

A new species of flycatcher in the *Tolmomyias assimilis* radiation from the lower Sucunduri-Tapajós interfluvium in central Amazonian Brazil heralds a new chapter in Amazonian biogeography

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In July, 1995, BMW and Sally Conyne departed by boat from Santarém, Pará to travel up the Rio Tapajós to make tape-recordings of a number of species of birds at their type localities. They anchored at the old, left-bank town of Boím on 16 July, and made their way into tall *terra firme* forest about 25 km west of the river via a recently opened logging road. Over the course of work at this site and a week or so later, above Itaituba at the important Sneath locality “Vila Braga,” BMW heard and recorded a distinctive song from a canopy flycatcher that he recognized as an undescribed, species-level representative of the widespread *Tolmomyias*³ *assimilis* (Yellow-margined Flycatcher) complex based on parallels in its vocalizations and behavior and the biogeography of the group. He made further recordings of the bird near the town of Maués in the state of Amazonas in July, 2002, and organized a collecting expedition to that area through the Museum of Zoology of the University of São Paulo (MZUSP) in July, 2008. Several specimens of the new *Tolmomyias* were voice-recorded and collected on that expedition, but it was decided to wait to describe the species until its western range limit could be determined, which BMW hypothesized to be the right bank of the Rio Canumã/Sucunduri, where turnover to nominate *T. assimilis* was expected to occur. A week of solo fieldwork on the lower Canumã and Sucunduri in July, 2010, confirmed that these rivers mark the longitudinal limits of the two *Tolmomyias* species as well as many other species-pairs of birds under study. In July–August, 2012, BMW directed a joint field expedition of the MZUSP and the Louisiana State University Museum of Natural Science (LSUMNS), largely funded by The National Geographic Society, to that region that resulted in collection of an additional specimen of the new flycatcher and samples of many other common birds.

Most importantly, however, that expedition, through the description of this new species, introduces two previously undescribed avian distribution patterns crucial to interpreting paleohistorical determinants of Amazonian biogeography in general: 1) the Rio Canumã/Sucunduri has been the most influential barrier to population expansion, thus directing speciation dynamics, across the entire Madeira-Tapajós interfluvium; and 2) there exists a pervasive pattern of replacements and drop-outs among named and unnamed taxa along a broad latitudinal and ecological gradient independent of any rivers. Focused study of both of these patterns and the processes that gave rise to them together with documentation of genetic introgression levels among numerous populations of birds across the Madeira-Tapajós interfluvium are the subjects of ongoing research to be illuminated in detail in future publications. For the present, to call particular attention to the seminal role of the Rio Sucunduri, we propose that this unnamed *Tolmomyias* flycatcher be henceforth known as:

Tolmomyias sucunduri Sucunduri Yellow-margined Flycatcher *Bico-chato-do-sucunduri* (Portuguese)



Holotype.— MZUSP 86976, adult female from Brazil: Amazonas; left bank rio Parauri about 6 km above cachoeira Tambor (05°04'02"S/58°02'40"W) at about 70 m elevation; collected 22 July 2009 by Fabio Schunck and Marco Antonio Rêgo, prepared by Paulo César Balduino. Voice recorded by Bret M. Whitney, original numbers BMW-7236 and 7237; Macaulay Library of Natural Sounds (ML) 169979. Pectoral muscle tissue preserved in approximately 96% alcohol: MZUSP 86976, field number 306.

Diagnosis: Morphology.— Distinguished from neighboring *T. a. assimilis*, *T. a. calamae*, and *T. a. paraensis* by notably darker and more uniformly leaden gray crown and slightly darker green back. **Voice.**— Distinguished in the field and in spectrographic

analysis by the widely modulated structure of the two or three loudest (most clearly audible) notes in the song resulting in a distinctive “washboard” quality to these notes strikingly different from all other taxa (see *Vocalizations*, below).

Distribution.— Central Amazonian Brazil from the right bank of the Rio Canumã and Rio Sucunduri in Amazonas east to the left bank of the lower Rio Tapajós in Pará south to approximately 05°40'S (Fig. 1; see *Range delimitation and Relationships*, below).

Description of holotype.— See color illustration and Figure 2 (paratype MZUSP 86974). Capitalized color designations (corresponding number in parentheses) from Smithe (1975). Alphanumeric color designation of the crown deter-

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³ Genus *Tolmomyias* 9: 338.

