



HYBRID, SUBSPECIES, OR SPECIES? THE VALIDITY AND TAXONOMIC STATUS OF *PHAETHORNIS LONGUEMAREUS AETHOPYGA* ZIMMER, 1950 (TROCHILIDAE)

VÍTOR DE Q. PIACENTINI,^{1,3,4} ALEXANDRE ALEIXO,^{2,3} AND LUÍS F. SILVEIRA^{1,3}

¹Laboratório de Ornitologia, Instituto de Biociências e Museu de Zoologia da Universidade de São Paulo,
Rua do Matão, travessa 14, n. 101, 05508-090 São Paulo SP, Brazil; and

²Coordenação de Zoologia, Museu Paraense Emílio Goeldi, Caixa Postal 399, CEP 66040-170, Belém PA, Brazil

ABSTRACT.—*Phaethornis longuemareus aethopyga* was described by John T. Zimmer in 1950 and treated as a valid subspecies until it was proposed that the three known specimens were hybrids between *P. ruber* and *P. rufurumii amazonicus*. On the basis of some recently collected specimens, we reevaluated the validity of *P. l. aethopyga*. Despite showing some differences related to age and sex, all specimens agree in the general plumage pattern and are fully diagnosable when compared with any other taxon of the genus. The hypothesis of a hybrid origin becomes unsustainable when one notes that (1) *P. l. aethopyga* has characters that are unique and absent in the purported parental species, such as the white outer margins at the base of the rectrices; and (2) *P. l. aethopyga* occurs far from the distribution of one of the alleged parental species. Furthermore, field data show that *P. l. aethopyga* has attributes typical of a valid and independent taxon, such as lekking behavior. Therefore, given its overall diagnosis, *P. aethopyga* could at least be treated as a phylogenetic species. Yet its morphological and vocal distinctiveness with respect to other *Phaethornis* spp. in the “*Pygmornis* group” is greater than that observed between some species pairs traditionally regarded as separate biological species within the group, which supports its recognition as a species under the biological species concept. Received 13 July 2008, accepted 9 March 2009.

Key words: distribution, hybridization, Little Hermit, *Phaethornis aethopyga*, *P. longuemareus aethopyga*, Tapajós Hermit, taxonomy, Trochilidae.

Híbrido, subespécie ou espécie? Validade e status taxonômico de *Phaethornis longuemareus aethopyga* Zimmer, 1950 (Trochilidae)

RESUMO.—*Phaethornis longuemareus aethopyga* foi descrito por John Zimmer em 1950 e tratado como subespécie desde então. Nas últimas décadas sua validade foi questionada por alguns autores em favor da hipótese de que os três espécimes conhecidos e atribuídos ao táxon seriam híbridos entre *P. ruber* e *P. rufurumii amazonicus*. Coletas recentes de novos espécimes permitiram uma nova análise sobre a validade de *P. l. aethopyga*. Apesar de apresentarem diferenças de plumagem relacionadas a sexo e idade, todos os espécimes estudados concordam com o holótipo quanto ao padrão geral de plumagem e são plenamente diagnosticáveis quando comparados a qualquer outro táxon do gênero. A hipótese de origem híbrida não se sustenta quando se percebe que: 1) *P. l. aethopyga* apresenta caracteres únicos e que não estão presentes nas supostas espécies parentais, tal como a base branca do vexilo externo das retrizes; 2) *P. l. aethopyga* ocorre em áreas distantes da distribuição de um dos supostos táxons parentais. Além disso, dados obtidos em campo mostram que a população de *P. l. aethopyga* possui diversos atributos típicos de um táxon válido e independente, e.g. a reunião de machos em arenas de exibição. Não obstante configure uma clara espécie filogenética, a distinção de *P. l. aethopyga* em relação a qualquer outro *Phaethornis* do “grupo *Pygmornis*” é maior do que aquela observada entre alguns pares de espécies tidos como válidos dentro deste mesmo grupo, apoiando o tratamento como espécie plena mesmo sob o Conceito Biológico de Espécie.

IN 1950, WHILE working on the series of publications entitled *Studies on Peruvian Birds*, John T. Zimmer came across two distinct specimens of *Phaethornis* from Caxiricatuba, on the east bank of the Tapajós River in Brazil. On the basis of the male specimen, he described *Phaethornis longuemareus aethopyga*, which

he considered closely allied to the Black-throated Hermit (*P. atrimentalis*), by that time often considered a subspecies of the Little Hermit (*P. longuemareus*; Zimmer 1950). The existence of these two specimens supported the inclusion of the Little Hermit in the Brazilian avifauna (Pinto 1978, Grantsau 1988, Sick 1997).

³The authors are members of the Comitê Brasileiro de Registros Ornitológicos (www.cbro.org.br).

⁴E-mail: vitor.piacentini@gmail.com

Subsequently, Hinkelmann (1996) proposed a hybrid origin of *P. l. aethopyga*, considering the Reddish Hermit (*P. ruber ruber*) and the Streak-throated Hermit (*P. rupurumii amazonicus*) the most likely parental species; he examined the type material of *P. l. aethopyga* in addition to a female at the Carnegie Museum of Natural History collected at Santarém, Pará, and related each morphological character of *P. l. aethopyga* to either parental species. Curiously, Hinkelmann (1996:8) dismissed one of the main diagnostic characters of *P. l. aethopyga*—the white coloration at the base of the rectrices (Zimmer 1950)—as restricted to the male (the holotype) and interpreted it as “a (possibly individual) lack of pigments . . . missing in both probable parental species.” He considered the measurements of *P. l. aethopyga* intermediate between those of the supposed parental species (Hinkelmann 1996).

