

Notes on the taxonomy and geographic variation of *Phaethornis bourcieri* (Aves: Trochilidae) with the description of a new subspecies

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Abstract. *Phaethornis bourcieri* in the past has been treated as a polytypic species with two generally accepted subspecies, *bourcieri* and *whitelyi*. Their respective distributions have been a matter of intensive discussion. Examination of study skins from virtually all parts of the species' range revealed that no continuous, geographically-based differences exist in either colouration or measurements to support the validity of *whitelyi*. However, a slight, probably clinal decrease of the measurements is recognizable from E to W. Size differences are striking between the poorly-known populations from the E bank of the lower Rio Tapajós, Brazil, and the remaining populations. Thus, the isolated, S Amazonian, birds are separated as a new subspecies, *P. b. major*.

Key words. *Phaethornis bourcieri*, taxonomy, geographical variation, Trochilidae, new subspecies.

Introduction

Phaethornis bourcieri is a member of the hermit hummingbird subfamily (Phaethornithinae) inhabiting tropical rain forests between E Ecuador and Amapá, Brazil. Mainly confined to lowland sites north of the Amazon river, *P. bourcieri* occurs in terra firme forest up to 1600 m in the S Venezuelan Pantepui region (Meyer de Schauensee & Phelps 1978). Males and females do not differ in colouration, but males proved to have slightly larger bills and wings (Table 1). However, there seems to exist no difference in body masses between the sexes.

Relationships within the genus

Based on its straight bill, *Phaethornis bourcieri* was considered to belong to the "Ametrornis" group (Weske & Terborgh 1977). Reichenbach (1854) had introduced the name *Ametrornis* to accentuate the supposed close relationship with *P. philippii*, the only other straight-billed *Phaethornis* known at that time. The placement of *bourcieri* and *philippii* in a separate genus *Ametrornis* was followed by some authors, e. g., Cabanis & Heine 1860, Boucard 1895, and Simon 1921, whereas others (e. g. Salvin & Elliot 1873, Hartert 1900, Peters 1945) still regarded both as very closely related within *Phaethornis*. Based on morphological characters, however, *P. philippii* appears to be most closely related to the recently described, straight-billed *P. koepckeae* (Weske & Terborgh 1977). These latter species are the sister group of *P. syrmatophorus*. Apart from the strongly curved bill there are virtually no major differences between *P. syrmatophorus columbianus* and *P. koepckeae*. Thus, the existence of a straight bill in both *bourcieri* and *philippii/koepckeae* appears to be due to convergence. Based on morphology, *P. bourcieri*, however, is either the sister group

to the monophyletic *P. superciliosus/malaris/longirostris* species group (these four species, in turn, represent the sister group to the *P. syrmatophorus/koepckeae/philippii* species group) or the sister group to all six species mentioned above. Because synapomorphic morphological characters within the possible systematic entity of *P. superciliosus/malaris/longirostris* and *P. bourcierii* are lacking, the position of this latter species cannot be determined with certainty (Hinkelmann 1988).

Material used for this investigation

A total of 149 museum specimens were examined, representing all major regions of the species' range. The study skins were kindly provided by the authorities of the following institutions (museum acronyms and number of specimens investigated):

American Museum of Natural History, New York, USA (AMNH; 42); Field Museum of Natural History, Chicago, USA (FMNH; 32); Louisiana State University Museum of Zoology, Baton Rouge, USA (LSUMZ; 25); National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA (USNM; 12); Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (RMNH; 8); Carnegie Museum of Natural History, Pittsburgh, USA (CMNH; 8); Delaware Museum of Natural History, Greenville, USA (DMNH; 4); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ; 4); The Academy of Natural Sciences of Philadelphia, USA (ANSP; 3); Naturhistorisches Museum Wien, Austria (NHMW; 3); Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt/Main, West Germany (NMFS; 2); Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia (UNCB; 2); Peabody Museum of Natural History, New Haven, USA (PMNH; 1); Übersee-Museum Bremen, West Germany (ÜMB; 1); Museum of Zoology, University of Michigan, Ann Arbor, USA (UMMZ; 1); Zoologische Staatssammlung, München, West Germany (ZSM; 1).

