest in the (NW) and in the (SE) 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 beauharnaesi) 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., Ortilis 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 R 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; Xingu, Tocantins: muelleri; Marañon, Napo: moorei), although other rivers (Amazon, Negro, Madeira, Tapajós) delimit the range of taxa.

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APPENDIX I

Museums, with their acronyms, 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
FNMH Field Museum of Natural History, Chicago
IVIC Instituto Valdecaucano 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
MZUSB Museu de Zoologia da Universidade de São Paulo

LONGTAILED HERMIT HUMMINGBIRDS
APPENDIX II

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

**Phaethomis longirostris**

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 *R. I. mexicanus*. Larger than remaining subspecies. Bill curvature less pronounced than in *R. I. longirostris*.  
Rectrical margins pure white.  
Distribution: W Mexico, states of Colima, Jalisco, and Nayarit (Fig. 4).

**Phaethomis superciliosus**

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 *R. I. mexicanus*. Larger than remaining subspecies. Bill curvature less pronounced than in *R. I. longirostris*.  
Rectrical margins pure white.  
Distribution: W Mexico, states of Colima, Jalisco, and Nayarit (Fig. 4).

**Phaethomis mexicanus**

*Phaethomis 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 Colima, Jalisco, and Oaxaca (Fig. 4).

**Phaethomis cephalus**

*Phaethomis 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. I. 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. I. 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.).
Phaethornis longirostris susurrus

Phaethornis longirostris susurrus Bangs, 1901. Type specimen: MCZ. Type locality: "Chiruca, 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. I. cephalus.

Distribution: Sierra Nevada de Santa Marta area, N Colombia; adjacent Venezuela, W Zulia (Fig. 4).

Phaethornis baroni

Phaethornis baroni Hartert, 1897. Type specimen: AMNH. Type locality: "Naranjal, near the Rio Pesca-do, in Western Ecuador" (Hartert 1897a).

Characters: Barred appearance of the throat feathers on both sides of the midthroat streaking similar to P. I. cephalus and P. I. susurrus; different from these taxa by pure white rectrical margins. Smaller than P. I. mexicanus and P. I. griseoven-tris. More greyish underparts than P. I. longirostris.

Distribution: W Ecuador; adjacent NW Peru, Dept. of Tumbes (Fig. 4).

Phaethornis malaris

P. malaris malaris

Phaethornis malaris 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).

Phaethornis malaris

Phaethornis malaris insolitus Zimmer, 1950. Type specimen: AMNH. Type locality: "Río Huayna, 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).

Phaethornis malaris

Phaethornis malaris moorei Lawrence, 1858. Type specimen. AMNH. Type locality: "Ecuador" (Lawrence 1858), "Napo" (specimen's label).

Synonyms: Trochilus consobrinus Bourcier, MS; Reichenschach, 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 uacayalii 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).

Phaethornis malaris boliviana Gould, 1861. Type specimen: BMNH. Type locality: "Bolivia" (Gould 1861).

Synonyms: Phaethornis superciliosus insignis Todd, 1937 (Type specimen: CMNH; type locality: "Itaituba, Rio Tapaj6z, Brazil", Todd 1937)


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 boliviana 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).

Phaethornis malaris


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 Espírito Santo (Fig. 6).

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

Phaethornis superciliosus

Phoethornis (sic) affinis ochraceiventris Hellmayr, 1907. Type specimen: 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 Marañón and Napo and the W bank of the lower Madeira (Fig. 6).

Phaeothornis 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: Phaeothornis fraterculus Gould, 1861 (nom. nov.)

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