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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 12. *Amazilia bangsi* Ridgway, 1910, is an intrageneric hybrid, *Amazilia tzacatl* × *Amazilia rutila*

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Abstract.—*Amazilia bangsi* Ridgway, 1910, collected at Volcan de Miravalles, Costa Rica, is shown to be a hybrid between *Amazilia tzacatl* and *Amazilia rutila*.

The unique type of *Amazilia bangsi* Ridgway, 1910, was collected by C. F. Underwood (1896) at Volcan de Miravalles, Costa Rica, on 7 September 1895. Early references treated *A. bangsi* as a valid species (Ridgway 1911, Cory 1918) until Simon (1921) suggested that it represents an aberrant specimen of *A. rutila*. Bangs (1930:218) later noted in a catalog of avian types in the Museum of Comparative Zoology:

> "Simon (1921, p. 106) gives it as his opinion, without, however, having seen the type, that *bangsi* is simply an example of *rutila* with an undue amount of green feathers on the sides of the breast. I do not think that this is so, but regard the type, which is unique, as a hybrid. The type in its coloring is nearly intermediate between *A. rutila* and *A. tzacatl*, both of which are common birds in the region whence it came."

Although Bangs' brief comment was insufficient to verify the taxonomic status of *A. bangsi*, subsequent authors accepted this treatment without additional comment (Peters 1945, Gray 1958, Panov 1989, Weller 1999). Here I provide a more comprehensive assessment of *A. bangsi* employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990), as modified by the findings of Graves (1998, 1999).

Methods

The type of *Amazilia bangsi*, originally part of the E. A. and O. Bangs Collection (No. 16682), was eventually cataloged in the Museum of Comparative Zoology, Harvard University (No. 116682). Sexed as ♂ on the Bangs Collection label, the specimen appears to be adult as judged by the absence of striations on the maxillary rhamphotheca. I compared the type with all trochiline species (n = 26) that occur in the Cordillera de Guanacaste and adjacent lowlands of northwestern Costa Rica (see Underwood 1896, Carriker 1910, Slud 1964, Stiles & Skutch 1989) in the Museum of Comparative Zoology (Appendix 1). Detailed descriptions and photographs of the type were compared with series of Costa Rican species in the National Museum of Natural History, Smithsonian Institution. Descriptions in this paper refer to definitive male plumage.

Measurements of selected specimens (Table 1) were taken with digital calipers and rounded to the nearest 0.1 mm: wing chord; bill length (from anterior extension of feathers); and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix). Rectrices (R1–R5) and primaries (P1–P10) are numbered from the innermost to the outermost.

General color descriptions presented in Appendix 2 were made under natural light. I evaluated the color of the lower back and abdominal plumage (3 mm lateral of the midline) with a calibrated colorimeter (CR-

Table 1.—Range (mean ± standard deviation) of measurements (mm) of wing chord, bill length, and rectrix length (R1–R5) of adult male *Amazilia tzacatl*, *A. rutila*, and probable hybrid, *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

	Amazilia tzacatl[a] (n = 13–15)	*Amazilia rutila*[b] (n = 10–14)	"*Amazilia bangsi*" MCZ 116682
Wing	54.6–58.7 (56.9 ± 1.3)	54.9–57.0 (56.2 ± 0.8)	58.8
Bill	18.5–22.7 (20.4 ± 1.2)	18.2–20.7 (19.3 ± 0.8)	20.7
R1	30.7–32.9 (31.8 ± 0.7)	30.4–34.0 (31.9 ± 1.3)	32.1
R2	32.3–35.1 (33.8 ± 0.7)	32.1–35.9 (33.8 ± 1.3)	34.2
R3	33.3–35.7 (34.6 ± 0.6)	33.2–36.9 (34.9 ± 1.2)	35.7
R4	33.1–36.2 (35.0 ± 0.8)	33.1–37.2 (35.3 ± 1.4)	36.7
R5	32.4–35.9 (34.5 ± 1.1)	32.7–36.4 (34.7 ± 1.3)	35.7

[a] Costa Rica.