Here, we test the hypothesis of a hybrid origin of *P. l. aethopyga* and provide new evidence for its validity at the species level, regardless of the species concept adopted. We also review *P. l. aethopyga*'s distribution and present new data on its biology and habitat requirements.

METHODS

We examined 257 skins of the taxa related to the *Phaethornis longuemareus* species-group (*sensu* Peters 1945), and 66 and 211 skins of the two alleged parental species, Streak-throated and Reddish hermit, respectively. These specimens, which include some types, are housed in the following collections: American Museum of Natural History (AMNH), New York; Academy of Natural Sciences, Philadelphia (ANSP); Carnegie Museum of Natural History (CMNH), Pittsburgh, Pennsylvania; Coleção Ornitológica Marcelo Bagno (COMB), Universidade de Brasília, Brasília, Brazil; Colección Ornitológica Phelps (COP), Caracas, Venezuela; Delaware Museum of Natural History (DMNH), Wilmington; Field Museum of Natural History (FMNH), Chicago, Illinois; Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Museu de Biologia Mello Leitão (MBML), Santa Teresa, Brazil; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts; Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil; Museu Paraense Emílio Goeldi (MPEG), Belém, Brazil; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; and Coleção Rolf Grantsau (RG), São Paulo (see Appendix).

The following measurements were taken following Baldwin et al. (1931): length of bill to feathers on the side of maxilla, maximum length of flattened wing, and tail length. In some cases, we also measured “tail projection,” defined here as the distance between the tips of rectrix 1 (central) and rectrix 2 (subcentral).

We mapped the specimen records of *P. l. aethopyga* as well as our own sight records and tape-recordings with ARCVIEW, version 3.3. When geographic coordinates were not readily available from specimen labels, we consulted gazetteers (Paynter and Traylor 1991, Vanzolini 1992). Data on the biology of *P. l. aethopyga* were gathered mainly by one of us (A.A.) in 2005 and 2007 while conducting field work in the Tapajós center of endemism (*sensu* Silva et al. 2005).

RESULTS

Morphology and age-related plumage development.—We examined 18 skins of *Phaethornis* clearly assignable to the taxon diagnosed by Zimmer (1950) as *P. l. aethopyga*. To our knowledge, those are the totality of specimens of *P. l. aethopyga* housed in museum collections worldwide.

The plumage color pattern of *P. l. aethopyga* is very distinct from that of its alleged parental species, *P. ruber ruber* and *P. rupurumii amazonicus*. Some characters posited by Hinkelmann (1996) as inherited from one of the parental species should be reinterpreted. The throat of *P. l. aethopyga* is solid dark, rather than scaled as in *P. r. amazonicus*. The rufous underparts are much darker than in *P. ruber*. None of these characters can be interpreted as intermediate; thus, along with the white base of the rectrices, they are best treated as absent in the purported parental species.

Given its body size, tail shape, and overall appearance, *P. l. aethopyga* is readily linked to the *P. longuemareus* species-group (*sensu* Peters 1945); nonetheless, *P. l. aethopyga* possesses a unique combination of characters and is consistently distinct from any other taxon within that group and, therefore, is of uncertain affinities. Within the *P. longuemareus* species-group, two other taxa share the same pattern of predominantly rufous underparts with solid dark throat, as well as similar morphological measurements and, therefore, can be postulated as candidates for the closest relative of *P. l. aethopyga*: *P. atrimentalis* Lawrence, 1858 (as suggested by Zimmer 1950) and nominate *P. longuemareus* Lesson, 1832. However, despite its sparse coverage of taxa within the “Pyg-mornis” group (*sensu* Salvin 1892), a recent phylogeny (McGuire et al. 2007) showed with good statistical support that these two species are not closely related. Thus, in the absence of a robust phylogeny of *Phaethornis* with a dense taxon-sampling regime, and given the overall uncertainty regarding the phylogenetic position of most taxa within the *P. longuemareus* species-group (including *P. l. aethopyga*), morphological comparisons will contrast *P. l. aethopyga* with *P. atrimentalis* and *P. longuemareus*, following Zimmer's (1950) implicit hypothesis regarding the phylogenetic affinities of *P. l. aethopyga*.

As pointed out in the original description, *P. l. aethopyga* differs from *P. atrimentalis* (as well as from *P. l. longuemareus*) by its white chin, deep rufous under-tail coverts, and strongly rufescent rump and upper-tail coverts. Other characters of *P. l. aethopyga* that distinguish it from both *P. atrimentalis* and *P. l. longuemareus* are the reddish rachis of the rectrices (blackish in the other two species) and the rufous terminal margins of rectrices, which range in *P. atrimentalis* and in *P. l. longuemareus* from whitish in the central pair to pale buff or buffy ochraceous in the two outermost rectrices, respectively (Table 1). The strongly rufescent belly further distinguishes *P. l. aethopyga* from *P. l. longuemareus*. A distinctive plumage character of *P. l. aethopyga* is the white base of the outer margins of the rectrices (except those of the external pair); all skins examined show this character, which is unique in *Phaethornis* (Fig. 1).

Adult male *P. l. aethopyga* have a different tail shape and color than young males and females (Fig. 2). Adult males (MPEG 53833, MZUSP 78717, and MZUSP 81173) have a round tail with the rufous latero-terminal margin very reduced. On the other

TABLE 1. Summary of color differences on several plumage characters between *Phaethornis longuemareus aethopyga* and two purported closest relatives (*sensu* Peters 1945, Zimmer 1950).