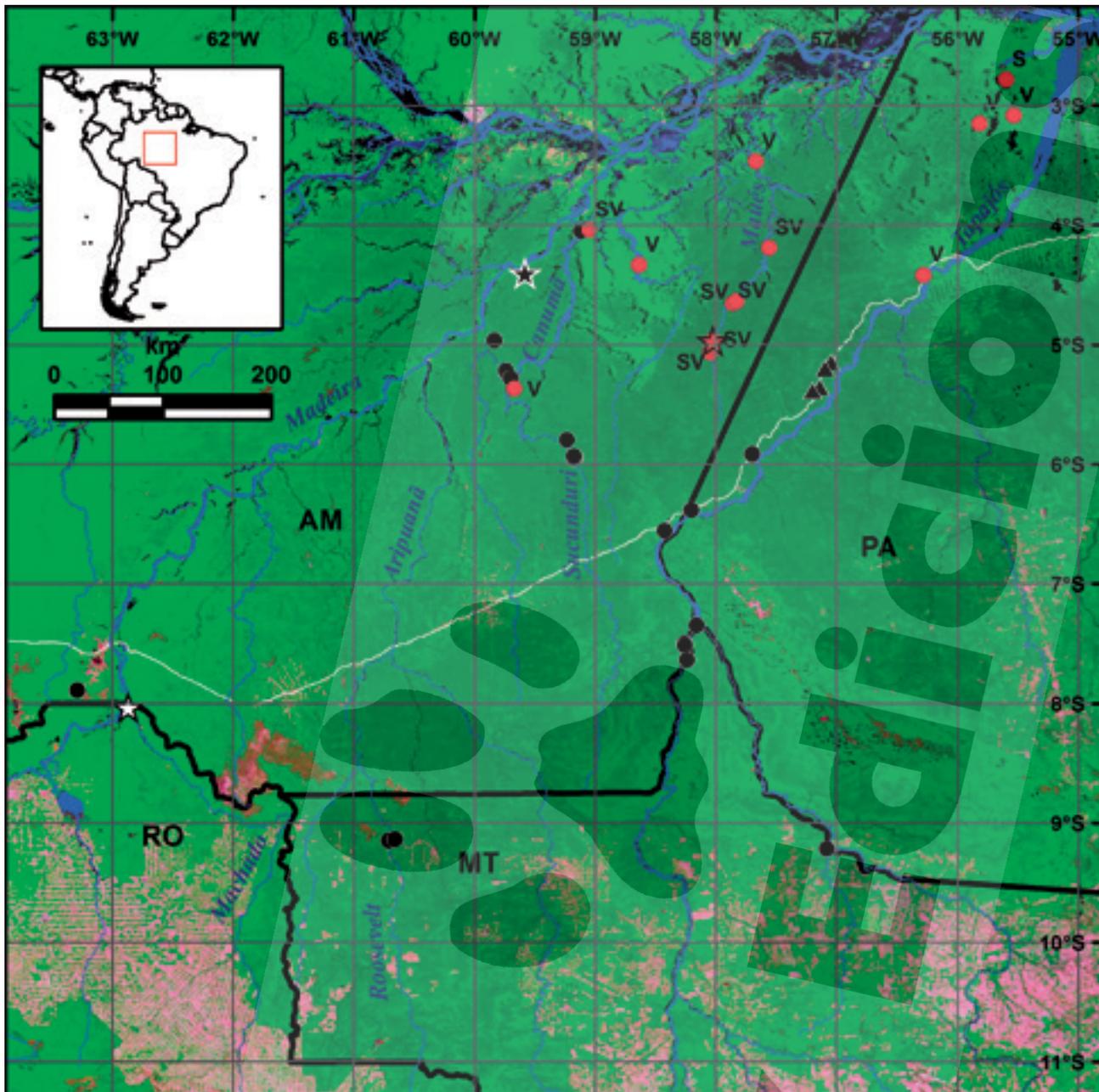


Figure 1. Geographic distribution of *Tolmomyias sucunduri* and some other members of the *T. assimilis* complex in central Amazonian Brazil. Red dots = *T. sucunduri*. Red star = type locality of *T. sucunduri* near Maués, Amazonas, Brazil. Letters adjacent to red locality dots provide documentation: S = specimen; V = vocal recording. Black dots = other members of the *T. assimilis* complex represented by specimens voice-recorded before collection (see SI for a list with specimen numbers; we have many other localities represented by either specimens or recordings). Black star = type locality of *T. assimilis assimilis*. White star = type locality of *T. assimilis calamae*. Black triangle = postulated hybrid or intergrade between *T. sucunduri* and *T. a. assimilis/calamae*, specimen voice-recorded before collection. Black lines mark the boundaries of Brazilian states as indicated by their official abbreviations: AM = Amazonas; RO = Rondônia; MT = Mato Grosso. The federal highway BR-230 ("Transamazônica") is shown in white.