[b] Costa Rica (n = 8), Honduras (n = 6).

221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture (Table 2). The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicularly from the specimen surface is collected for color analysis. To reduce measurement variation, I held the aperture flush with the plumage without depressing the surface. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure twice (five times for the type of *A. bangsi*), removing the aperture between trials. Thus, each datum summarized in Table 2 represents the mean of 6 (parental species) or 15 (type of *A. bangsi*) independent colorimetric measurements.

Colorimetric characters are described in terms of opponent-color coordinates (L, a, b) as per Hunter & Harold (1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), green-red ($+a/-a$), and blue-yellow ($+b/-b$). The rationale is that a color cannot be perceived as red and green or as yellow and blue at the

Table 2.—Minima, maxima, and means (± standard deviation) of opponent color coordinates (L, a, b) of rectrix 1 (R1) of adult male *Amazilia tzacatl*, *A. rutila*, and probable hybrid, *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

		Amazilia tzacatl (n = 15)			*Amazilia rutila* (n = 8)			"*Amazilia bangsi*"
		Min.	Max.	Mean (± SD)	Min.	Max.	Mean (± SD)	MCZ 116682
Back	L	28.7	35.4	32.9 (± 1.7)	32.8	37.4	35.5 (± 1.6)	35.0
	a	−10.3	1.1	−3.4 (± 3.1)	−3.0	1.0	−1.0 (± 1.5)	1.9
	b	16.7	29.5	23.8 (± 3.9)	14.7	21.5	18.1 (± 2.3)	24.7
Abdomen	L	35.3	47.7	40.6 (± 3.0)	42.5	49.1	46.8 (± 2.3)	42.6
	a	−1.2	3.0	1.3 (± 1.5)	5.0	14.6	10.4 (± 2.7)	10.5
	b	7.7	18.5	12.3 (± 3.1)	16.5	28.3	24.4 (± 3.5)	23.1

same time. Therefore "redness" and "greenness" can be expressed as a single value *a*, which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by $+b$ for yellows and $-b$ for blues. The third coordinate, *L*, ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage, the higher the *L* value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans, and the relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. In any case, the *L,a,b* color system permits plumage color to be unambiguously characterized for taxonomic purposes.

Results and Discussion

I considered three hypotheses proposed by previous authors: *Amazilia bangsi* represents (1) a subdefinitive plumage, color morph, or geographic variant of *Amazilia rutila* or some other species (Simon 1921); (2) a hybrid, *Amazilia tzacatl* × *Amazilia rutila* (Bangs 1930); or (3) a valid species (Ridgway 1910). For brevity I use the epithet, *bangsi*, in the remainder of the paper.

Populations of *Amazilia tzacatl* and *A. rutila* from northwestern Costa Rica are adequately represented in museum collections (Carriker 1910). I found no evidence that *bangsi* represented a subdefinitive plumage, color morph, or geographic variant of either of these species or any other taxon. Rather, all evidence suggests that *bangsi* represents an intrageneric hybrid.

The hybrid diagnosis focuses on the identification of apomorphic character states in putative hybrids (Graves 1990). However, complete dominance and polygenic inheritance of plumage characters may preclude or obscure the expression of parental apomorphies in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of a suite of plesiomorphic characters. Plumage and soft-part characters of *bangsi* that facilitated the identification of its parental species include: (a) ventral plumage from chin to undertail coverts predominately cinnamon-buff (Fig. 1); (b) feathers along the sides of the throat and breast spangled with dull pale green subterminal spots; (c) rectrices (R1–R5) dark rufous tipped with bronze; (d) mandibular ramphotheca predominately yellowish-brown (probably reddish-orange or red in life); and (e) shallowly forked tail (fork depth = 5.6 mm). Perhaps as informative, *bangsi* lacks several conspicuous traits that are present in some potential parental species (Appendix 1): (a) contrasting rump band; (b) brilliant frontlet or coronal patch; (c) brilliant gorget; (d) pronounced blue or violet iridescence on body plumage; (e) white spots on rectrices; and (f) thickened rachises of primaries (P8–P10).