Character	Taxon		
	<i>P. l. aethopyga</i>	<i>P. atrimentalis</i>	<i>P. l. longuemareus</i>
Chin	White	Blackish	Blackish
Belly	Strongly rufescent	Rufescent	Ochraceous
Dark pectoral band (on adult males only)	Absent	Present	Absent
Under-tail coverts	Deep rufous	Buff (females) or white (adult males)	Whitish
Rump and upper-tail coverts	Strongly rufescent	Rufous	Rufous
Terminal margin of rectrices	Rufous	Whitish to pale buff	Whitish to buffy ochraceous
Rachis of rectrices	Reddish	Dark	Dark

hand, young males (MPEG 59119, RG 10237) and females (CMNH 74518, MNRJ 33105) have a V-shaped tail with a wider rufous margin and a longer and whitish-tipped central pair of rectrices; the same applies to the type specimen. Also, young males may present some dorsal feathers with pale edges, which are most noticeable on the upper wing coverts. Other male specimens may have an intermediate tail shape between fully adult and young patterns (e.g., MPEG 59118, in which the fifth right side rectrix shows a narrow rufous terminal margin).

Another apparently age-related difference, at least among males, is the change in color on the (blackish) throat and (rufous) chest and belly. Young males (MPEG 59119 and 59120) have a more sharply limited blackish throat patch, whereas older males show a more gradual transition in colors, thus showing a slightly darker foreneck than young and female specimens. The holotype also shows a well-limited black throat (Fig. 2). Females usually have some rufous edging on the throat feathers, thus resulting in a much reduced dark patch (e.g., CMNH 74518) or in a somewhat diluted, not-so-solid dark throat (MNRJ 33105, AMNH 285951, MZUSP 81175; Fig. 2).

Measurements of *P. l. aethopyga* are similar to those of the taxa that look most like it (Table 2). Adult males have slightly shorter tails than young ones and females, as a result of tail shape.

Distribution.—All known specimens of *P. l. aethopyga* were collected south of the Amazon, on the right bank of the Teles Pires and Tapajós rivers and along some of their eastern-bank tributaries (Fig. 3 and Appendix). An apparently young male photographed by K. Aguiar on the left bank of the lower Xingu River is the easternmost record (photo available from the senior author by request). Therefore, *P. l. aethopyga* is strongly allopatric with respect to any taxon of the “*Pygmornis*” group except *P. ruber ruber*, with which it is sympatric.

Regarding the distribution of the two alleged parental species of *P. l. aethopyga* as suggested by Hinkelmann (1996), one (*P. rufipurpureus amazonicus*) occurs along the middle and lower reaches of the Negro, Amazon (east of Manaus), and lower Tapajós and Xingu rivers, always in association with riverine habitats (Fig. 3), whereas polytypic *P. ruber* occurs over most of South America east of the Andes, with its southern limit in Paraná State, Brazil.

Habitat.—Between 24 November and 1 December 2005, A.A. and colleagues netted and subsequently collected a single specimen of *P. l. aethopyga* in lightly disturbed upland (*terra firme*) forest near a small stream at Fazenda Jamanxin, Altamira (8°23'S, 55°22'W), where the species was uncommon compared with the other species of *Phaethornis* present (*P. ruber* and *P. bourcieri*). On 4 December 2005, a lek of *P. l. aethopyga* was found in heavily



FIG. 1. Dorsal view of the tails of some specimens of *Phaethornis longuemareus aethopyga*, showing the most distinguishing character of the taxon, the white base of the outer margins of the rectrices. From left to right: AMNH 285949 (holotype, [young] male), MPEG 59119 (young male), MPEG 53833 (adult male), and MNRJ 33105 (female).



FIG. 2. Ventral view of some specimens of *Phaethornis longuemareus aethopyga*, showing the differences in plumage pattern related to age and sex. From left to right: AMNH 285949 (holotype, [young] male), MPEG 59119 (young male), MPEG 53833 (adult male), and MNRJ 33105 (female).

disturbed *terra firme* forest ~20 km southwest of Novo Progresso (7°11'S, 55°29'W), where several individuals were tape-recorded and two specimens (MPEG 59119 and 59120) collected through 6 December. The lek included no fewer than five actively singing males, and activity was high during most of the day, with conspicuous noisy chases among individuals displaying and visiting the lek; time and logistical constraints prevented gathering more extensive information.

From 22 November to 5 December 2007, A.A. surveyed birds at Floresta Nacional de Altamira and Parque Nacional do Jamanxin, where *P. l. aethopyga* was found at only 4 of 18 localities sampled and was regarded as uncommon. At all those localities, only lone individuals of *P. l. aethopyga* were observed briefly calling and flying along or over nearly dry streams surrounded by lightly disturbed or undisturbed *terra firme* forest.

DISCUSSION

Age-related plumage development.—Most (and perhaps all) small *Phaethornis*, sometimes (e.g., Bonaparte 1854, Gould 1861, Salvin 1892) placed in the genus *Pygmornis*, show a clear distinction between fully adult male and young male and female plumages,

especially in the tail. The differences are well known in *P. idaliae* (Ruschi 1967, Grantsau 1988) but can also be seen in other taxa such as *P. r. ruber*, *P. r. episcopus*, *P. l. aethopyga*, and others (V. Q. Piacentini unpubl. data). Zimmer (1950) briefly discussed the differences between adult males and females in small *Phaethornis* and argued that the tail of the type specimen of *P. l. aethopyga* was closer to the female pattern than the male pattern of *P. atrimentalis*. Not surprisingly, he wondered whether the type was juvenile. Ruschi (1967) argued that young male *P. idaliae* would have round and narrowly margined tails (i.e., that sexual dimorphism would appear during immaturity), contrary to that pattern of dimorphism. The plate of *P. idaliae* in Grantsau (1988) followed Ruschi's (1967) view. On the other hand, Vielliard (1994) also discussed those differences in *P. idaliae* and contended that the dimorphic male is the adult rather than the juvenile. Therefore, all evidence gathered so far strongly suggests that the type specimen of *P. l. aethopyga* is an immature bird. Besides differences in tail shape, adult males of *P. l. aethopyga* are darker in general than young males and females, a pattern similar to that in *P. idaliae*.

