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DISTRIBUTION, VARIATION, AND TAXONOMY OF *TOPAZA* HUMMINGBIRDS (AVES: TROCHILIDAE)

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Abstract. We review the distribution, variation, and taxonomy of the Crimson Topaz (*Topaza pella*) and the Fiery Topaz (*Topaza pyra*). Both taxa show sexual dimorphism of foot color and notable age-related variation in plumage. *Topaza pyra* shows distinct and reliable differences from *T. pella* and warrants specific status. We describe a new subspecies, *T. pyra amaruni*, and delineate diagnostic features for *T. pella pella*, *T. pella smaragdula*, and *T. pella microrhyncha*. *Topaza pella pamprepta* is based on specimens with incorrect locality data and should be regarded as a synonym of *T. p. smaragdula*. We note recent range extensions for both species. Our findings serve, we hope, to illuminate directions for further research on these hummingbirds. *Accepted 10 June 1999.*

Resumen. Revisamos la distribución, la variación, y la taxonomía del Topacio Carmesí (*Topaza pella*) y del Topacio Fuego (*Topaza pyra*). Los dos taxa demuestran dimorfismo sexual en el color del pie y notable variación en el plumaje con relación a la edad. *Topaza pyra* se distingue claramente de *T. pella* y merece la categoría de especie. Describimos una nueva subespecie, *T. pyra amaruni*, y presentamos los elementos diagnósticos para *T. pella pella*, *T. pella smaragdula*, y *T. pella microrhyncha*. *Topaza pella pamprepta* fue descrita en base a especímenes con localidades incorrectas y debe ser considerada como un sinónimo de *T. p. smaragdula*. Observamos extensiones recientes en la distribución de las dos especies. Esperamos que nuestros hallazgos sirvan para guiar investigaciones en estos colibríes.

INTRODUCTION

Although the hummingbirds of the genus *Topaza* are among the most distinctive and commonly illustrated trochilids, much remains uncertain about their systematic relationships, taxonomy, and natural history. Earlier authors placed *Topaza* near *Sephanoides, Trochilus,* and *Hylonympha* (Elliot 1878), or between *Trochilus* and *Oreotrochilus* (Cory 1918), or near *Hylonympha, Sternoclyta,* and *Oreotrochilus* (Simon 1921, Peters 1945). More recently, Schuchmann (1982), citing anatomical, ethological and nest-form considerations, allied *Topaza* with *Anthracothorax*, *Eulampis,* and *Sericotes,* while Ruschi (1986) and Grantsau (1988) suggested *Heliodoxa* and *Augastes* as the closest Brazilian genera. Bleiweiss *et al.* (1997) were unable to include *Topaza* in their matrix of DNA hybridization distances involving 26 hummingbirds.

The genus is generally considered to comprise two species, the Crimson Topaz *(Topaza pella)* and the Fiery Topaz *(Topaza pyra)*, although Schuchmann (1982) and Ruschi (1986) regarded them as conspecific. *Topaza pella* has been divided into four subspecies, but the validity of some of these has been questioned (Cory 1918, Peters 1945, Schuchmann 1982, Rushi 1986). *Topaza pyra* has been

TABLE 1. Measurements of *Topaza* hummingbirds.

		T. pella (all specimens)		*T. pyra* (all specimens)		*T. p. pella*		*T. p. microrhyncha*		Rondônia		*T. p. smaragdula*	
		M	F	M	F	M	F	M	F	M	F	M	F
Exposed	Mean	22.9	22.9	20.9[1]	20.9[1]	23.5[2]	23.3[3]	20.0[4]	20.7[5]	21.5	22.0	23.0	23.3
culmen (mm)	SD	1.4	1.2	0.98	0.99	1.2	0.86	0.71	0.58	0.71	0.0	0.84	0.86
	n	60	33	18	10	34	18	5	3	2	2	17	7
	Range	19–25	19–25	19–22	20–23	21–25	22–25	19–21	20–21	21–22	22	22–24	21–24
Flattened	Mean	78.6	73.0	83.5[1]	76.2[6]	79.7	73.8	72.3	70.3	80.0	76.5	78.8	72.1
wing (mm)[7]	SD	3.6	3.1	2.0	2.5	3.2	3.1	6.1	1.5	—	2.1	1.9	3.3
	n	31	35	13	10	13	18	3	3	1	2	13	8
	Range	67–86	67–80	81–87	70–79	76–86	68–80	67–79	69–72	—	75–78	75–81	67–76
Tail chord	Mean	101	—	108[8]	—	96.3[9]	—	102[10]	—	93	—	107[11]	—
(mm)	SD	8.1	—	6.6	—	6.0	—	1.5	—	—	—	7.5	—
	n	32	—	13	—	13	—	3	—	1	—	13	—
	Range	86–122	—	99–118	—	86–102	—	100–103	—	—	—	97–122	—
Mass (g)	Mean	13.6	10.8	14.2	11.1	14.3	11.4	12.4	—	11.8	9.6	14.0	9.8
	SD	1.9	1.3	1.6	0.63	1.8	0.8	2.0	—	0.76	0.64	2.2	1.7
	n	19	18	7	4	9	11	2	—	3	2	5	4
	Range	11–18	9–12.5	12–17	10.5–12	12.5–18	10–12.5	11–13.8	—	11–12.5	9.1–10	11–17	9–12

[1]*pyra* vs *pella*, $P < 0.001$; [2]ANOVA among *pella* groups, $F_{(3,54)} = 17.767$, $P = 0.000$; [3]ANOVA among *pella* groups, $F_{(3,26)} = 8.602$, $P = 0.000$;

[4]*p. pella* vs *p. microrhyncha*, $P < 0.001$; *p. smaragdula* vs *p. microrhyncha*, $P < 0.001$; [5]*p. pella* vs *p. microrhyncha*, $P = 0.006$; *p. smaragdula* vs *p. microrhyncha*, $P = 0.002$;

[6]*pyra* vs *pella*, $P = 0.004$; [7]For males, includes only specimens with fully grown elongated rectrices, as mature males have longer wings;

[8]*pyra* vs *pella*, $P = 0.003$; [9]ANOVA among *pella* groups, $F_{(3,26)} = 6.108$, $P = 0.003$; [10]*p. pella* vs *p. microrhyncha*, $P < 0.020$;

[11]p. *pella* vs *p. smaragdula*, $P = 0.001$; *p. smaragdula* vs *p. microrhyncha*, $P = 0.41$.

regarded as monotypic. In this paper we address species limits and assess individual and geographic variation within the species.

