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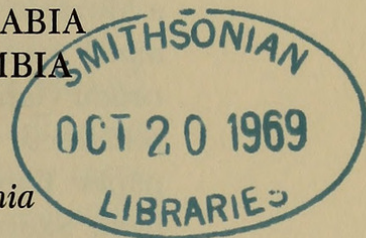
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THE RED-THROATED ANT-TANAGER (*HABIA FUSCICAUDA*) IN PANAMA AND COLOMBIA

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The Red-throated Ant-tanager (*Habia fuscicauda*) is principally a species of Middle America (see map in Willis, 1960: 151). It was formerly considered to be conspecific with the isolated Sooty Ant-tanager (*H. gutturalis*) of the middle Magdalena and other valleys of the Colombian Andean region (Meyer de Schauensee, 1966: 484-485), and much of the literature of the Red-throated Ant-tanager appears under the specific name *Habia gutturalis*. Both morphological and behavioral evidence (*fide* E. O. Willis) indicate that *gutturalis* and *fuscicauda* are best kept as separate species.

At the southern end of its range *H. fuscicauda* appears to have a rather interrupted distribution, in eastern Panamá and Colombia. Meyer de Schauensee (1966: 485) gives the South American range as follows: "COLOMBIA, Caribbean coastal region west of the río Magdalena from Atlántico to Córdoba (upper Sinú valley), possibly Santa Marta but no authentic records." Carriker (1955: 60) doubted the Atlántico "sight" record (Santa Cruz, Los Pendales) that had earlier been accepted by Meyer de Schauensee (1951: 1054), although Carriker conceded that the species might occur north to the hills of central Atlántico. Hellmayr (1936: 314) examined a specimen alleged to have been taken at Barranquilla, Atlántico, but Meyer de Schauensee (1951: 1054) placed this locality in quotation marks, presumably an indication that he believed the "Barranquilla" specimen to have been a native trade skin of uncertain origin.

The name *Phoenicotheraupis erythrolaema* Sclater, 1862, was based on a manuscript name of Bonaparte, attached to specimens in the Verreaux collection attributed to "S. Martha, New Grenada" (= Santa Marta, Colombia). Sclater compared his *erythrolaema* only to "*Phoenicotheraupis rubicoides*," which is a Mexican subspecies of another species, *Habia rubica*. Sclater's name was placed in the synonymy of *Phoenicotheraupis fuscicauda* Cabanis (Costa Rica) by Lawrence (1863: 9), where it remained until revived by Bangs (1900: 30). In the latter paper Bangs attributed to *erythrolaema* a range "extending from Santa Marta to Panama," but later Thayer and Bangs (1906: 222) expressed some doubt as to the correctness of the alleged provenience of the type, as no ant-tanagers had been collected subsequently in the Santa Marta region. Todd and Carriker (1922: 483) agreed, and considered the Santa Marta locality to be almost certainly erroneous. They did not, however, venture to conjecture about the actual origin of the type of *erythrolaema*, mentioning merely that the name had been applied to the Panamá form by Bangs.

As a brief digression, it should be mentioned that since 1922 the generic name *Habia* Blyth, 1840, has been used for the ant-tanagers in place of *Phoenicotheraupis* Cabanis, 1851. The latter generic name (and, in fact, its root *Thraupis*) has been variously treated in the literature as being of masculine or feminine gender. To avoid confusion, all names in the present paper, except when quoted directly, will be treated as feminine, in agreement with the current generic name *Habia*.

In January 1916 Carriker collected for Carnegie Museum a series of ant-tanagers near Turbaco, Bolívar, Colombia, just inland from Cartagena. Tood (1917), in a brief "preliminary diagnosis," described the Turbaco birds as a new species, *Phoenicotheraupis rubiginosus*. He compared the male with "*Phoenicotheraupis salvini salvini*" (= *Habia fuscicauda salvini*, type locality Vera Paz, Guatemala), and the female with Costa Rican *fuscicauda*. He did not mention *erythrolaema*. Todd's unpublished notes, filed at Carnegie Museum, go into more detail than did his formal published diagnosis of "*rubiginosus*." He dismisses the name *erythrolaema* from consideration for his