Validity of the taxon.—The larger series of specimens now available for *P. l. aethopyga* allowed us to study the validity of this taxon more properly than would be possible with only the three

TABLE 2. Mean measurements (mm) of *Phaethornis longuemareus aethopyga* and two purported closest relatives (*sensu* Peters 1945, Zimmer 1950), with maximum and minimum values in parentheses. Number of individuals measured is given in parentheses after sex and age. Superscript letters indicate cases where it was impossible to measure all individuals.

Taxon	Sex and age	Character			
		Bill	Wing	Tail	Tail projection
<i>P. l. aethopyga</i>	Adult males (7)	24.9 (24–27)	41 (39–44)	31.6 (30.5–32.5)	3.1 (2.5–4)
	Young males (5)	23.9 (23.5–24)	44 (41–47)	34.2 (32–35)	4.9 (3.5–5.5)
	Females (6)	23.5 (23–24.5)	42.3 (40–43)	33.5 ^a (32–35)	6.4 ^a (4.5–7)
<i>P. atrimentalis</i>	Adult males (16)	24.2 (22–26)	40.6 (37–45)	34.4 (31.5–36.5)	2.1 (1–3)
	Young males (10)	23.8 (22–25)	41.4 (39–45)	38.1 (35.5–42)	7.4 ^b (7–7.8)
	Females (18)	23.6 (22–25)	42.4 (40–46)	36.6 ^c (34–40.5)	7.8 ^d (5.5–11)
<i>P. l. longuemareus</i>	Adult males (17)	23.75 ^d (23–24.5)	42.9 (40–45)	36.6 (33.5–38)	5.3 (4–6.5)
	Young males (11)	24.4 ^b (22–27)	43.5 (42–45)	40.9 ^e (39–42.5)	9.75 ^e (7.5–12.5)
	Females (12)	24.1 ^b (23–25.5)	43.6 (40.5–46)	39.2 (37–41)	9.8 ^f (7.5–11)

^an = 4, ^bn = 9, ^cn = 17, ^dn = 16, ^en = 10, ^fn = 8.

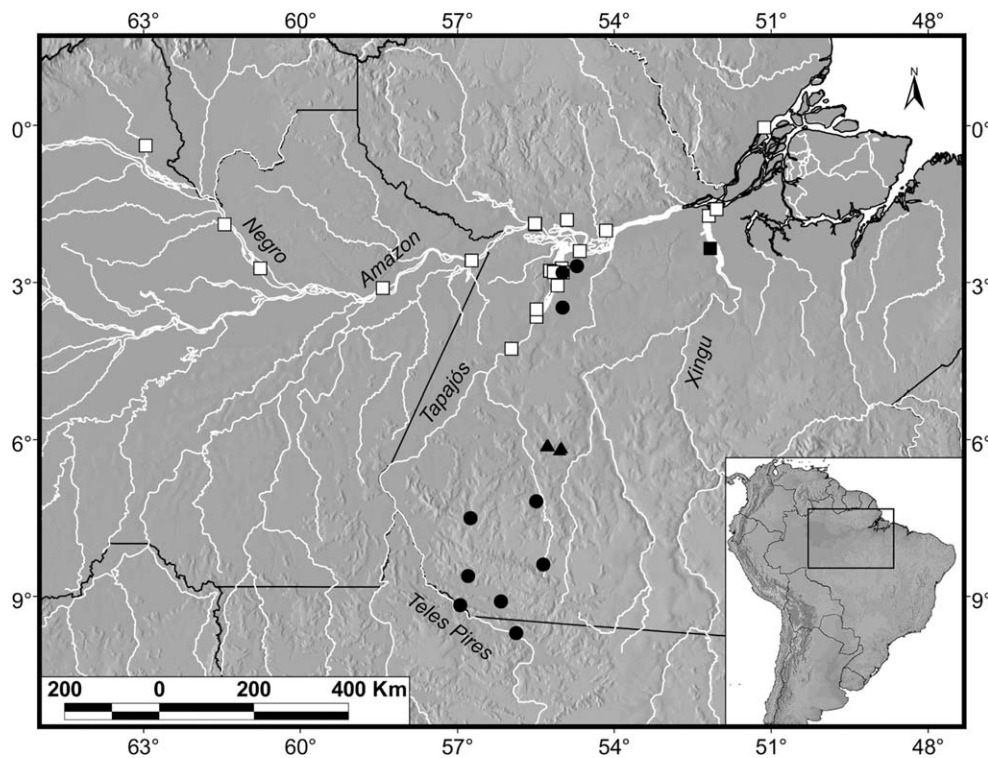


FIG. 3. Collecting localities of specimens of *Phaethornis rupurumii amazonicus* (white squares) and *P. longuemareus aethopyga* (black circles) analyzed. Black square indicates a record based on a photograph, and black triangles indicate sight records, of *P. l. aethopyga*. For more detailed locality data, see Appendix.

specimens studied by Hinkelmann (1996). The first evidence against a hybrid origin for *P. l. aethopyga* is its diagnostic plumage characters, which remain constant over a wide geographic area, as indicated by the larger series of specimens studied. Our analysis failed to find any intermediate morphological characters between those of *P. ruber ruber* and *P. rupurumii amazonicus* or a color pattern expected as a result of “mosaic expression of parental autapomorphies” involving the latter two species (Hinkelmann 1996:5). The homogeneity in plumage color found in the specimens (of the same age and sex) studied, which were collected over a wide area, also points against a hybrid origin of *P. l. aethopyga*. It is well known that hybrid specimens between the same parental species are likely to show heterogeneity in plumage, not constancy. Furthermore, *contra* Hinkelmann (1996), *P. l. aethopyga* has characters that are absent in its postulated parental species, particularly the white base of the rectrices. The only exception is a female (AMNH 285951), in which the light color at the base of the rectrices is gray instead of pure white, as noted by Zimmer (1950). Measurements of *P. l. aethopyga* are intermediate between those of *P. ruber* and *P. rupurumii amazonicus*, but this alone provides no evidence of a hybrid origin.