MATERIALS AND METHODS

All specimens of *T. pyra* (n = 29)from the Academy of Natural Sciences (Philadelphia, Pennsylvania, USA; ANSP), American Museum of Natural History (New York, New York, USA; AMNH), Field Museum of Natural History (Chicago, Illinois, USA; FMNH), Moore Laboratory of Zoology (Los Angeles, California, USA; MLZ), Museum of Comparative Zoology (Cambridge, Massachusetts, USA; MCZ), and Smithsonian Institution (Washington, District of Columbia, USA; USNM), and 99 specimens of *T. pella* from the above collections plus the Museu Paraense Emílio Goeldi (Belém, Pará, Brazil; MPEG) were examined. Collection data and selected morphometric and coloration data from 25 *T. pyra* and 143 *T. pella* specimens in 16 other collections were obtained. Standard measurements and observations on color and morphology were made by Hu, and the data were used to describe age-related, geographic, and individual variation. Exposed culmina were measured using calipers. Flattened wing measurements were taken using a wing rule marked off in mm. In males with elongated rectrices the longer of the two elongated rectrices (R2) was measured from its point of insertion using calipers. Both chordal and flattened measurements were taken. The chordal measurements were used for data analysis as this was more easily comparable to previously reported measurements. Plumage was examined for evidence of body, rectrix, and remex molt. Color observations were standardized using comparison with British Colour Council color charts (1938, 1941). Statistical analyses were run using MYSTAT 1.1. For comparisons between the two species t-tests were used. For comparisons within *T. pella* a one-way ANOVA was used on each dependent variable to test for differences among the four groups. If the omnibus group was significant at $P < 0.05$ follow-up pair-wise comparisons between groups were conducted using t-tests. Due to the small sample size $P < 0.05$ was used for all comparisons in order to maintain adequate statistical power. The specimens were examined in five different locations (ANSP, AMNH, Dartmouth College, MCZ, USNM). The literature was searched for relevant information.

RESULTS AND DISCUSSION

Species limits

Table 1 summarizes morphometric data. *T. pyra* averages shorter-billed, longer-winged, possibly slightly heavier, and, at least in the males, longer-tailed than *T. pella.*

In Table 2 we summarize the diagnostic plumage differences between adults of both sexes for both species. In addition, *T. pella* males are almost always a distinctly more purplish-red on the back, breast, and abdomen, and usually retain a greenish cast on the inner secondaries. Perhaps as a result of this color difference, the abdominal iridescence of *T. pella* is generally also duller than that of *T. pyra*, though this difference is less marked than on the breast and back. *Topaza pella* often has a wider gorget than *T. pyra,* with a less well-defined, narrower green border and a yellow center less orange and less shining. The uppertail-coverts may be a yellower green. One adult *T. pella* (USNM 586322) was described on the specimen label as having yellow feet; *T. pyra*'s feet are always blackish.

In the females the gorget of *T. pella* always extends to the base of the bill, whereas the gorget of *T. pyra* rarely does; it is almost always both narrower and shorter. *T. pella* never has orange/red feathers interspersed among the green of the back and abdomen, which *T. pyra* sometimes does. Usually *T. pella*

TABLE 2. Differences in plumage between *Topaza pyra* and *T. pella*.

	Males		Females	
	T. pyra	*T. pella*	*T. pyra*	*T. pella*
Gorget coloration	Border bright medium green	Border yellowed medium green to greenish yellow, less bright	No gray edges to feathers	Gray edges to feathers[1]
Black on head	Covers nape and auricular areas, well-demarcated	Replaced by body color on nape and auricular areas, gradual transition to body color		
Width of black breast-band	Wide	Narrow		
Iridescence of back and breast	Shining	Subdued		
Feathers of breast and abdomen			No gray edges to feathers	Gray edges to feathers[1]
Secondaries, inner primaries	Blackish	Cinnamon-rufous[2]		
Green under tail coverts	Bluer	Yellower[2]		
Rectrix coloration	R4, inner web of R5 black	R4, inner web of R4 cinnamon-rufous	Inner web of R5 mostly blackish, vane of R4 black	Inner web of R5 mostly cinnamon, vane of R4 cinnamon

[1]Most apparent when viewed at an angle that reduces iridescence, giving a scaled appearance.

[2]Absent in some immature males.

has less or no yellow to the green of the back, which is always yellow-green in *T. pyra*. One *T. pella* had rufous at the base of some secondaries. *Topaza pella* almost always has more cinnamon on R4, usually both the distal web and a substantial portion of the proximal web, where in *T. pyra* these are usually blackish.

In both sexes *T. pella* tends to have wider and more obtuse rectrices, and may have white tips to the lower abdominal feathers, which are all blackish in *T. pyra*. The tibial feathers in *T. pella* are always white, while they usually have some black in *T. pyra*. Perhaps related to immaturity, *T. pella* may show yellow, pink, or gray on portions of the mandible, rather than the overall black which is characteristic of *T. pyra*.

The most diagnostic identification characteristics appear to be the color of the rectrices and, in males, the color of the secondaries and inner primaries (Table 2). In the males, the extent of black on the head, if determinable, will always be diagnostic, and gorget color and body color will almost always be so. In certain geographic regions tibial feather coloration will also be diagnostic. Most of these

features are readily observable in the field.

Both species share two apparently previously unremarked physical characteristics. In the adults there is sexual dimorphism in foot color, with the males having gray to black feet, and the females having yellow to rosy feet. In both immature and adult birds the rufous underwing-coverts at the base of the leading edge of the wing combine with the axillaries to form a tuft, which protrudes from beneath the folded wings of many study skins. This tuft is more consistent and more prominent than in any of the other trochilid genera we examined and appears *in vivo* in several of Greenewalt's slides of *T. pella*, most noticeably when the birds are stretching (Visual Resources for Ornithology G02/4/451, G02/3/650 WC, ANSP). Another characteristic of the genus, noted by Elliot (1878) but not generally mentioned now, is that the feet are, in proportion to size, relatively large for a hummingbird.

Are *T. pyra* and *T. pella* distinct species? Arguments for and against have focused on the degree of similarity of the two taxa and their geographic distributions. While they are clearly closely related, we suggest that species-level distinction is favored by the obvious differences between the two taxa in coloration and morphometric characteristics of both sexes, differences which are consistent across their geographic ranges. Neither intermediate forms nor hybrids have been reported, and we have found no specimens that showed any combination of the characteristics of the two taxa.

The Ecuadorian population of *T. pella*, which is based on three male specimens collected in 1899, is separated by 1500 km from the other known *T. pella* populations. This range has been cited as support both for and against conspecificity. Norton (1965) and Hilty & Brown (1986) suggested that the overlap of *T. pyra* and *T. pella* in Ecuador precluded conspecificity. Schuchmann (1982) argued that *T. pyra*'s range bridged the gap between the Ecuadorian and Venezuelan populations of *T. pella*, thereby demonstrating conspecificity. We will show later that the record of *T. pella* in Ecuador is likely erroneous. This obviates the need to consider sympatry vs. parapatry of the two species in Ecuador in the question of species limits; they might be parapatric in southeastern Venezuela or in southwestern Amazonian Brazil, from which region both taxa are only recently and poorly known.