The combination of plumage characters observed in *bangsi* can be derived from only a single pair of species—*A. tzacatl* × *A. rutila* (see Appendix 2 for comparative description of plumages). Other pairwise combinations of species can be eliminated from consideration because they either lack characters found in *bangsi*, or possess one or more distinctive characters that are not expressed, even subtly, in *bangsi*. Colorimetric values largely corroborate the visual impression that plumage color of *bangsi* is intermediate between that of the postulated parental species (Table 2, Fig. 2).

I tested the parental hypothesis by examining size and external proportions (Table 1). Measurements of trochiline hybrids invariably fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (Banks & Johnson 1961; Graves 1990, 1996). *Amazilia tzacatl* and *A. rutila* are very similar in size and the percent difference in character means is negligible (larger species divided by smaller): wing chord (1.2%), bill length (5.7%), R1

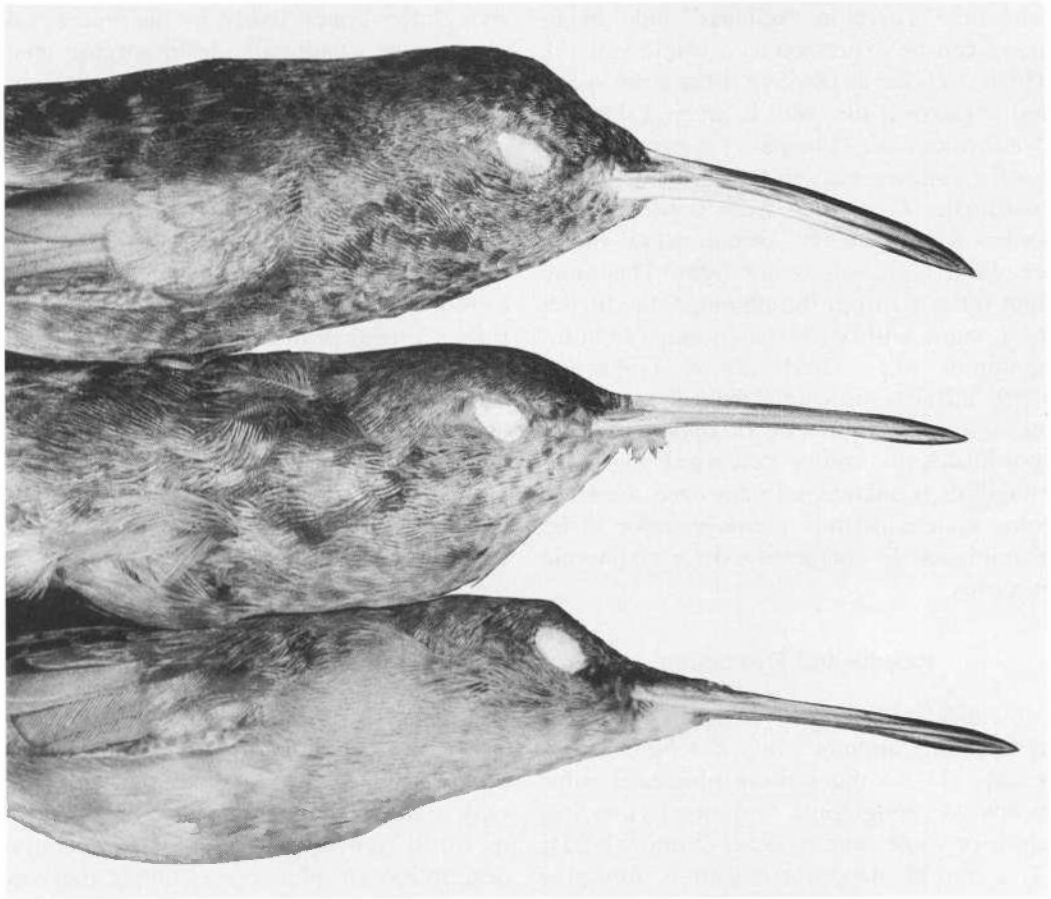

Fig. 1. Lateral views of adult males: *Amazilia tzacatl* (top), *A. rutila* (bottom), and probable hybrid (middle), *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