new Colombian species, partly on the basis that the type locality Santa Marta was probably erroneous, and partly because several authors had considered males of *erythrolaema* inseparable from *fuscicauda*, whereas in Todd's opinion males of "*rubiginosus*" were barely separable from *salvini*. Todd did not list his comparative material of *salvini*, but it was presumably the series from British Honduras then available in Carnegie Museum, which is indeed best referred to *salvini*, *contra* Russell (1964: 173). Later Todd added to his notes the following statement: "Panama skins (*erythrolaema*) prove upon comparison to be so exactly intermediate in all respects between *fuscicauda* and *rubiginosa* that the only course open is to make all three forms conspecific." These observations are undated, and were probably made independently of those of Dwight and Griscom (1924: 5). In any case, the latter authors were the first to point out in print that *three* forms were possibly involved: *fuscicauda* of Costa Rica; *erythrolaema* from "somewhere on the north coast of Colombia," with *rubiginosa* Todd as a synonym; and an *unnamed* Panamanian race of *fuscicauda*, to which the name "*erythrolaema*" had been erroneously applied by Thayer and Bangs. In the principal standard reference work on New World birds, Hellmayr (1936: 314) briefly reviewed this history, and synonymized *rubiginosa* Todd with *erythrolaema*, on the basis that he could not separate an adult male from Baranquilla from a series from along the Panamá Railroad (but see above on the status of this "Barranquilla" specimen). Hellmayr, in a lengthy footnote, paraphrased a letter from Todd concerning the latter's opinion of the validity of *rubiginosa* after having examined specimens at the British Museum. Hellmayr's wording is ambiguous, and it is not always clear whether Hellmayr or Todd is responsible for a given statement. I therefore consulted the carbon of Todd's original letter to Hellmayr, dated 1 August 1934. Todd's findings were (1) as he had already noted on his file card, his *rubiginosa* was not a good species but was conspecific with *fuscicauda* of Costa Rica; (2) Panamá specimens were "clearly intermediate" between those of Costa Rica and those of Colombia, for which he advocated use of his name *rubiginosa*; (3)

the type of *erythrolaema* was "rather faded" but appeared to belong to the Panamá race; (4) the name *erythrolaema* was therefore available for the Panamá birds, but Todd's inclination was to recognize only the extreme forms *fuscicauda* and *rubiginosa*, suppressing the name *erythrolaema* entirely. Hellmayr obviously disagreed with these findings, preferring to unite Panamanian and Colombian birds under the older name *erythrolaema*.

No further developments in the nomenclatorial history of these ant-tanagers took place until 1955, when Carriker designated the type locality of "*erythrolaemus*" [*sic* = *erythrolaema*] as Turbaco, Colombia (where he had collected ant-tanagers in 1916), stating that the type specimen probably came from near Cartagena. Carriker inadvertently gave the original supposed origin of the type as "Magdalena"; as stated above, the type locality was given as "S. Martha," or Santa Marta. This action of Carriker's would make *rubiginosa* Todd an objective synonym of *erythrolaema* Sclater, unless it could be demonstrated that the type of *erythrolaema* probably did *not* come from the vicinity of Cartagena (International Code of Zoological Nomenclature, 1964, Recommendation 72E). Carriker did not examine the type of *erythrolaema*, and accepted without question its identity with the birds of Turbaco.

The suggestion of Dwight and Griscom (1924: 5) that the Panamanian population of *fuscicauda* might need a name was never pursued, all subsequent writers having accepted Hellmayr's usage. As pointed out by Carriker (1955), the only modern specimens from Caribbean Colombia, and the only ones with accurate locality data, are those he himself collected in 1916 and 1942. The former series, as stated above, is in Carnegie Museum, the latter in the Smithsonian Institution. Far more material is now available than was true when Hellmayr, Todd and other previously mentioned writers studied these ant-tanagers. Central to the problem remained the status of the name *erythrolaema*. Through the courtesy of Dr. David Snow I was able to borrow Sclater's type specimen, in order to try to settle the matter once and for all.

Upon comparison of the type of *erythrolaema* (BM 1885-6-

12-681) with Panamanian birds and with the type series of *rubiginosa*, I disagree with Todd on two counts. This specimen, although now well over a century old, does *not* appear to me to be "rather faded"—no more so than the now 53-year-old specimens of *rubiginosa*, or a 69-year-old Panamanian specimen at hand. And I do *not* consider it to be "identical" (Hellmayr's word) with the Panamanian birds.