The breeding season for *T. pella* has been reported to be July to November in Guyana (Nicholson 1931, Davis 1958); the breeding season for *T. pyra* is not fully known but may be different from that of *T. pella*. While Whitney, Oren, & Pimentel (pers. comm.) observed *T. pyra* nesting and collected one nest with two eggs (specimen at MPEG) in July in Acre, Brazil, and an Ecuadorian *T. pyra* male collected in August (ANSP 186789) had enlarged testes (6x6 mm), Arvin (pers. comm.) observed behavior along the Río Tiputini, Napo, Ecuador, in February that may have indicated a nearby nest, and two Venezuelan *T. pyra* females with slightly enlarged ovaries, one collected in February (FMNH 318844; 5x3 mm), one in May (FMNH 318842; 5x4 mm), suggest that breeding may occur near those months. This raises the possibility that there are ethological differences between the two taxa.

We conclude that the best hypothesis at present is that *T. pella* and *T. pyra* are distinct allopatric or parapatric species.

Distribution, variation, and systematics

Topaza pyra

Of the two species, *T. pyra* is the less well-known and the less well-represented in collections. We located 54 specimens of which eight lack locality data, in 23 collections. The only recent considerations have been in the context of reviews of the hummingbirds of

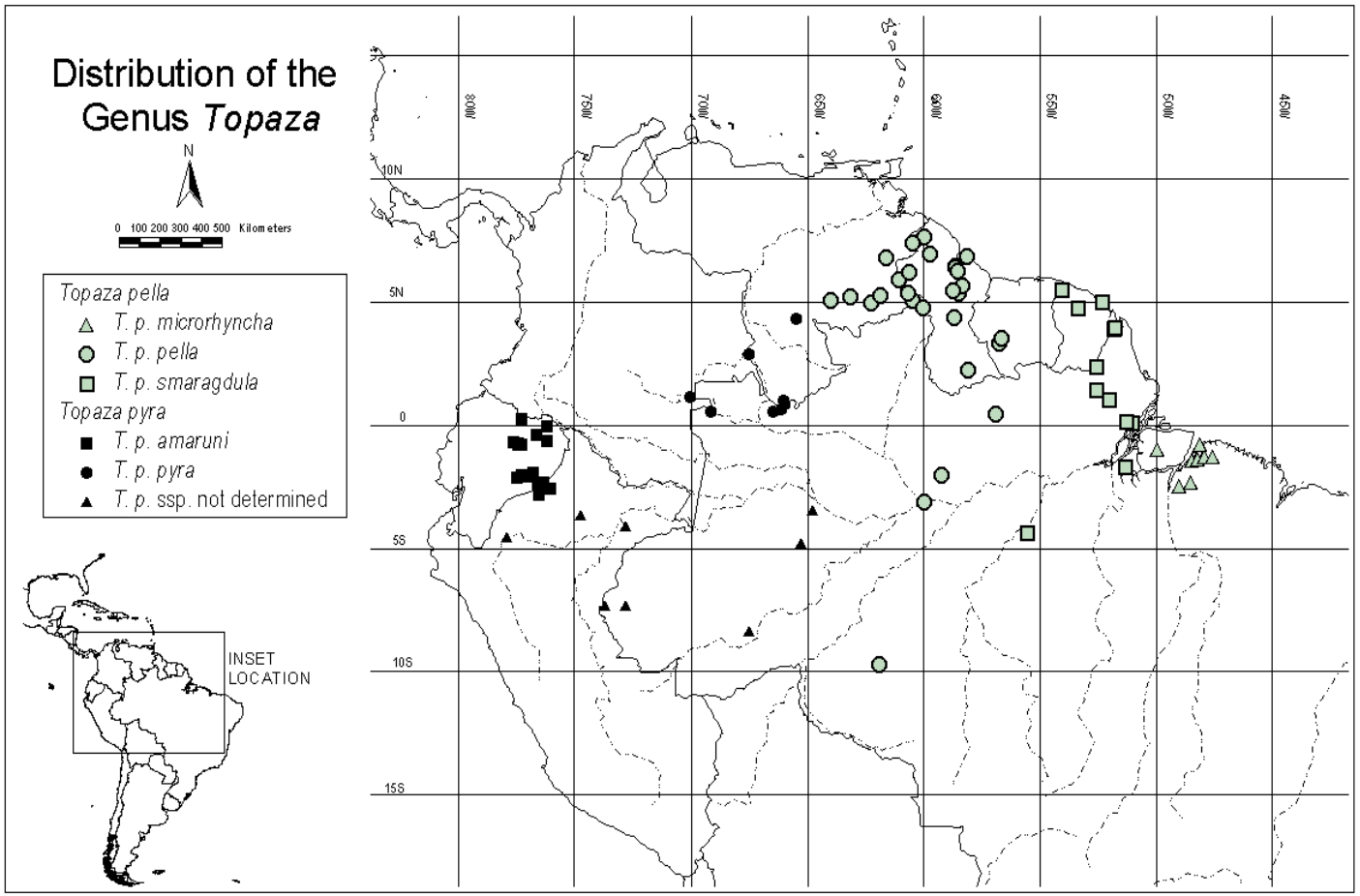

FIG. 1. Distribution of *Topaza pella* and *T. pyra*, including locations of specimens and sightings.

specific geographical regions: Peru (Zimmer 1951) and Brazil (Ruschi 1986). Field observations have been reported infrequently. Appendix 2 summarizes locality data for the specimens and observations that we found.

T. pyra appears to be uncommon over much of its range and may engage in some temporal movements, perhaps seasonal and/or resource-based (Whitney, pers. comm.). Habitat, as with *T. pella,* is restricted to forest on sandy soil, particularly at the margins of blackwater streams and in palm swamps (Whitney, pers. comm.). Sightings and specimens have generally been from two areas: one in Ecuador-Peru centered around the Río Napo-Río Corrientes area of Ecuador, and a more diffuse one in Venezuela-Brazil in the region of the upper Rio Negro, the type locality.

The Ecuador-Peru records are more frequent. Determination of which old records were from Peru was complicated by the 1942 boundary changes affecting that country. Data collected since the 1960s have shown that *T. pyra* ranges well into Amazonian Peru, including the Río Nieva, Kigkis, Amazonas (LSUMZ 34069 and 34070), the Río Tahuayo, Loreto (Siegel, pers. comm.), the middle Río Tigre, including near Intuto, Loreto (Alvarez, pers. comm.), and Andoas. On the other hand, there are no records from the lower Río Napo (Cardiff & O'Neill, pers. comm.) or the Río Marañon upriver at least to Iquitos (Wust *et al.* 1990, Alvarez, pers. comm.).