A second line of evidence against the hybrid origin is that some localities where *P. l. aethopyga* is found are far from the range of one of the suggested parental species, *P. r. amazonicus*; *P. l. aethopyga* occurs as far south as Alta Floresta, Mato Grosso State, which is >600 km from the nearest locality where *P. r. amazonicus* has been recorded. The southern distributional limit of *P. l. aethopyga* reported herein is corroborated by the lack of records of this taxon west of the Teles Pires River. A. Lees (pers. comm.) spent ~440 days surveying birds in the Alta Floresta region and did not find *P. l. aethopyga* on the left bank of the Teles Pires or in the Serra dos Caiabis, 100 km south of Alta Floresta (Lees et al. 2008).

The third line of evidence against the hybrid origin is the existence of leks where male *P. l. aethopyga* congregate and display. In addition to the lek southwest of Novo Progresso in Pará, B. Carlos (pers. comm.) found one at the Cristalino Jungle Lodge, Alta Floresta (~280 km to the south). The existence of these leks conflicts with the hybrid hypothesis, because it is unlikely that different male hybrids would recognize each other as conspecifics and aggregate at lekking territories exclusive to hybrids birds, stable through time, and over a large area.

Although common in hummingbirds, hybridization among Phaethornithinae was unknown until Hinkelmann (1996) reported examples. The case of *P. l. aethopyga* raises the question of whether more of Hinkelmann’s (1996) proposed hybrids may prove to be valid taxa (especially “*P. l. imatacae*”; V. Q. Piacentini unpubl. data).

Taxonomic rank.—*Phaethornis l. aethopyga* presents several unambiguous diagnostic characters (Table 1) in addition to an allopatric distribution among the *P. longuemareus* species-group and, thus, is recognizable as a valid species under the phylogenetic species concept (or any other lineage species concept; de Queiroz 1998) or, minimally, as a subspecies under the biological species concept. Zimmer (1950) considered *P. l. aethopyga* close to *P. [longuemareus] atrimentalis*; therefore, if *P. l. aethopyga* is ranked as a subspecies and if *P. atrimentalis* is treated as a species separate from *P. longuemareus* (e.g., Schuchmann 1999, Remsen et al.

2008), one possibility would be to treat *P. l. aethopyga* as a subspecies of *P. atrimentalis*. However, using the comparative approach for ranking allopatric taxa under the biological species concept as outlined by Johnson et al. (1999), *P. l. aethopyga* shows the same degree of distinctiveness in plumage found between closely related biological species in the same genus, such as *P. atrimentalis* and *P. longuemareus*. Actually, *P. l. aethopyga* is even more distinct from *P. atrimentalis* or *P. longuemareus* than they are from each other. The distinctiveness of *P. l. aethopyga* among the “*Pygornis*” group in the genus *Phaethornis* parallels that of *P. idaliae*, the Atlantic Forest representative of the *P. longuemareus* species-group that has virtually always been ranked as a separate biological species. Therefore, we suggest that this taxon should be treated as

***Phaethornis aethopyga* Zimmer, 1950**

Tapajós Hermit

Rabo-branco-do-tapajós (Portuguese)

The suggested English name highlights the river basin and center of endemism (*sensu* Silva et al. 2005) to which the species seems restricted. Current evidence (Henriques et al. 2003, present study) suggests that *P. aethopyga* occurs only in *terra firme* forest with varying degrees of disturbance, especially along streams. Therefore, it could be tentatively regarded as a habitat specialist associated with streams of varying sizes bisecting *terra firme* forest. That some skilled observers surveying sites within the range of *P. aethopyga* missed this species (Pacheco and Olmos 2005) could indicate that it is patchily distributed.

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APPENDIX

SPECIMENS EXAMINED (FOR ABBREVIATIONS, SEE TEXT)

Phaethornis aethopyga ($n=18$)

Brazil: Pará: Altamira (MPEG: 1 ♂), Alto Cururu (MNRJ: 1 ♀), Caxiri-catuba (AMNH: 1 ♂ [type], 1 ♀), Floresta Nacional de Tapajós (MPEG: 1 ♂), Jacareacanga, right bank of Cururu River and right bank of São Benedito (MZUSP: 2 ♂♂), Jacareacanga, near the mouth of Apiacás River (MZUSP: 3 ♂♂, 3 ♀♀), Novo Progresso (MPEG: 2 ♂♂), Colônia do Mojuí, Santarém (CMNH: 1 ♀); Mato Grosso: Alta Floresta–Novo Mundo, Cristalino River (RG: 2 ♂♂).

P. longuemareus ($n=59$)

British Guyana: “Guyana” (FMNH: 1 ♀), Rockstone, Essequibo River (FMNH: 1 ♂).

French Guyana: Approuague (AMNH: 4 ♂♂, 3 ♀♀), Cayenne (AMNH: 2 ♂♂; CMNH: 2 ♂♂), Roche Marie (AMNH: 1 ♂).

Suriname: near Paramaribo (AMNH: 3 ♂♂, 1 ♂, 1 ♀, 1 unsexed; MCZ: 5 ♂♂, 2 ♀♀ [♂♂?], 2 unsexed), Kwata (AMNH: 1 ♂).