(0.3%), R2 (0.0%), R3 (0.9%), R4 (0.9%), and R5 (0.6%). Measurements of *bangsi* fall within the cumulative range of parental measurements for six of the seven measurements (the wing chord of *bangsi* was 0.1 mm longer than the largest value recorded for that character in the parental species). There have been no well-documented cases of morphological luxuriance (where the size of hybrid offspring exceeds that of the parental species) among avian hybrids (Graves 1990, 1996). I suspect that the cumulative range of measurements for wing chord in the parental species would overlap the hybrid value if the sample size was increased. Had the measurements of *bangsi* occurred well outside (e.g., >3% larger) the range of those of *A. tzacatl* and *A. rutila*, this particular hybrid hypothesis would have been rejected.

In summary, concordance of results from analyses of plumage color and external measurements provides strong support for the hypothesis that *bangsi* is an intrageneric hybrid between *A. tzacatl* and *A. rutila*. *Amazilia bangsi* Ridgway, 1910, is thus available in taxonomy only for the purposes of homonymy. The parental species are sympatric from the Yucatan Peninsula (Howell & Webb 1995) south to northwestern Costa Rica, particularly in the transition zone between dry thorn forest and semi-humid forest (Underwood 1896, Carriker 1910, Slud 1964, Stiles & Skutch 1989).

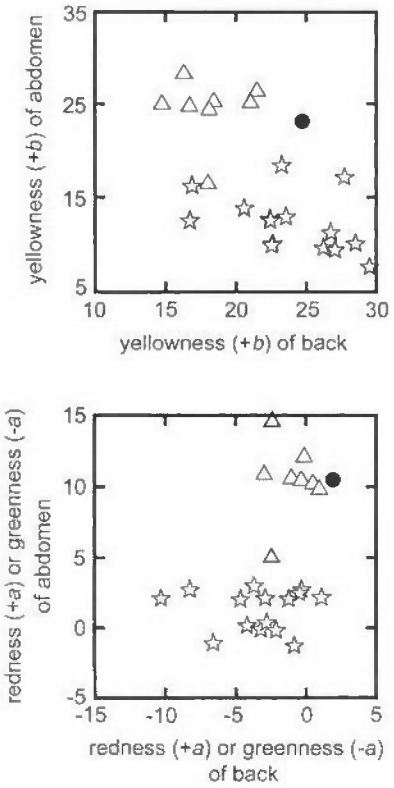

Fig. 2. Bivariate relationships of *L*, *a*, *b* color coordinates: *Amazilia tzacatl* (☆), *A. rutila* (△), and probable hybrid (●), *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