The second group of records comprises a few scattered reports from southern Venezuela, adjacent Colombia, and northwestern Brazil. Northern Brazilian records we found include the two syntypes in the British Museum (BMNH 1997.16.2 and 1997.16.3), labeled "Rio Negro"; one specimen in the Colección Ornitológica Phelps (COP 69823), collected at Mision Maturacá, Amazonas, and Whitney's observations (pers. comm.) of the taxon on the Rio Cauaburi, Amazonas, and along the main road linking São Gabriel da Cachoeira, Amazonas, Brazil, with Cucuí, Amazonas, Venezuela, (mostly within Brazil's Pico da Neblina National Park) where it was common and conspicuous in September and October and uncommon to rare in December and March, albeit of different years.

Recent data have extended the known range of *T. pyra* into Brazil substantially south of the Rio Solimões: along the Rio Urucu, Amazonas (Peres & Whittaker 1991), in the Serra do Divisor region, Acre (Whitney, Oren, & Pimentel, pers. comm.), northwest of Cruzeiro do Sul in extreme southern Amazonas (Whitney, pers. comm.), at Tefé, Amazonas (Wheatley 1995), and along the Igarapé Mapiá, Amazonas (Hu). It therefore appears likely that *T. pyra* ranges continuously from Ecuador through western Brazil to Amazonian Venezuela (Fig. 1), with patchy occurrence closely paralleling the distribution of blackwater drainages (Whitney, pers. comm.). Whether its range also includes some part of the 600 km hiatus across southern Colombia remains unclear. It has not been recorded in this area in Caquetá (Borrero 1982), or Puerto Nariño (Pearman 1993), and Wheatley's sources (1995) did not report it in Colombia. However, this region of Colombia remains poorly known ornithologically.

Topaza pyra is a highly sexually dimorphic hummingbird of striking plumage in both sexes. While there are multiple published descriptions of *T. pella*, descriptions of *T. pyra* are generally based on comparison to *T. pella.* A full description of *T. pyra* is provided in Appendix 1.

Sub-adult males differ from mature males as follows: green edge of gorget bluer and wider, yellow center less intense, less orange and smaller; black of the head duller or with scattered greenish-black feathers; body color less intense, less iridescent, more orange, with green reflections or interspersed green feath-

ers; rump perhaps more yellow-green, less orange, feathering less full; upper- and undertail-coverts a bluer green, with less orange gloss, and feathers shorter and tighter in texture; R2 may be non-elongated or less elongated than in mature males; wing length is generally shorter. Coloration of dried feet suggests that the feet darken with maturity; this would be consistent with the observed sexual dimorphism of foot color and the juvenile's likely having light feet.

The range of non-adult plumage variation is so great as to suggest the possibility that in males there are two distinct sub-adult plumages between immature and adult plumages. In the first sub-adult plumage, characteristics noted above would appear in varying combinations, but always with green in the body; in the possible second sub-adult plumage, some green or greenish reflections would persist on the upperwing-coverts and inner secondaries, the remainder of the plumage being typical of the adult. Perhaps most importantly, we draw attention to the need for clarification of immature and sub-adult plumages in males. Immature females may differ from mature females in having shorter wings, and gorgets that are less extensive near the base of the bill.

We propose that two populations of *T. pyra* are distinguishable by the following characters: 1) the color of the puffy tibial feathering, and 2) the prominence of the nasal fossa at the base of the bill. There are no demonstrable morphometric differences.

Topaza pyra pyra (Gould)
Trochilus (Topaza) pyra Gould, 1846, Proc. Zool. Soc. London 14:85. Rio Negro, Brazil.

Characters. Typical for the species (Appendix 1). Tibial feathering fully white to white with blackish feathers anteriorly. Nasal fossa readily apparent.

Range. Venezuela: Amazonas (Cerro de la Neblina; Sabana, upper Río Asisas; Caño Pimichin), southeastern Colombia (Río Vaupés, Mitú), Brazil: upper Rio Negro (including Mision Maturacá) and Rio Cauaburi (Whitney, pers. comm.).

Specimens examined. Colombia: Vaupés: Opposite Tahuapunto, Rio Uaupés (1, AMNH). Venezuela: Amazonas: Cerro de la Neblina (4, FMNH).

Remarks. We are aware of 11 specimens of both sexes from this area. Gould (1846, 1851) did not comment on the coloration of the tibial feathers. The tibial feathering cannot now be seen on the type specimens at BMNH (Walters, pers. comm.). However, Martin (1861) noted that the thighs of Gould's specimens were white.

Topaza pyra amaruni, new subspecies

Holotype. MLZ 10339, adult male, collected at Cabeceras, Río Guataraco, Ecuador, 27 May 1933, by Olalla & Sons.

Diagnosis. Differs from the nominate subspecies in having significantly more black in the tibial feathering, which is completely blackish or blackish with narrow white edge. The nasal fossa is also usually smaller than in *T. p. pyra*, being either absent or short and shallow.

Range. Amazonian Ecuador, along Río Napo and Río Corrientes; western Amazonian Peru.

Paratypes. Ecuador: Napo: Cabaceras, Río Guataraco (MLZ 10338), Coca, Río Napo (USNM 174293), Concepción (MLZ 1136, 1138, 1139, 14708), Cotapino (MCZ 298752), Provincia Sucumbíos, 14 km north of Tigre Playa (ANSP 186789), Río Pucuno (MCZ 266864), Sumaco, Guaticocha (MCZ 298751); Pastaza: Montalbo (AMNH 802113, 802114), Río Conambo (ANSP 168093), Río Corri-

entes (ANSP 160360, 163057, 163058), Río Copotaza (MCZ 266863), Río Tigre (MLZ 10456).

*Other specimens examinea***.** Ecuador: No further locality (FMNH 46135). Peru: Loreto: Upper Amazon (AMNH 37709). Ecuador or Peru: Napo River (AMNH 46072).

Etymology. Amarun is a Quichua word meaning anaconda. The Canelos Quichua of Amazonian Ecuador refer to the anaconda, related snakes, and the rainbow as *amarun*. The *amarun* contains the power of and encompasses the waters, earth, forest, and sky (Whitten 1976).

Remarks. The nasal fossae show some variation with 4 of the 20 specimens overlapping the range observed in *T. p. pyra.* The male specimens also demonstrate two other possible minor color differences, a central gorget more orange, less yellow, and a body color more orange, less red, but the sample is insufficient to establish whether these are reliable.

With regard to local names, one specimen (MLZ 1139) is labelled "Urcuquinde o Curiquinde". Three (MLZ 10338, 10339, 10456) are labelled "Curiquide". One (ANSP 163058) is labelled "Nina Quinde", and one (AMNH 802114) is labelled "Minaquinde" (?or "Ninaquinde"; difficult to read). In Ecuadorian Quichua "quinde" means "hummingbird" (Cordero 1955, Whitten 1985).