Collecting localities of the specimens examined (for details or coordinates see gazetteers listed below):

Colombia (Paynter & Traylor 1981): Araracuara (0028 S, 7213 W; UNCB), Florencia (AMNH), Guamués (FMNH), Cerro de Mitú (= Las Guacamayas; FMNH), Morelia (AMNH, ANSP);

Ecuador (Paynter & Traylor 1977): Andoas (USNM), Avila (UMMZ, CMNH), Lago Agrio to Baeza (DMNH, PMNH), Limóncocha (MCZ, LSUMZ), Méndez (NHMW), Montalvo (ÜMB), Río Pucuno (MCZ), San José abajo (AMNH), Río Suno (AMNH);

Peru (Stephens & Traylor 1983): Apayacu (AMNH), Boca Río Curaray (AMNH), Calientillo, Contamana (FMNH), Huampami (LSUMZ), 157 km NNE Iquitos (LSUMZ), Río Kagka (LSUMZ), Libertad (LSUMZ), Maynas (NHMW), Quebrada Orán (5 km N Río Amazonas, 85 km NE Iquitos; LSUMZ), Puerto Galilea (FMNH), Puerto Indiana (AMNH), Urakusa (LSUMZ), Río Yanuyacu (LSUMZ);

Venezuela (Paynter 1982): Arabopó (AMNH), Brazo Casiquiare (AMNH), Chapazón (USNM), Chimantá-tepui (FMNH), Cerro Duida (AMNH), Cerro de La Neblina (AMNH, FMNH), Boca Río Ocamo (AMNH), San Carlos de Río Negro (FMNH), Cerro Urutani (AMNH), Cerro Yapacana (LSUMZ);

Brazil (Friedmann 1948, Haffer 1974, Novaes 1974): Rio Amapari (USNM), Rio Cauabury (USNM), Caxiricatuba (MCZ), Manacapuru (CMNH), Marabitanas (NHMW), Porto Platón (USNM), Salto do Huá (USNM), Serra do Navio (USNM), Tatú (AMNH), Tonantins (CMNH);

Guyana (Stephens & Traylor 1985): Courantyne River (FMNH), Kamakusa (AMNH, ZSM, NMFS), Merume Mountains (AMNH, FMNH), Minnehah Creek (AMNH);

Surinam (Stephens & Traylor 1985): Baruba Creek (RMNH), Kayser Gebergte Airstrip (FMNH), Lelydorp (MCZ), Lely Gebergte (RMNH), Neger Kreek (RMNH), Paloemeu (FMNH, RMNH), Raleigh Vallen (RMNH), Rama (RMNH), Zanderij (RMNH);

French Guiana (Stephens & Traylor 1985): Approuague (AMNH), "Cayenne" (AMNH, NMFS), Tamanoir (CMNH).

Table 1: Linear character measurements and body masses of *Phaethornis bourcieri bourcieri* (incl. "*whitelyi*") specimens.

	♂					♀					♂ - ♀	
	n	\bar{x}	s	Min	Max	n	\bar{x}	s	Min	Max	p	Si
BL [mm]	76	32.70	1.08	30	35	63	31.17	1.39	28.5	35	3.06-10	+
WL [mm]	78	58.28	1.25	56	61	66	54.64	1.60	50	59	0	+
TL* [mm]	71	35.20	3.27	29	42	57	36.01	2.68	31	42	0.16	—
BM** [g]	20	4.26	0.35	3.9	5.0	21	4.15	0.43	3.6	5.0	0.19	—

BL = bill length; WL = wing length; TL = tail length; BM = body mass.

* tail measurements indicate the shortest distance between the tips of the outermost (V) and central (I), i. e., longest feathers; in case of differences between left and right half, the left side was taken for calculation.

** body mass data were taken from freshly collected specimens as indicated on their labels.

n = number of measurements; \bar{x} = mean; s = standard deviation; Min = minimal value; Max = maximal value.

p = two-tailed probability; significance level (Si) fixed at $p < 0.001$ = +; n. s. = —.