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Appendix 1

Species of trochiline hummingbirds that occur regularly in the Cordillera de Guanacaste and adjacent lowlands of northwestern Costa Rica (see Underwood 1896, Carriker 1910, Slud 1964, Stiles & Skutch 1989). Taxonomy follows Sibley & Monroe (1990). Parentheses enclose a representative list of characters or traits that would probably be expressed in hybrid progeny of these species, but that do not occur in the type of *Amazilia bangsi* Ridgway, 1910 (MCZ 116682): *Phaeochroa cuvierii* (white spots on R4–R5; thickened rachises of P8–P10); *Campylopterus hemileucurus* (purple head and breast; white spots on R3–R5; thickened rachises of P8–P10); *Florisuga mellivora* (blue head and breast; white collar; R1–R5 white with black tips); *Colibri delphinae* (violet auricular patch); *Anthracothorax prevostii* (black throat; purple rectrices); *Klais guimeti* (violet crown and throat; white tips on R2–R5); *Lophornis helenae* (elongated black head plumes; white rump band); *Chlorostilbon canivetii* (black tail); *Thalurania colombica* (purplish-black rectrices; violet crown, lower breast, flanks, and abdomen); *Panterpe insignis* (brilliant coppery-orange throat; blue crown; bluish-black rectrices); *Hylocharis eliciae* (golden-green tail; blue throat); *Amazilia amabilis* (bluish-violet upper breast; black rectrices); *Amazilia saucerrottei* (steel-blue tail); *Amazilia cyanura* (blackish-violet rectrices); *Amazilia rutila; Amazilia tzacatl; Eupherusa eximia* (white medial vanes of R2–R5); *Elvira cupreiceps* (R2–R5 white); *Microchera albocoronata* (white crown; white vanes on R2–R5; deep maroon body plumage); *Chalybura urochrysia* (bronzy-black rectrices; pale feet in dried skin); *Lampornis castaneoventris* (brilliant green crown; purple gorget; bluish-black rectrices); *Heliodoxa jacula* (brilliant green crown; small blue gorget spot; bluish-black rectrices); *Heliothryx barroti* (R3–R5 white; violet crown; white ventral plumage); *Heliomaster constantii* (red gorget; white facial stripe; white tips on R3–R5); *Heliomaster longirostris* (reddish-violet gorget; white facial stripe; brilliant bluish-green crown; white tips on R4–R5); *Philodice bryantae* (purple gorget; white pectoral band; white flank tufts).

Appendix 2

Abridged description of adult male *Amazilia tzacatl*, *A. rutila*, and a probable hybrid, *A. tzacatl* × *A. rutila* (= *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

The forecrown and crown of *tzacatl* are dark bronze becoming dark green on the hind neck, lesser and median wing coverts, and back, changing to bronzy-green or bronze on the upper tail coverts. The dorsum of *rutila* is similar in color but slightly paler and less iridescent (particularly on the lower back and rump) owing to narrow buffy feather margins. The color and quality of iridescence of the dorsum in *bangsi* are intermediate to those of *tzacatl* and *rutila*. The rectrices (R1–R5) of *tzacatl*, *rutila*, and *bangsi* share a similar color pattern. Rectrices are chestnut broadly tipped with bronze in *rutila*, slightly darker in *tzacatl*. The rectrices of *bangsi* are intermediate in appearance between those of *rutila* and *tzacatl*. Likewise, the greater wing coverts, secondaries, and primaries of *bangsi* are intermediate in appearance between those of the postulated parental species. Underwing coverts are dark glossy green in *tzacatl*, dull green broadly tipped with buff or rufous in *rutila*, and intermediate in appearance in *bangsi*. Primaries and secondaries of *tzacatl*, *rutila*, and *bangsi* lack rufous or chestnut pigmentation. Rachises of *tzacatl*, *rutila*, and *bangsi* are unmodified.

The chin, throat, breast, and flanks of *tzacatl* are dark green (the throat and upper breast are glowing golden-green when viewed head-on). Grayish feather margins on the abdomen become progressively wider from the sides to the ventral midline; the center of the abdomen is buffy-gray. Undertail coverts are chestnut or dark rufous. The ventral plumage of *rutila* from chin to undertail coverts is buffy-cinnamon, palest on the throat (feathers with narrow buffy margins in many individuals). Ventrally, *bangsi* is most similar to *rutila* but shows the influence of a "green breasted" parental species, particularly along the sides of the throat and upper breast where feathers have dull, pale green, subterminal disks which are broadly margined with buff. Feather of the chin and upper throat of *bangsi* are cinnamon-buff margined with very pale buff. Scattered feathers across the center of the lower throat have small greenish-bronze subterminal disks. The midline of the abdomen of *bangsi* is cinnamomeous as in *rutila* but duller with grayish tones. Undertail coverts of *bangsi* are intermediate in color but closer to *rutila* than to *tzacatl*. The maxillary and mandibular rhamphotheca of *tzacatl*, *rutila*, and *bangsi* are pale yellowish-brown (red in life) tipped with dark brown or blackish-brown (20–30% of the bill length).