Topaza pella

Four subspecies have been described in *T. pella*: *T. p. microrhyncha* of Pará south of the Amazon, *T. p. smaragdula* with type locality "Cayenne", *T. p. pella* of Suriname, Guyana, Venezuela, and adjacent Brazil, and *T. p. pamprepta,* isolated in the Río Suno region of Ecuador. The validity of some, especially *T. p. smaragdula*, has been doubted. Of these, Schuchmann (1982) recognized only *T. p. pella*, ascribing observed color variation to interbreeding ("vermischen") with *T. pyra.*

The reported range of *T. pella* has for the most part changed little over the past fifty years: eastern Venezuela, the Guianas, and northern Brazil to eastern Pará, with additional data slowly extending the range farther south in Amazonas and Pará, e.g., the Baía de Caxiuana (Whitney, pers. comm.). Specimens collected recently in Rondônia (Stotz *et al.* 1997) extend the range 600 km south of even those limits. Whether these represent an isolated population is not known. Figure 1 displays the known distribution for this taxon, based on the specimens we examined and information from other sources about additional areas of occurrence. Appendix 3 summarizes these locality data.

Nicholson (1931) described the juvenal plumage of *T. pella*, and Ruschi (1986) published a photograph of two juveniles. The juvenile male we examined (MPEG 43720) largely resembles Ruschi's photograph (although iris color in the specimen was recorded as yellow and the irides in the photograph are dark), but Nicholson's description does not accord with the specimen or the photograph, e.g., in throat, belly, undertail-covert, and rectrix color. One possible explanation is that Ruschi's photograph is of two juvenile males and Nicholson's description is of a juvenile female. The immature plumage of the males appears to follow a partial post-juvenal molt and consists of a patchwork of juvenal orange/green feathers, with loose gray webs and edges on the abdomen, and iridescent crimson and orange feathers of adult structure.

What may be a sub-adult plumage is variable, much like the adult male, but with the black of the head duller and the body color mixed with green and often less intense. The undertail-coverts may be greener, less yellow,

the uppertail-coverts less coppery. The remiges may not be cinnamon-rufous but dark brown as in the juveniles and females. The subcentral rectrices (R2) may not be elongated, which may partly account for scarcity of "adult males" noted by observers (Nicholson 1931, Davis 1958). Wing length is usually shorter. The feet may still be pale. A possible second sub-adult plumage approximates the mature male except for continued green reflections on the upperwing-coverts and inner secondaries.

The immature plumage of the female primarily differs from the adult female ventrally, the gorget consisting of loose gray feathers with small spots of yellow-green iridescence, and the abdomen feathered with loose juvenal feathers, green with loose gray proximal webs and edging. A possible sub-adult plumage is much like the adult female but with shorter wings and a gorget at least partially gray instead of iridescent, especially at the base of the bill. The body color may be duller overall as well.

Vielliard (1994) has pointed out that partial albinism is not uncommon in this bird. Several of the specimens we examined showed a few white contour feathers. This was apparently not related to geographical location.

Topaza pella pella (Linné)
Trochilus Pella Linné, 1758, Syst. Nat., ed. 10, 1:119. "in Indiis" (= Suriname, *ex* Edwards [Peters 1945])

Characters. Typical for the species; two of the fuller descriptions published are in Simon (1921) and Ruschi (1986). Adult males demonstrate significant color variation. Body color ranges from deep purplish-crimson to, in one specimen (AMNH 482443), orange-red. The gorget varies in width, intensity and color of the border, and intensity and color (greenish yellow to deep yellow-orange) of the center.

Range. Eastern Venezuela, Guyana, Suriname; Brazil: Roraima, northwestern Pará, Amazonas (including Manaus [Wheatley 1995]), eastern Rondônia.

Specimens examined. Brazil: Amazonas: Rio Uatumã (1, MPEG); PARÁ: Foz do Igarapé Tramalhetinho, Rio Trombetas (2, MPEG); Rondônia: Rio Jiparaná (1, FMNH), Cachoeira Nazaré, Rio Jiparaná (1, FMNH; 2, MPEG). Guayana: Essequibo River (2, AMNH; 1, USNM), No further locality (4, AMNH; 2, MCZ; 1, USNM); East Demerara-West Coast Berbice: Demerara (1, MCZ; 4, USNM); Mazaruni-Potaro: Carimang River/ River Carimang (1, AMNH; 1, USNM), River Carimany (?= Kamarang River) (1, FMNH), Cuyuni River (3, AMNH; 1, ANSP), Kalicoon (1, AMNH), Kartabo (10, AMNH), Upper Mazaruni River (4, AMNH), Waruma River (1, USNM); North West: Baramita (2, USNM); Rupununi: Iwokrama Reserve (7, ANSP). Suriname: Nickerie: Kaiserberg Airstrip, Zuid Rivier (1, FMNH).

Topaza pella smaragdula (Bosc)
Trochilus smaragdulus Bosc, 1792, in Lamarck *et al.*, *Choix de Mémoires sur Divers Objets D'Histoire Naturelle* (= *Journal D'Histoire Naturelle*). Paris. Vol. 1, No. 10, pp. 385–6. Cayenne.

Diagnosis. Chubb (1913) reported that *Trochilus smaragdulus* was based on a female *Topaza pella*. After examining the original description and figure, we agree. Bosc (1792) did not effectively diagnose this taxon with respect to *T. p. pella*. Simon (1921) stated that compared to *T. p. pella* males have brighter orange-red on the back and abdomen, with a clear delineation between the carmine of the upper back and the orange-red of the lower back, and a gorget with generally less orange in the center and more green at the edges. Vielliard (1994)

TABLE 3. Comparison of *Topaza pella pamprepta* and *T. p. smaragdula*.

		T. p. pamprepta	*T. p. smaragdula*
Exposed	Mean	23.0	23.0[1]
culmen	SD	1.4	0.8
(mm)	n	2	15
	Range	22–24	22–24
Flattened	Mean	79.0	78.7[2]
wing	SD	1.4	2.0
(mm)	n	2	11
	Range	78–80	75–81
Tail	Mean	114	105[3]
chord	SD	10.6	6.4
(mm)	n	2	11
	Range	107–122	97–115

[1]*p. smaragdula* vs *p. pamprepta*, $P = 0.979$.

[2]*p. smaragdula* vs *p. pamprepta*, $P = 0.854$.

[3]*p. smaragdula* vs *p. pamprepta*, $P = 0.448$.

felt that this was individual variation. Our examination did not substantiate a difference in body or gorget color, but did demonstrate one morphometric difference: a statistically significantly longer tail for the males.

*Range***.** Presumably French Guiana; Brazil: Amapá, central Pará, probably including the Baía de Caxiuana.