Trinidad and Tobago: Trinidad: Aripo (AMNH: 1 ♀), Caparo (AMNH: 2 ♂♂; MCZ: 2 ♂♂), Carebage (AMNH: 1 ♂), Savannah Grande (AMNH: 2 ♀♀), Valley (AMNH: 1 ♂), “Trinidad” (AMNH: 1 ♂, 2 [♂♂], 1 unsexed; FMNH: 1 [♂]).

Venezuela (all in COP): Amacuro: Capure (3 ♂♂, 1 ♀), Caño Merejina (1 ♂), Curiaipo (1 ♀), Misión Araguaimujo (1 ♂), mouth of Amacuro River (1 ♀, 1 unsexed), Tucupita (1 ♂); Sucre: Guaraunas (1 ♂), Tunapu (1 ♂), Yaguaraparo (1 unsexed).

No locality: AMNH: 1 unsexed; ANSP: 1 unsexed

P. atrimentalis ($n=59$)

Colombia: Guaviare: San José del Guaviare (ICN: 2 ♂♂); Meta: Parque Nacional Natural la Macarena (ICN: 1 unsexed), Los Micos (CMNH: 1 ♂), La Macarena norte (ICN: 1 ♂), La Macarena Sur (ICN: 1 unsexed), Paujiles (ICN: 1 ♂, 2 ♀♀, 1 unsexed), Rio Guapaya, Serranía de la Macarena (FMNH: 2 ♂♂, 1 ♀), San Martín (ICN: 1 ♀?), San Juan de Arama (ICN: 1 ♂); Putumayo: San Antonio Guamez (FMNH: 2 ♂♂, 1 ♀), Umbria (ANSP: 1 ♀); Santa Rosa: Cauca Piamonte (ICN: 1 ♂).

Ecuador: Napo: Avila, Río Cochayacu (MNRJ: 1 ♂; MCZ: 1 ♂), Baeza, road to Lago Agrio (DMNH: 1 ♂, 1 ♀), Concepción (MCZ: 4 ♂♂); “Napo” (AMNH: 3 [♂♂], 3 unsexed [type], MCZ: 1 unsexed).

Peru: Amazonas: Rio Cenipa (AMNH: 1 ♀); Huánuco: 15 km north-northeast Tingo Maria (AMNH: 1 ♂), Estacion Bid. Panguana, Rio Lullapichis (AMNH: 1 ♀), Jaupar (FMNH: 1 unsexed); Junin: Puerto Yessup (ANSP: 1 ♀); “Loreto” (MBML: 1 ♂); Loreto: 40 miles east of Iquitos (FMNH: 2 ♂♂, 2 ♀♀), 59 km west of Pucallpa (AMNH: 2 ♂♂, 1 ♀; DMNH: 1 [♂]), Puerto Indiana, Rio Amazonas (AMNH: 1 ♀), Rio Pichana (FMNH: 2 ♂♂, 1 ♀); Pasco: Chuchurras (AMNH: 1 ♀), Puerto Bermudez (FMNH: 1 ♀), 25 miles east of Nevati (FMNH: 1 ♂); San Martín: Moyobamba (ANSP: 1 ♀); Ucayali: Yarina-Cocha (FMNH: 1 [♂], 1 ♀).

P. striigularis striigularis ($n=11$)

Colombia: Cesar: El Cauca (CMNH: 1 ♂); La Guajira: Chirúa (CMNH: 1 ♂), La Concepción (MCZ: 2 ♂♂); Magdalena: Don Diego (CMNH: 1 ♀); Santander: El Tambor (CMNH: 2 ♂♂, 2 ♀♀, 1 unsexed); “Colombia” (FMNH: 1 [♂]).

P. s. ignobilis ($n=5$)

Venezuela (all in COP): Mérida: El Vigía (1 unsexed), Santa Helena, El Moro River (2 unsexed); Táchira: La Fría (1 ♂); Zulia: Mene Grande (1 ♂).

P. s. subrufescens ($n=54$)

Colombia: Antioquia: Murindo (CMNH: 1 ♀); Chocó: Andagoya (ANSP: 1 [♂]; CMNH: 2 ♂♂), Quibdo (CMNH: 3 ♂♂), Rio Baudo (ANSP: 2 ♂♂), Rio Jurado (ANSP: 1 ♂, 1 ♀), Rio Jurubida (ANSP: 1 ♂), Rio Salaqui (ANSP: 1 ♂, 2 ♀♀), Sautata (CMNH: 2 ♀♀); Nariño: Barbacoas (AMNH: 1 unsexed [type]; MCZ: 1 ♂, 1 unsexed), La Guayacana (ANSP: 1 ♂; FMNH: 1 ♀); Valle del Cauca: Córdoba (CMNH: 1 ♂), Rio San Juan de Macay (FMNH: 1 ♀); “Colombia” (FMNH: 1 ♀).

Ecuador: Azuay: Manta Real (ANSP: 1 ♂); Chonta Pamba (MBML: 1 ♂), Gualala (MNRJ: 2 ♂♂); Esmeraldas: Cabeceras de Bilsa (ANSP: 1 ♂), 30 km south of Chonchaduro (ANSP: 1 ♀), El Guayabo (ANSP: 1 ♂), El Placer (ANSP: 1 ♀); Guambi (MNRJ: 2 ♂♂); Guayas: Bucay (ANSP: 1 ♀); La Granada (MBML: 2 ♂♂), Mindo (MNRJ: 1 ♂; MBML: 1 ♂), Nanegalito (MNRJ: 1 ♂), Pichincha, Mindo (ANSP: 1 [♂]; MCZ: 1 ♂; MNRJ: 2 ♂♂), Rio Palenque (FMNH: 1 ♀), San José Cachari (MNRJ: 1 ♀), Santo Domingo de los Colorados (ANSP: 2 [♂♂]; MBML: 1 ♂), “West Coast” (MBML: 1 unsexed; MCZ: 1 ♂).