Results

Type locality

Phaethornis bourcieri was described by Lesson (1832) as "*Trochilus bourcieri*" from "Brésil". Berlepsch (1908) regarded this origin not only as inaccurate but also as a mistake and replaced the type locality to Cayenne, French Guiana: ". . ."Brésil"-erre!-hab. substit. Cayenne." This statement obviously was overseen by Griscom & Greenway (1941) who restricted the type locality to the Rio Tapajós, and later by Friedmann (1948) who proposed Caxiricatuba, Rio Tapajós as a more exact type locality, as well as by Peters (1945) who indicated "Brazil". As will be shown below, all populations occurring north of the Amazon and in the E Andean lowlands exhibit neither geographically based variation of the colouration nor any major size variation and are thus treated as a single subspecies. Due to Berlepsch's (1908) restriction of the type locality, these are to be designated as *P. bourcieri bourcieri*.

Taxonomy

Unfortunately, Lesson (1832) described the species as bearing a slightly curved ("peu recourbé") bill which is also recognizable on his colour plate (Pl. 18). Consequently, Pelzeln (1871) regarded a similar, although slightly larger bird with an entirely straight bill collected by J. Natterer at Marabitanas, Rio Negro, Brazil, as a distinct species and named it *Ametrornis abnormis* (based on field notes of Natterer, Reichenbach [1854] had already used this name as a nomen nudum). Salvin & Elliot (1873), Salvin (1892), and Hartert (1900) later confirmed the identity of *abnormis* as a synonym of *bourcieri*.

Until present, *P. bourcieri* was considered to be separable in two subspecies, their ranges being a topic of numerous discussions. These started with the description of *Phaethornis whitelyi* from Guyana (formerly British Guiana) by Boucard (1891). As stated by the author, the new species differs from *P. bourcieri* in the dorsal colouration as well as in having rufous grey instead of white underparts. Recognizing that in *P. bourcieri* the colouration of the back is indeed highly variable and that the underparts are never white, Boucard (1895) himself considered *whitelyi* a "darker

variety" and thus a synonym of *bourcieri* which was confirmed by Hartert (1900) and Simon (1921). Chapman (1926) compared a small series of 12 birds from Ecuador with specimens from Guyana and concluded that the Ecuadorian birds are paler and less uniform below than those from Guyana. Stimulated by this note of an apparently geographic difference, Griscom & Greenway (1941) examined 22 specimens from various parts of the species' range and finally accepted the subspecies *P. b. bourcieri* (Rio Tapajós, Peru, Ecuador, Colombia, and possibly the upper Rio Negro, Brazil) and *P. b. whitelyi* (British Guiana, Surinam, S Venezuela). *P. b. whitelyi* differed from *P. b. bourcieri* "in being much less white and grey below, the underparts almost uniform pale mouse brown, paler on chin, throat and belly, instead of whitish and greyish with a faint brownish tinge on the sides". Specimens from SE Colombia (Caquetá) were regarded as intermediate (Griscom & Greenway 1941). Peters (1945) listed two valid subspecies: *P. b. bourcieri*, distributed in E Ecuador, adjacent Peru, and in the Amazonian lowlands of Brazil towards the Rio Tapajós, and *P. b. whitelyi* from SE Colombia, S Venezuela, the Guyanas, and probably from the upper Rio Negro without considering the priority of *abnormis* Pelzeln. Although later examinations of morphological characters within the species yielded different results with respect to the subspecies' distributions, Peters' (1945) point of view was generally accepted until today (e. g., Mayr & Phelps 1967, Pinto 1978, Grantsau 1988).