Specimens examined. Brazil: Amapá: Serra do Navio (1, FMNH; 1, USNM); PARÁ: Rio Tapacurazinho (1, MPEG). French Guiana: No other locality (3, ANSP); Cayenne: No other locality (14, AMNH; 2, USNM), Oyapoc (1, USNM), Pied Saut, Oyapock (2, FMNH); Saint-Laurent du Maroni: Saint-Jean (1, MCZ); Ecuador: Napo: "Suno, Río Napo" (2, USNM, including the holotype of *T. pella pamprepta* Oberholser 1902; see Remarks).

*Remarks***.** Table 1 shows morphometric comparisons of the *T. p. pella*, *T. p. microrhyncha*, Rondônia, and *T. p. smaragdula* specimens. The few Rondônia specimens were generally smaller than the *T. p. pella* specimens, though none of the differences reached statistical significance. The *T. p. smaragdula* males had statistically significantly longer tails than any of the other groups. The difference in tail length between *T. p. pella* and *T. p. smaragdula* was still present but did not reach statistical significance when only the *T. p. smaragdula* specimens with definite localities were included ($P = 0.125$); the others were labelled "Cayenne," which may have been the point from which they were sent to Europe. "Cayenne" was a common nominal type locality that does not necessarily indicate that the specimens were collected there (Stephens & Traylor 1985). The specimens from northwestern Brazil had relatively short culmens, the Rio Uatumã specimen (MPEG 43650) in particular having a short (21 mm), thick bill as well as short wings and a short tail. Neither culmen length nor tail length appeared to show clinal variation, i.e., the range of variation was distributed geographically throughout each group and did not appear to show any gradual change across the geographic range.

A further subspecies, *T. p. pamprepta* Oberholser 1902, is known only from three specimens supposedly collected by Goodfellow and Hamilton in Ecuador (Suno, Río Napo) in 1899. We examined two of these, including the holotype; one was sent to Germany on exchange from USNM in 1931 (Schmidt, pers. comm.). We were unable to find any other specimens or sightings of *T. pella* from Ecuador. Agro and Ridgely examined the two specimens labelled *T. pella* in the Museo Ecuatoriano de Ciencias Naturales, Quito (MECN), and they are *T. pyra*, not *T. pella*.

Although Rounds (1990) credited Goodfellow and Hamilton with careful, credible

documentation, others have questioned their Ecuadorian records (Ridgely, pers. comm.) including Zimmer (1951), who noted that specimen labels were reputedly added by a dealer in London. One of the *T. p. pamprepta* specimens we examined (USNM 174296) has been annotated "Locality Wrong/Cayenne - skin!/C.E.H. [Charles E. Hellmayr]".

Morphometrically, the two *T. p. pamprepta* specimens we examined were not significantly different from the *T. p. smaragdula* specimens from Brazil and French Guiana (Table 3). The *T. p. pamprepta* tail chord of 107 mm is exceeded in three *T. p. smaragdula* specimens. The 122 mm chord is notably longer than the longest *T. p. smaragdula* (115 mm), but Grantsau (1988) cites a tail length of 122 mm for a *T. pella* specimen from Serra do Navio, Amapá.

The style of preparation of the *T. p. smaragdula* specimens does not match that of multiple other Goodfellow and Hamilton hummingbird specimens, all of which show a style of preparation which while similar among themselves is different from that of the *T. p. pamprepta* specimens.

Taking these data together, we conclude that *T. p. pamprepta* was based on specimens with incorrect location data and should be synonymized with *T. p. smaragdula.*

Topaza pella microrhyncha Butler
Topaza pella microrhyncha Butler, 1926, Bull. Brit. Orn. Club 46:56. Matta de Igapó, Utinga, Pará.

Diagnosis. Butler did not cite specific diagnostic characteristics, but mentioned generally small size, shorter bill, and a very ruddy gorget in the males. Grantsau (1988) described the males being more red-gold on the lower back and belly, and both sexes having a shorter bill. Ruschi (1986) did not recognize it as a valid taxon. Our data corroborated the shorter culmen (Table 1) and revealed a longer tail and non-statistically significant tendency towards a shorter wing, but we found no consistent differences in color.

Range. Brazil: northeastern Pará east of the Rio Tocantins, and the Ilha de Marajó.

*Specimens examined***.** Brazil: Pará: Anajás, Ilha de Marajó (1, MPEG), Belém (1, MCZ), Castanhal (1, ANSP), No other locality (1, ANSP), Prata, near Pará (1, AMNH), Rio Moraitena (1, ANSP), Santa Rosa, Município de Vigia (2, MPEG).

Remarks. One of the three females we examined (AMNH 482448) had rufous at the base of some secondaries.

The recently-collected specimens from Rondônia (Stotz *et. al.* 1997) are not, as the authors suggested, *T. p. microrhyncha.* Hu examined these specimens and found that their culmina fall outside the range for *T. p. microrhyncha* and that culmen, wing, and tail measurements are closer to *T. p. pella* (Table 1).

Systematics of Topaza pella *in summary***.** Though we recognize subspecific divisions in *T. pella* to describe its morphometric variation, we note that interpretation of this variation is still clouded by uncertain locality data for some *T. p. smaragdula,* and small sample size for the *T. p. microrhyncha* and Rondônia specimens. We suggest that *T. p. pella* and *T. p. microrhyncha* are valid. *T. p. microrhyncha* is both significantly and consistently different in culmen length and appears to occupy a clearly-defined geographic range. *T. p. smaragdula* is likely valid, although study of additional specimens with specific locality data is needed to clarify this. *T. p. pamprepta* should not be recognized. Further specimens from Rondônia may demonstrate that subspecific distinction is warranted for the population there.

CONCLUSION

Much remains to be learned about the *Topaza* hummingbirds. Recent data have extended their known ranges and suggest that there may be other undiscovered populations. The work of previous observers on *T. pella* suggests areas for behavioral study, e.g., whether both sexes indeed share in protecting the nest (Nicholson 1931), the significance of lek-like behavior (Davis 1958), or the meaning of the observed paucity of "adult males". Almost any behavioral observations on *T. pyra* would add to our present knowledge. Both species have loud, complex songs and conspicuous calls that, to date, have been recorded only rarely and remain unstudied (Whitney, pers. comm.). For both taxa intraspecific and age-related variation are incompletely understood. While none of the diagnostic characters we found appeared to show clinal variation, geographic gaps between the specimens we examined still allow for this possibility. Consideration of material in European and South American collections might help to clarify this. We hope these aspects of distribution and natural history can be investigated before these wondrous species are too adversely affected by the increasing anthropogenic changes in South America, and that this paper can help to focus where further work may best be conducted.