The type of *erythrolaema* is an almost perfect match for CM 52413, the only specimen in the type series of *rubiginosa* that was *not* taken at Turbaco. It was collected by Carriker at Puerto Zapote, Bolívar, which (according to Meyer de Schauensee, 1948: 324) is the same as Cispata, on the east side of Cispata Bay, opposite the mouth of the Río Sinú, or about 125 kilometers farther southwest along the coast (toward Panamá) than Turbaco. Both the type and the Cispata bird are somewhat intermediate between the Turbaco series and the Panamanian form. In view of the extensive deforestation that has taken place all along this part of Caribbean Colombia, it is impossible to say whether this species may not once have had an essentially uninterrupted range from eastern Panamá to the vicinity at least of Cartagena; the intermediacy of the Cispata bird at least suggests that there has been gene flow. Since the type of *erythrolaema* does *not* match Turbaco birds, I would reject Carriker's designation of Turbaco as the type locality, and substitute "vicinity of the mouth of the Río Sinú"; the specimen was probably obtained from a professional collector, or native plumage hunters, for the Verreaux collection. Specimens of this era labelled "Santa Marta" (or one of the variant spellings) could have come from any of several different parts of Colombia (Todd and Carriker, 1922: 21-22). The type locality, therefore, may best be fixed on the basis of the characters of the type specimen, which, as stated above, match the bird from the mouth of the Río Sinú.

Although *erythrolaema* is therefore not absolutely identical with Todd's *rubiginosa*, I would recommend using the name *erythrolaema* for all of the Caribbean Colombian *Habia fuscicauda*, considering *rubiginosa* as a synonym. Contrary to Todd, I find the type of *erythrolaema* nearer the Turbaco series than

to those of Panamá in color. In the light of the extensive deforestation, it will be interesting to see whether any remnant populations of this species are rediscovered in what is now the apparent distributional gap between eastern San Blas, Panamá, and the Río Sinú in Colombia. One would predict that such birds might well represent additional intermediates, stages along a former cline between the extreme ("*rubiginosa*") type of the Turbaco region and the "typical" Panamanian birds of central Panamá.

The Panamanian birds remain to be discussed. In spite of the fact that they have hitherto been included nomenclatorially with the Colombia birds, those of Panamá are (as predicted by Dwight and Griscom, 1924) a perfectly recognizable subspecies, rather more like Costa Rican *fuscicauda* than like the Turbaco birds. The Panamá birds may be known as:

***Habia fuscicauda willisi* new subspecies**

Holotype: United States National Museum no. 445515, adult ♂, from Boca del Río Indio, Colón, Panamá, collected by Alexander Wetmore and W. M. Perrygo on 15 February 1962 (original number 16757).

Characters: Definitively plumaged males differ from *erythrolaema* as follows: throat deeper and richer red; throat/breast color transition more abrupt (whereas in *erythrolaema* there is a fairly abrupt breast/abdomen transition); breast and abdomen much darker and grayer; flanks heavily washed with gray; midventral region and under tail coverts dark red with either a scarlet or bluish tinge, not rose or orange; black spot of malar region averaging more extensive, occupying much of subocular region; ear coverts darker; crest feathers somewhat more elongated; crown patch larger, darker and more intensely red; dorsum darker, more purplish red; wings and tail much darker, almost black in some individuals. Females differ from *erythrolaema* as follows: throat patch deeper, more intense yellow, abruptly contrasting with breast rather than blending with breast color; posterior underparts very much darker—dark, dull olive brown with a yellowish wash medially, rather than grayish yellow, somewhat browner on the flanks as in *erythrolaema*; under tail coverts darker and browner; ear coverts dark olive brown rather than light yellowish brown; back, wings, and tail all darker.

Definitively plumaged males differ from *fuscicauda* as follows: throat more brilliantly red; posterior underparts, on the average, less shaded with gray, the red tending toward pinkish or bluish rather than toward brownish or orange; dorsum averaging lighter and brighter, of either a purer or bluer, less brick red; crest purer, less orange red; tipping of crest feathers in fresh plumage browner, less black. Females differ from

fuscicauda as follows: throat deeper, more brilliant yellow; little or no brownish band across breast; posterior underparts paler, less washed with dark brown; abdomen with much more yellow wash; dorsum less brownish, more greenish; crown more greenish yellow, less ochraceous yellow.

Range: central Panamá, chiefly on the Caribbean slope. Specimens were examined from the provinces of Colón, northeasternmost Coclé, Panamá, and westernmost San Blas (Mandinga), as well as from the Canal Zone. Western Bocas del Toro province (Almirante and vicinity) is inhabited by typical *fuscicauda*. A series of 9 specimens in the AMNH collection from Santa Fé, northern Veraguas, is highly variable, and represents intergradation between *fuscicauda* and *willisi*. Santa Fé is just about halfway between Almirante and the type locality of *willisi*. Eugene Eisenmann has kindly supplied the following information: "In Panamá this species is primarily a bird of the humid Caribbean slope, though it has crossed over to the Pacific slope at low divides in Veraguas, as at Santa Fé, and eastward in Panamá province and the Canal Zone, where sufficiently humid conditions and shady woodland exist." The apparent gap in the range of the species between northwestern Bocas del Toro and central Colón (except for the one series from Santa Fé) is interpreted by Eisenmann as due partly to inadequate collecting and partly to unsuitably mature forest with too little undergrowth. As in the case of the bird from the Río Sinú in Colombia, the intermediacy of the Santa Fé specimens suggests populations in sufficient contact for gene exchange.