Investigating the avifauna of S. Venezuela and adjacent Brazil, Friedmann (1948) was not able to assign *P. bourcieri* from that area to either *bourcieri* or *whitelyi* without doubt. If *whitelyi* is to be regarded as a valid subspecies, he suggested to define its range according to Peters (1945). He, however, also disregarded the priority of *abnormis* (see above). Zimmer (1950) accentuated that the specimen collected by Natterer at the upper Rio Negro (*Ametrornis abnormis* Pelzeln, 1871) has greater affinities with *bourcieri* than with *whitelyi*. Furthermore, he found no differences between specimens from Ecuador and Peru on the one hand and those from S Venezuela and adjacent Brazil on the other hand. Thus, he concluded that if *whitelyi* is a valid subspecies that its range is to be confined exclusively to the Guyanas. A specimen from SE Colombia, however, "shows a close approach to *whitelyi*, but others from the same locality (La Morelia) do not" (Zimmer 1950). Dickerman & Phelps (1982) regarded *P. b. whitelyi* as confined to the eastern Pantepui region (SE Venezuela and adjacent Guyana) without mentioning specimens from Surinam or French Guiana. Birds from the Cerro Urutaní (along the SE Venezuelan border with Brazil), however, differ "in having well-marked paler midthroat streakings, and greyer, less buffy underparts" representing the easternmost known specimens of the nominate race, *P. b. bourcieri* (Dickerman & Phelps 1982). In fact, birds from the lower Rio Tapajós (type locality suggested by Griscom & Greenway 1941, and Friedmann 1948) as well as specimens from Amapá, Brazil (USNM), are usually considered nominate *bourcieri* in contrast to Novaes (1974) who listed specimens from Amapá as *P. b. whitelyi*. Meyer de Schauensee & Phelps (1978) limited the range of *whitelyi* in Venezuela to N Amazonas and SE Bolívar considering the Cerro Duida populations as *bourcieri* which were explicitly referred to *whitelyi* by Peters (1945). Recently, Cracraft (1985) regarded *P. b. whitelyi* and *P. b. bourcieri* as endemic taxa of the "Gran Sabana Subcenter" and the "Duida Subcenter" of the "Pantepui Center", respectively; both areas are limited almost entirely to S and SE Venezuela.

Geographical variation

Examination of large numbers of specimens from virtually all parts of the species' range revealed that the differences in colouration are not associated with geographical distribution. Side-by-side occurrence of typical *bourcieri* colourations (greyer, less buffy underparts; more or less well-defined whitish midthroat streaking) as well as the *whitelyi* colourmorphs (buffier, less greyish underparts; a lighter midthroat area, not definable as a stripe, fades into the dark colouration of the underparts) (first reported by Zimmer 1950) is observable in various parts of the species' range, e. g. in SE Colombia, E Ecuador, NE Peru, S Venezuela, Surinam, and Amapá, Brazil. Thus, the separation of any subspecies based exclusively on colouration does not seem to be possible. On the other hand, it is difficult to determine if these morphological differences are based on age or individual variation. It is evident, however, that they are not sex-dependant.

Whereas there is no geographically-correlated colour variation in *P. bourcieri*, the species exhibits pronounced differences in some linear measurements. In order to discover possible geographical correlations, specimens were assigned to seven "population groups" (Fig. 1) which were tested against each other. The analysis showed a slight, probably clinal, decrease of mensural characters of populations from E to W (Table 2).

Unfortunately, no birds from the Manaus area (Willis 1977) were available for examination. However, the single specimen from Manacapuru (CMNH 98355) does not differ from NW Brazilian birds (population group 3). These localities represent the only collecting sites known from the ornithologically poorly investigated N Amazonian Brazil (unhatched area between the population groups 3, 4, 5, and 6; Fig. 1).

Although the scarcity of specimens examined ($n = 2 \sigma$) prevented statistical confirmation, the isolated S Amazonian populations from the E bank of the lower Tapajós in Brazil (population group 7) clearly exceed the variation of bill and wing measurements found in all remaining populations of the species (Fig. 1). When comparing the Tapajós specimens with larger series of conspecifics from other areas, their general larger size is obvious at first glance. To accentuate the size difference, the birds from the E bank of the lower Rio Tapajós are separated from the remaining populations as:

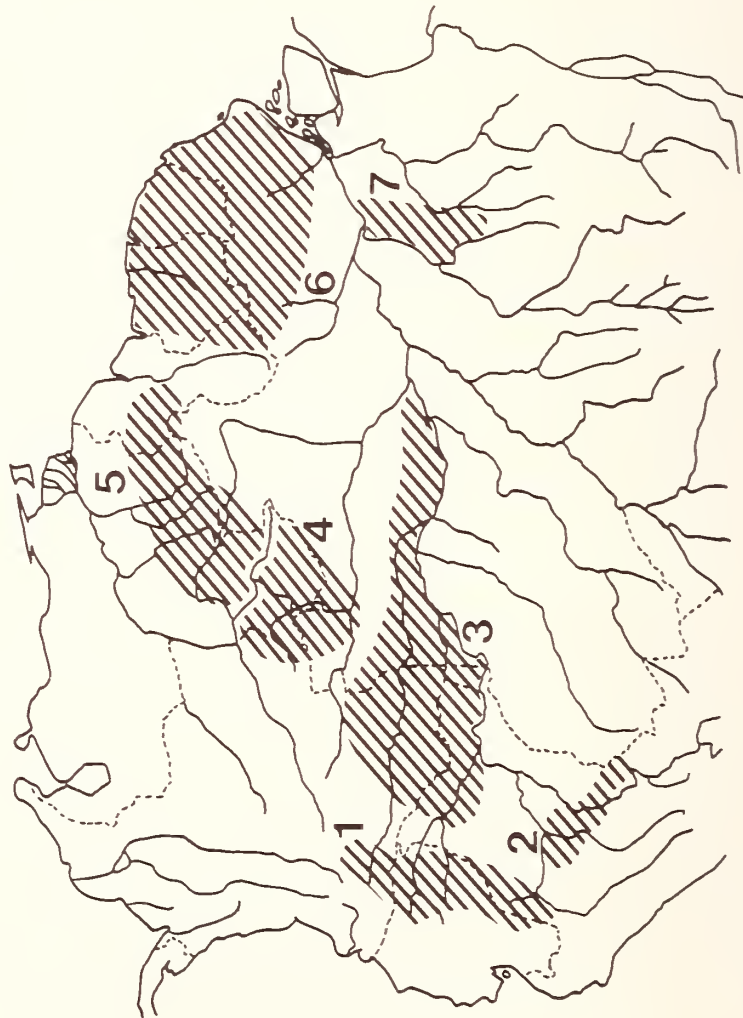
Phaethornis bourcieri major subsp. nov.

Type: MCZ 173642, σ , Caxiricatuba, Rio Tapajós, Brazil; leg. A. M. Olalla, August 4, 1932.

Diagnosis: Specimens of this subspecies exhibit "typical *bourcieri*" colouration, i. e. a brownish grey throat and breast as well as a more or less defined whitish chin and midthroat streaking. Males are distinctly larger than those of the remaining populations (Fig. 1). This is particularly evident in the measurements of bill and wing. Females could not be investigated. Probably due to the limited knowledge of the *major* populations at the moment, the "*whitelyi*" colouration cannot be confirmed in this subspecies.

Distribution: Collecting localities along the E bank of the lower Tapajós are Ca-

PG = population group
 BL = bill length [mm]
 WL = wing length [mm]
 TL = tail length* [mm]
 n = number of measurements
 \bar{x} = mean
 s = standard deviation
 Max = maximal value
 Min = minimal value
 * (for details of tail measuring see Table 1)



Subsp.	bourcierii							(n. ssp.)
	1	2	3	4	5	6	7	
PG								
♂	BL	n	26	14	10	10	7	2
		\bar{x}	32.87	32.5	32.11	32.3	32.79	33.15
		s	0.74	---	1.32	1.11	1.63	0.93
		Max	34.5	---	34	34.5	35	34
		Min	31.5	---	30	31	30	30.5
	WL	n	25	1	14	11	8	2
		\bar{x}	57.92	58	57.86	58.86	58.69	58.61
		s	1.11	---	1.34	1.25	1.03	1.38
		Max	60	---	60.5	61	60	61
		Min	56	---	56	57	57	56
	TL	n	22	1	13	11	7	2
		\bar{x}	32.06	36	34.04	37.09	36.57	36.97
		s	2.52	---	3.14	2.12	3.46	3.09
		Max	38	---	39	41	40	42
		Min	29	---	30	35	32	33
♀	BL	n	30	0	9	5	7	0
		\bar{x}	31.4	---	30.11	30.0	30.43	32.33
		s	1.12	---	0.96	1.06	1.13	1.51
		Max	34	---	31.5	31	32	35
		Min	30	---	29	28.5	29	29
	WL	n	29	1	9	7	8	0
		\bar{x}	53.91	54.5	54.56	55.43	55.19	55.67
		s	1.43	---	1.13	2.37	1.56	1.07
		Max	56	---	56	59	59	57
		Min	50	---	53	53	52	54
	TL	n	25	1	7	7	6	0
		\bar{x}	35.02	38	34.57	35.86	37.83	38.09
		s	1.92	---	1.51	2.54	2.93	3.30
		Max	39	---	36	38	42	42
		Min	31	---	33	31	34	33