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APPENDIX 1. Description of *Topaza pyra*

Male: Gorget with a golden yellow/orange-yellow center and a medium green edge. Rest of the head and a wide breast band velvety black, sometimes glossed with violet-red. Back, lower breast, upperwing-coverts, and outer webs of the innermost two remiges shining orange-red, becoming more orange on the belly, shading over the rump into the yellow-green/green uppertail-coverts. Rump feathering relatively full. Feathers of the lower abdomen loose-webbed and blackish. Undertail-coverts yellow-green/green. Upper- and undertail-coverts with orange highlights, and somewhat lengthened and loose-webbed. Central rectrices violet-glossed blackish overlaid by iridescent unsaturated yellow-green, sometimes with orange lights. Elongated subcentral rectrices and outer rectrices are black with a violet gloss. Outer webs of R5 sometimes rufescent; this may indicate immaturity. Underwing-coverts rufous. Remiges dark brown with faint violet reflections. Tibial feathers completely blackish to fully white. Bill black. Feet gray. Iris dark brown.

Female: Gorget iridescent red/orangish-red, bordered by a narrow orange-yellow-green band. Rest of the head medium to bluish-green. Breast less bluish. Back, upperwing-coverts, and abdomen yellowish-green with a yellow-orange/orange gloss, sometimes with orange-red edging or feathers interspersed. Upper- and undertail-coverts blue-green. Central rectrices violet-glossed blackish overlaid with iridescent unsaturated medium green. Other rectrices black with a violet gloss. Outer web of R5, sometimes tip of inner web of R5, outer web of R4, or the tip of R4, cinnamon. Outer webs of the two innermost secondaries bluish-green/green. Underwing-coverts rufous. Remiges dark brown with a violet gloss. Bill black. Feet orange/flesh. Iris brown.

APPENDIX 2. Locality of data for *Topaza pyra.* This list includes all specimens and sources from which we obtained information. Latitudes and longitudes in brackets are general locations, e.g., the mouth of the indicated river.

Location	Date	Source	Latitude	Longitude
Topaza pyra pyra				
BRAZIL				
Amazonas				
Mision Maturaca	10.X.1970	COP 89623	?[0040N	6608W]
Rio Cauaburi		Whitney (pers. comm.)	[0017S	6556W]
Rio Negro		BMNH 1997.16.2		
		BMNH 1997.16.3		
		AMNH 37710		

APPENDIX 2. Continuation.

Location	Date	Source	Latitude	Longitude
		(?presumptive location)		
North of São Gabriel da Cachoeira		Whitney (pers. comm.)	[0008S	6705W]
COLOMBIA				
Vaupés				
Mitú		Hilty & Brown (1986)	0108N	7003W
Opposite Tahuapunto, Rio Uaupés	21.VII.1929	AMNH 434189	[0036N	6912W]
VENEZUELA				
Amazonas				
Cerro de la Neblina	27.IV.1984	FMNH 318841	0050N	6600W
	04.V.1984	FMNH 318842		
	20.II.1985	FMNH 318843		
	19.II.1985	FMNH 318844		
Caño Pimichin	02.III.1946	COP 34235	0252N	6732W
Sabana, Alto Río Asisa	06.III.1949	COP 47084, 47085	[0418N	6530W]
T. pyra amaruni				
ECUADOR				
Río Uskino		LACM 78157		
Napo				
?Coca, Río Napo[1] (= Puerto Francisco de Orellana)	VI.1899	USNM 174293	0028S	7658W
Concepción	01.II.1930	MLZ 1136	0048S	7725W
	01.II.1930	MLZ 1138		
	23.VII.1928	MLZ 1139		
	13.VIII.1935	MLZ 14708		
Cotapino	11.VII.1964	MCZ 298752	0045S	7725W
Cuyabeno Reserve		Wheatley (1995)	0001S	7611W
Limoncocha		Wheatley (1995)	0024S	7637W
Panacocha (near Río Pañayacy)		Wheatley (1995)	[0027S	7606W]
Prov. Sucumbios (14 km N of Tigre Playa)	02.VIII.1993	ANSP 186789	0015N	7715W
Río Bermejo	07.VIII.1994	Molina (Ortiz-Crespo, pers. comm.)	0017N	7706W
Headwaters of Río Guataraco	26.V.1933	MLZ 10338	[0040S	7737W]
	27.V.1933	MLZ 10339		
Río Pucuno	22.VII.1939	MCZ 266864	[0048S	7716W]
Sumaco, Guaticocha	18.VIII.1964	MCZ 298751	0045S	7724W
Tiputini Biological Diversity Station	I.1997	English (pers. comm.)	0038S	7611W

APPENDIX 2. Continuation.

Location	Date	Source	Latitude	Longitude
Pastaza				
Montalbo/Montalvo	06.VIII.1949	AMNH 802113	0204S	7658W
	05.VIII.1949	AMNH 802114		
	31.VIII.1949	CU 27250		
	06.VI.1958	MML 941		
	02.VI.1958	MML 942		
	14.VII.1957	MML 943		
Río Conambo	03.III.1952	ANSP 168093	[0207S	7603W]
Río Corrientes	V(?).1936	ANSP 160360	[0221S	7626W]
	V.1936	ANSP 163057		
	V.1936	ANSP 163058		
Río Copotaza, Andoas	04.III.1939	MCZ 266863	[0234S	7648W]
Río Rotuna		BMNH 1997.16.1	[0144S	7729W]
Río Tigre	24.II.1933	MLZ 10456	[0207S	7604W]
ECUADOR or PERU				
Napo River		AMNH 46072		
PERU				
Loreto				
Near Andoas		O'Neill (pers. comm.)	[0250S	7630W]
?Mouth of Río Curaray[1]	VI.1899	USNM 174293	222S	7405W
Upper Amazon		AMNH 37709		
Topaza pyra (indet. subspecies)				
BRAZIL				
Acre				
Mun. Mâncio Lima alto Rio Moa	11.VII.1996	MPEG 52719, 52720	0721S	7341W
	12.VII.1996	MPEG 52721		
Amazonas				
Northwest of Cruzeiro do Sul	IV.1997	Whitney (pers. comm.)	[0738S	7236W]
Igarapé Mapiá	28.V.1996	Hu	0824S	6732W
Upper Rio Urucu	30.VII.1989	Peres & Whittaker (1991)	0450S	6516W
Tefé		Wheatley (1995)	0322S	6442W
PERU				
Amazonas				
Río Nieva, Kigkis, Depto. Amazonas	VII.1964	LSUMZ 34069, 34070	0452S	7757W
Loreto				
Near Intuto	05.X.1995	Alvarez (pers. comm.)	[0339S	7444W]
Río Tahuayo	1984	Siegel (pers. comm.)	[0415S	7304W]
Río Tigre	08.X.1992	Alvarez (pers. comm.)	[0426S	7405W]
Upper Amazon		AMNH 37709		

[1]Goodfellow and Hamilton specimen of disputed locality (Zimmer 1951)

APPENDIX 3. Locality of data for *Topaza pella*. This list includes all specimens we examined plus information from other sources that we felt helped to establish this taxon's distribution. Latitudes and longitudes in brackets are general locations, e.g., the mouth of the indicated river.