No locality: ANSP: 1 [♂], 1 unsexed.

P. idaliae ($n=51$)

Brazil: Espírito Santo: Baixo Guandú (AMNH: 2 ♂♂; MNRJ: 1 ♂), Barra Seca (RG: 1 ♀), Colatina (RG: 1 ♀), Conceição da Barra (MBML: 3 ♂♂, 2 ♀♀), Córrego do Sabiá (MZUSP: 1 unsexed), Governador Lindeberg (MBML: 1 ♂), Lagoa Juparaná (AMNH: 1 ♂, 1 ♀), Linhares (RG: 2 ♂♂, 2 ♀♀; MBML: 2 ♀♀; MNRJ: 1 ♀), Porto Cachoeira (MZUSP: 1 ♂), Santa Leopoldina (RG: 1 ♂), Santa Teresa (MBML: 9 ♂♂, 7 ♀♀, 2 unsexed, MNRJ: 1 ♂, 1 ♀), São Mateus (MBML: 1 ♀), Vitória (MBML: 1 ♂); Minas Gerais: Rio Doce (MZUSP: 1 ♂, 1 ♀; FMNH: 1 ♂); “Rio [de Janeiro]” (AMNH: 1 ♂, 1 ♀). “Brazil” (MCZ: 1 unsexed).

P. rupurumii amazonicus ($n=66$)

Brazil: Amapá: Santana (MZUSP: 1 ♂; RG: 9 ♂♂); Amazonas: Araçá River, Barcelos (MPEG: 1 unsexed), Arquipélago de Anavilhanas, Novo Airão (MPEG: 1 ♂), Itacoatiara (MZUSP: 1 ♂), Negro River, Ilha Jussara, in front of mouth of Jaú River (MPEG: 1 ♂), “Villa Bella Imperatriz” [= Parintins] (AMNH: 2 ♀♀); Pará: Aramaí, Tapajós River (MZUSP: 1 ♂), Boim (MCZ: 1 ♀), Caxiri-catuba (AMNH: 2 ♂♂), Fordlandia (MZUSP: 1 ♀; RG: 1 ♂), Igarapé Boiussu, Amazon River (MZUSP: 1 ♂), Igarapé Brabo, Tapajós River (AMNH: 1 ♂), Igarapé Amorin, Tapajós River (AMNH: 3 ♂♂), Ilha de Goyana, Tapajós River (MPEG: 1 ♂), Itaituba (AMNH: 1 ♂, 1 ♀ [type]), Juriti (MPEG: 1 ♂), Lago Cuiepeua, Amazon River (ANSP: 1 ♂; MCZ: 4 ♂♂, 1 ♀♀), Monte Alegre (MPEG: 5 ♂♂, 3 unsexed), Obidos (AMNH: 1 ♀; MZUSP: 1 unsexed), Porto de Moz, Xingu River (AMNH: 1 unsexed), Santa Cruz–Maguari, Santarém (RG: 1 ♂), Santarém (AMNH: 2 ♀♀; CMNH: 4 ♂♂; MCZ: 2 ♂♂), Tapara, Xingu River (AMNH: 1 ♂, 3 unsexed), Tauarí, Tapajós River (AMNH: 1 ♂, 1 ♀; ANSP: 1 ♂), Urucurituba (AMNH: 1 ♂), Vista Alegre, Amazon River (MZUSP: 1 ♂).

P. ruber (*n* = 211)

Brazil: Roraima: Nova Esperança, Pacaraima (MZUSP: 1 unsexed); Amapá: Cajari River (MBML: 2 ♀♀), Macapá (MZUSP: 1 ♀; MPEG: 2 ♂♂, 1 ♀, 1 unsexed), Serra do Navio (MZUSP: 3 ♀♀; MPEG: 1 unsexed; MNRJ: 2 ♂♂, 1 unsexed; MBML: 1 ♂), Vila Velha do Caciporé, Oiapoque (MPEG: 1 ♂); Amazonas: Cuiuni River, right bank, Barcelos (MPEG: 1 ♂, 1 unsexed), Igarapé Caititu, right bank of Uatumã River (INPA: 1 unsexed), Itacoatiara (MZUSP: 1 unsexed; MNRJ: 1 ♂), João Pessoa, Juruá River (MZUSP: 1 ♀), Manaus (MNRJ: 1 ♂, 1 ♀), Maraã, Maguari, left bank of Japurá River (MPEG: 1 ♀), Novo Airão, Lago Miratuca, right bank of Jaú River (MPEG: 1 ♂), Pedra do Gavião, Moura, right bank of Negro River (MPEG: 2 unsexed), Rodovia do Estanho, Manicoré (MPEG: 2 unsexed), Santa Cruz, Juruá River (MZUSP: 1 ♂) Tapuruquara, Negro River (MNRJ: 1 ♂, 1 ♀, 1 unsexed); Acre: Estação Ecológica Rio Acre, ~78 km west of Assis Brasil (MPEG: 1 unsexed), Igarapé São Luiz, left bank of Juruá River, Porto Valter (MPEG: 1 ♀), Macauã River (MZUSP: 1 unsexed) Marechal Taumaturgo, left bank of Tejo River (MPEG: 1 ♂); Pará: Baião, right bank of Tocantins River (MPEG: 2 ♂♂), Belém (MPEG: 1 ♂, 2 ♀, 2 unsexed; MNRJ: 1 ♀), Benevides (MPEG: 2 ♂♂; MNRJ: 1 ♀), Cachoeira do Arari, Povoação Pedras, Marajó (MPEG: 1 ♂), Cametá, left bank of Tocantins River (MPEG: 1 ♂), Castanhal (MPEG: 1 ♂), Caviana, Faz. São Luiz (MPEG: 1 ♀), Flor do Prado, Quatipuru River (MPEG: 1 ♂), Gorotire, Fresco River, right bank of Xingu River (MPEG: 1 unsexed), Igarapé Pedral, right bank of Guamá River, Ourém (MPEG: 1 ♀), Ipixuna do Pará, Capim (MPEG: 1 ♂), Itaituba, Parque Nacional do Tapajós (MPEG: 2 ♀♀), Jacundá, left bank of Tocantins River (MPEG: 1 ♂, 1 unsexed), Juriti (MPEG: 1 ♂), Maguari (MPEG: 1 ♂), Mexiana, Faz. Santana (MPEG: 1 ♂, 1 ♀), Monte Alegre, Parque Estadual de Monte Alegre (MPEG: 1 unsexed), Murutucu (MZUSP: 2 ♂♂, 3 ♀♀, 1 unsexed), Paragominas, Faz. Vitória (MPEG: 1 unsexed), Ponta de Pedras, Faz. Santa Maria, Marajó (MPEG: 1 ♂), Portel, Floresta Nacional de Caxiuanã (MPEG: 1 ♀, 1 unsexed), Providência (MPEG: 1 ♀), Rodovia Belém-Brasília, km 26 (MPEG: 1 ♀), Santa Isabel do Pará (MPEG: 1 ♂, 1 unsexed), Santo Antônio do Prata, Maracanã River (MPEG: 1 ♀), Serra dos Carajás (MPEG: 2 unsexed), Tailândia, Faz. Agropalma (MZUSP:

2 ♂♂, 1 ♀, 1 unsexed), Tomé-açu (MPEG: 2 unsexed), Tucuruí, Tocantins River (MPEG: 3 unsexed), Upper Cururu River (MZUSP: 2 ♀♀), Utinga (MZUSP: 2 ♀♀; MNRJ: 1 ♂), Xingu River, right bank (MZUSP: 1 ♂); Rondônia: Cachoeira Nazaré (MPEG: 2 ♂♂, 2 ♀♀), Ouro Preto do Oeste (MPEG: 1 ♂), Pimenta Bueno (COMB: 1 unsexed), Porto Velho (MNRJ: 4 ♂♂, 2 ♀♀, 2 unsexed), Vilhena (COMB: 1 unsexed); Tocantins: Araguatins (MZUSP: 1 ♂), Dianópolis (COMB: 1 ♂, 1 unsexed); Mato Grosso: Jacaré, upper Xingu River (MNRJ: 1 ♂, 1 ♀), Peixoto de Azevedo River, Faz. São José (MPEG: 1 ♂), Ponte Branca, Araguaia River (COMB: 1 ♂), Sinop (MNRJ: 1 ♂, 1 unsexed), Xavantina, Rio das Mortes (MZUSP: 1 unsexed); Goiás: Anápolis, Nova Veneza (MNRJ: 2 ♂♂), Niquelândia, Serra Negra, Bagagem River (MZUSP: 1 ♀), Rio das Almas (MZUSP: 1 ♂) Rio Verde, Faz. Transwaal (MZUSP: 1 unsexed); Maranhão: Anil (MNRJ: 1 unsexed), Carutapera, Pedra Chata, Gurupi River (MPEG: 1 ♂), Lago Verde, Faz. São Francisco (MPEG: 1 unsexed), Reserva Indígena Alto Turiaçu (MPEG: 1 ♂), Turiaçu (MNRJ: 1 unsexed); Ceará: Serra do Castelo (MNRJ: 1 ♂); Paraíba: Mamanguape, Camaratuba (MZUSP: 2 ♂♂); Alagoas: São Miguel (MZUSP: 1 ♂); Bahia: Andaraí (MBML: 2 ♀), Itajuípe (MPEG: 1 unsexed), Porto Seguro, Estação Veracruz (MZUSP: 1 unsexed), Rio Mucuri (MNRJ: 2 ♀♀), Serra do Gongogi (MZUSP: 1 ♂?), "Bahia" (MBML: 2 ♂♂, 1 unsexed); Minas Gerais: Itambacuri (MBML: 1 ♂), São Paulo do Muriaé, Faz. Barra Alegre (MNRJ: 1 ♂, 1 unsexed); Espírito Santo: Conceição da Barra (MBML: 2 ♂♂, 1 ♀), Pedro Canário (MNRJ: 1 unsexed), Vitória (MBML: 1 ♂); Rio de Janeiro: Angra dos Reis, Faz. Japuiba (MZUSP: 2 ♂♂), Magé (MNRJ: 1 ♂, 1 ♀), Nova Friburgo, Lumiar (MNRJ: 1 ♀), Parati, Pedra Branca (MNRJ: 1 unsexed), Ponte Coberta, Faz. Colorado (MNRJ: 1 ♀), Represa Rio Grande (MNRJ: 10 ♂♂, 12 ♀♀, 6 unsexed), Rio de Janeiro, Floresta da Tijuca (MNRJ: 3 ♂♂, 2 ♀♀, 3 unsexed); São Paulo: Barra do Icapara (MZUSP: 2 ♀♀), Iguape (MZUSP: 1 unsexed), Piassaguera (MZUSP: 1 ♀), São Sebastião, mouth of Una River (MZUSP: 1 unsexed), Ubatuba (MZUSP: 1 ♂); "Brasil" (MNRJ: 1 ♂, 2 unsexed).

Ecuador: Montalvo, Andoas (MNRJ: 1 ♂).

Venezuela: Amazonas: Atures, caño Cataniapo (MBML: 1 ♂); Carabobo: La Planada (MBML: 1 ♂).