From the Pacific slope there are specimens from the Canal Zone and from adjacent Panamá province east to the Río Pacora, about 35 miles east of the city of Panamá (USNM—Wetmore). West of the Canal Zone and east of Santa Fé I have seen only a single first-year male in Carnegie Museum collected by A. C. Twomey at Capiरा, Panamá province. Both Willis and Eisenmann have observed this species (with army ants) on Cerro Campana, a few miles beyond Capiरा, which Eisenmann's notes characterize as "a low mountain right on the divide . . . extremely humid at the upper levels."

Hellmayr (1936: 314) listed a supposed record of "*Phoenicotheraupis fuscicauda*" from the Río Lara, Darien, based on a specimen collected by Festa in 1895 and published by Salvadori and Festa (Bol. Mus. Zool. Anat. Comp. R. Univ. Torino, 14, no. 339, 1899: 4—original publication not seen). Dr. Wetmore (letter of 16 January 1969) believes this record to be erroneous and probably based on a specimen of *Habia rubica*. Assuming Dr. Wetmore to be correct in this assumption, there are no specimen records of *Habia fuscicauda* east of the Río Pacora and Río Mandinga in Panamá or west of the Río Sinú in Colombia. One sight record from the intervening area is believed by Eisenmann to be worthy of serious consideration. According to information supplied to me by Eisenmann, Dennis R. Sheets reported "several pairs heard, one seen" low down in overgrown thickets above Puerto Obaldía, on the trail to La Bonga, 16–18 June 1965. Puerto Obaldía is in easternmost San

Blas, virtually on the Colombian border, and thus just about halfway between the extreme known specimen localities given above. Eisenmann informs me that Sheets was well acquainted with this ant-tanager in the Canal Zone, and in view of the highly distinctive nature of its vocalizations it is unlikely that another species was mistaken by Sheets for *H. fuscicauda*. The superficially similar Red-crowned Ant-tanager (*Habia rubica*), which is quite different in voice from *H. fuscicauda*, is not known from the Caribbean slope of Panamá (*vide* Eisenmann).

Etymology: it is most appropriate that this subspecies of ant-tanager should be named for Dr. Edwin O. Willis, who has contributed so much to our knowledge of the biology of the tanagers of the genus *Habia*.

Specimens examined: This study was based on the combined series of the pertinent forms belonging to Carnegie Museum, the United States National Museum, and the American Museum of Natural History, plus a series from the Museum of Comparative Zoology, and the type of *erythrolaema*. The total number examined is as follows: *H. f. fuscicauda*, 42 from Costa Rica and 11 from Panamá; *H. f. fuscicauda* \times *willisi*, 9 from Santa Fé, Veraguas, Panamá; *H. f. willisi*, 121 from Panamá; *H. f. erythrolaema*, 21 from Colombia.

Thayer and Bangs (1906: 222) claimed that specimens from the savannas near the city of Panamá, on the Pacific slope, were the same as *erythrolaema*, and more pallid than those from Loma del Leon (in the area now occupied by the Canal Zone). The latter they ascribed to "true *P. fuscicauda*." I have examined the two series involved, and find that the savanna series does, on the whole, average slightly paler. This may well be attributable, at least in part, to the fact that they are May specimens, and thus more worn than the March birds from Loma del Leon. The minor differences between the two series are bridged by individual variation, which tends to be strong in this species, and all may be called *willisi*. Loma del Leon birds are not *fuscicauda* nor are the savanna birds *erythrolaema*.

Acknowledgments: I am indebted to the authorities of the Smithsonian Institution and the American Museum of Natural History for access to their collections. Dr. David Snow of the British Museum (Natural History) was good enough to arrange to have the type of *Phoenicotheraupis erythrolaema* sent on loan. Dr. Raymond A. Paynter, Jr., lent the Panamá specimens from the Museum of Comparative Zoology that had been discussed by Thayer and Bangs. Dr. Alexander Wetmore allowed me to use collections of Panamanian and Colombian birds set aside for his personal research, and provided additional useful information about the distribution of *Habia fuscicauda* in those countries. Finally, Mr. Eugene Eisenmann kindly extracted from his notes on Panamá birds everything pertaining to the distribution and habitats of ant-tanagers in that country, and made this information freely available to me.

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