Location	Source	Latitude	Longitude
Topaza pella pella			
BRAZIL			
Amazonas			
Manaus	Wheatley (1995)	0308S	6001W
Rio Uatumã	MPEG 43650	[0226S	5737W]
Pará			
Foz do Igarapé Tramalhetinho, Rio Trombetas	MPEG 43720, 43721	[0155S	5535W]
Rondônia			
Cachoeira Nazaré, Rio Jiparaná	FMNH 343679 MPEG 39493, 39494	0944S	6153W
Rio Jiparaná	FMNH 330272	[0944S	6153W]
Roraima			
Rio Cotinga	Ruschi (1986)	[0355N	6030W]
Rio Maú (= Ireng River, Guyana)	Ruschi (1986)	[0333N	5951W]
GUAYANA			
Essequibo River	AMNH 482440, 482441 USNM 149383	[0659N	5832W]
Mashapu	ROM 43273		
East Berbice-Corentyne			
Haimara Camp, New River	FMNH 120094	[0323N	5736W]
Phantom Falls, New River	FMNH 120093	[0323N	5736W]
East Demerara-West Coast Berbice			
Demerara (= Georgetown)	MCZ 115450 USNM 55125, 55127, 55128, 87619	0648N	5810W
Demerara River, below Great Fall	Davis (1958)	[0519N	5831W]
Near Ituni	ROM 113115, 113116, 107324, 107327, 107531	[0530N	5814W]
Malali Rapid, Demerara River	Davis (1958)	0537N	5822W
Moraballi Creek	Nicholson (1931)	[0612N	5834W]
Mazaruni-Potaro			
Carimang River/River Carimang[1]	AMNH 482433 USNM 14982	[0554N	6035W]
River Carimany (?= Kamarang River)[1]	FMNH 46136	[0554N	6035W]
Cuyuni River	AMNH 806261, 806262, 806263 ANSP 167556	[0623N	5841W]
Kalicoon	AMNH 806260	0624N	5839W
Kartabo	AMNH 806264, 806265, 806266, 806267, 806268,		

APPENDIX 3. Continuation.

Location	Source	Latitude	Longitude
	806269, 806270, 821468, 821469, 821470	0623N	5841W
Upper Mazaruni River	AMNH 482434, 482435, 482437, 482438	[0625N	5838W]
Waruma River	USNM 609131	[0530N	6047W]
North West			
Arakaka, Rio Barima	MLZ 1132	0735N	6001W
Baramita	USNM 586322, 586323	0722N	6029W
Rupununi			
Iwokrama Reserve (several locations)	ANSP 187598, 187599, 187600, 187601, 187602, 187603, 187604	[0430N	5850W]
Rupununi River	ROM 94661	[0403N	5834W]
SURINAME			
Nickerie			
Kaiserberg Airstrip, Suid Rivier	FMNH 260235	0307N	5627W
West River, Wilhelmina Mountains	FMNH 264313	[0326N	5645W]
VENEZUELA			
Bolivar			
Eldorado	Ruschi (1986)	0644N	6138W
Gran Sabana	Meyer de Schauensee & Phelps (1978)	[0530N	6130W]
La Planada, Río Carabobo	MML 947, 951		
Monte Roraima	MML 948, 954	0512N	6044W
Upper Río Caroní	Ruschi (1986)	[0821N	6243W]
Caño Pácara	Phelps & Phelps (1958)		
Río Icabarú	Phelps & Phelps (1958)	[0445N	6215W]
Upper Río Caura, Mawoña	Phelps & Phelps (1958)	[0738N	6453W]
Upper Río Cuyuni, Carabobo	Phelps & Phelps (1958), Ruschi (1986)	0618N	6126W
Upper Río Paragua, Caño Antabari	Phelps & Phelps (1958)	[0503N	6411W]
Caño Tonoro	Phelps & Phelps (1958)	[0608N	6343W]
Cerro Guiaquinima	Phelps & Phelps (1958)	[0605N	6350W]
Salto Maisa	Phelps & Phelps (1958)	0426N	6256W
Salto María Espuma	Phelps & Phelps (1958)	0445N	6320W
Topaza pella smaragdula			
BRAZIL			
Amapá			
Clevelândia do Norte	MNRJ 18739	0349N	5152W
Macapá	USP 32042	0002N	5103W
Rio Amaparí	FMNH 295599	[0043N	5132W]

APPENDIX 3. Continuation.

Location	Source	Latitude	Longitude
Rio Maracá, Mun. Mazagão	USP 42772	0007S	5117W
Rio Maroni	Ruschi (1986)		
Serra do Navio	USNM 515479	0059N	5203W
Serra do Tumucumaque (= Tumuc-Humac Mountains)	Ruschi (1986)	[0220N	5500W]
Pará			
Baía de Caxiuana	Whitney (pers. comm.)	0145S	5120W
Rio Tapacurazinho, Transamazônica km 25	MPEG 47680	0418S	5554W
FRENCH GUIANA			
Cayenne			
Cayenne	AMNH 37698, 37699, 37701, 37703, 37704, 37705, 37706, 37707, 37708, 37762, 46070, 46571, 482442, 482445 ANSP 48226 USNM 149384, 24556	0456N	5220W
Oyapoc (= Saint-Georges)	USNM 332228	0354N	5148W
Pied Saut, Oyapock	FMNH 256767 FMNH 256768	[0354N	5148W]
Saut Tamanoir (Fleuve Mana)	CM	[0544N	5354W]
Saint-Laurent du Maroni			
Saint-Jean	MCZ 145634	0524N	5405W
Topaza pella microrhyncha			
BRAZIL			
Pará			
Anajás, Ilha de Marajó	MPEG 45767	0059S	4957W
Apehú (= Apéu)	Simon (1921)	0118S	4759W
Belém	MCZ 173829	0127S	4829W
Benevides	CM	0122S	4815W
Castanhal	ANSP 80451	0118S	4755W
Mocajutaba (?= Mocajatuba)	Simon (1921)	?0127S	4829W
Prata, near Pará (= São Jorge)	AMNH 482448	[0118S	4736W]
Rio Acará	Simon (1921)	[0140S	4825W]
Rio Mojú, Jaguaraí	MNRJ 29307	[0140S	4825W]
Rio Moraitena	ANSP 80450		
Santa Rosa, Municipio de Vigia	MPEG 30524, 30728	0048S	4808W
Utinga (mata)	USP 36409		

[1]Stephens & Traylor (1985) note that Carimang, Caramay and Caramani are alternate spellings for Kamarang River.