Fig. 1: Geographical variation of linear character measurements in *Phaethornis bourcierii* based on museum specimens.

Table 2: Comparison of linear character measurements within 7 population groups of *Phaethornis bourcieri* (see Fig. 1).

population group	BL							WL							TL						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	♀							♀							♀						
1		--	++	+	-	+	--		--	-	-	+	++	--		--	-	-	+	+	--
2	--		--	--	--	--	--	--		--	--	--	--	--	--		--	--	--	--	--
3	-	--		-	-	++	--	-	--		-	-	+	--	-	--		-	-	+	--
4	-	--	-		-	++	--	+	--	-		-	-	--	++	--	+		-	-	--
5	-	--	-	-		+	--	-	--	-	-		-	--	+	--	-	-		-	--
6	-	--	+	+	-		--	-	--	-	-	-		--	++	--	-	-	-		--
7	--	--	--	--	--	--		--	--	--	--	--	--		--	--	--	--	--	--	
	♂							♂							♂						

Results are based on the non-parametric Mann-Whitney-U-test; comparisons were made with at least 4 measurements.

-- = n < 4, not tested; - = n. s.; + = p < 0.05; ++ = p < 0.01; BL = bill length; WL = wing length; TL = tail length (for details of tail measuring see Table 1).

xiricatuba (MCZ), Miritituba (CMNH), Tucunaré and Rio Jamauchim (= Rio Jamauxim; Ruschi 1961).

Griscom & Greenway (1941) were the first to report on the bird collected by A. M. Olalla and designated "Rio Tapajoz" as a restricted type locality for the nominate form instead of Lesson's (1832) "Brésil" without mentioning the remarkable size difference; Friedmann (1948) suggested Caxiricatuba as a precise locality.

Griscom & Greenway (1941) in addition accentuated that the species "has been completely overlooked in our area". This is confirmed by a specimen from Miritituba (CMNH 77539) which Todd (1942) reported as being "*Phaethornis muelleri*" (= *P. superciliosus*). Thus, the obviously unique specimen from the lower Rio Tapajós area known at that time induced Zimmer (1950) to question the correctness of the collecting locality, and to propose to treat the restricted type locality Aramanay (sic, confusion with Caxiricatuba) as doubtful. Finally, Ruschi (1961) reported on additional localities from the area that were confirmed by Eisenmann (in Meyer de Schauensee 1966). Haffer (1978, 1988) listed *P. bourcieri* among the "Northern Amazonian birds" that were able to cross the stream in the estuary region.

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Zusammenfassung

Untersuchungen zur Merkmalsvariation des Schattenkolibris *Phaethornis bourcieri* ergaben, daß eine geographisch determinierbare Variation der Gefiederfärbung nicht existiert und die bislang als *P. b. whitelyi* bezeichneten Populationen, deren Gesamtverbreitung sehr uneinheitlich behandelt wurde, keine subspezifische Trennung rechtfertigen. Demgegenüber ließ sich eine leichte, möglicherweise klinale Größenzunahme linearer Meßstrecken von Westen nach Osten feststellen, deren Ausmaß allerdings nicht die Abtrennung einer validen Unterart ermöglicht. Deutlich größer als Individuen aller übrigen Populationen sind jedoch

die südlich des Amazonas am Ostufer des Tapajós lebenden Vögel, worauf hier durch die Beschreibung als neue Subspecies, *P. b. major*, aufmerksam gemacht wird.

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