mined through direct comparison with Munsell soil color charts (1994); the description in quotation marks is the chart designation. Plumage fresh and unworn, no wing molt (but P10 missing on left side); rectrices not fully grown on left side; skull ossification not recorded. Numerous long (some exceeding 10 mm) black rictal bristles at base of bill around commissure and over nares. Crown from base of bill through nuchal region uniform "dark bluish gray" (nearest chart 2 for Gley 4/5PB), some feather edges of nape tinged slightly olive contrasting notably with the uniform Greenish Olive (color 49) upperparts. Lores and tiny feathers above base of bill whitish. Visage plain, lacking any areas of strong contrast, dark or light, around the eyes or auriculars but photos of the bird at the time of collection (as in Fig. 2) show a pale eyering concentrated along the upper edge of the orbit. Lower facial region, chin and upper throat dull whitish contrasting moderately with the gray crown and blending posteriorly toward yellowish, picking up a weak olive tinge through the breast. Sides and flanks yellowish olive becoming clear yellow (brighter than Sulphur Yellow 157) on the belly and undertail coverts. Upperwing coverts black with pale markings as follows: lesser and median coverts with an Olive Green (aux. 47) spot on distal web at feather tip; greater coverts with well-defined and more contrasting yellow (near Sulphur Yellow 157) margins to distal webs extending to feather vane. Primaries 9 and 8 are of equal length and longest, about 1 mm longer than P7 which is about 2 mm longer than P6; P10 is about 2 mm longer than P4. Distal margins of primaries and, especially, secondaries conspicuously fringed same yellow as edging on upperwing coverts and contrasting inside the dark primary stack. Anterior edge of primary stack marked by an approximately 7-mm long, pale wedge formed by conspicuous, white distal margins near the bases of P7 and P6, with that on P5 slightly shorter, and only very short and

fainter margins on P8 and P4. This pale wedge contrasts sharply with a coterminous, similarly sized, deep black triangle formed by the unmarked blackish primary coverts. Alula dull blackish, tiny feathers at bend of wing dull yellowish white. Underwing coverts clear, pale yellow becoming slightly dusker at the wrist. Tail narrowly fringed with Olive Green (aux. 47) and not contrasting with upperparts. **Soft parts in life:** iris clear light brown, maxilla black, mandible gray, legs dark gray. **Standard measurements:** total length (just before specimen preparation) 149 mm; bill (culmen from base at skull) 13.1 mm; bill from anterior edge of nares 7.4 mm; bill width at anterior edge of nares 4.3 mm; wing (chord) 63.2 mm; tail 55.8 mm (somewhat short of fully grown?); tarsus 16.8 mm; mass 14.5 g.

Etymology.— The name refers to the Rio Sucunduri which marks the new species' western range limit; pronunciation of the river name is *soo-coon-doo-REE*, with the accent on the final syllable. The species-group name is a non-Latinized noun in the nominative singular case. The English name unambiguously allocates the new species to the "yellow-margined flycatcher" complex.

REMARKS

Type series.— The following eight specimens are the paratypes of *Tolmomyias sucunduri*: MZUSP 86974, 86975, 86977, 86980, 86981 male, female, male, sex unknown, and sex unknown, respectively (AM, Maués, left bank rio Parauri); 86978 male

Figure 2.
A paratype of *Tolmomyias sucunduri* (MZUSP 86974) from near the type locality, on the left bank of the Rio Paraúri above Maués, Amazonas, Brazil. Facial markings show better in this photo than in the prepared specimen. Audio and video recordings were made by Bret Whitney and photos by Fabio Schunck, including this one, on 20 July 2009 (see SI).

(AM, Maués, right bank rio Paraúri); 94841 male with spread wing (AM, right bank lower rio Canumã); and Museu Paraense Emilio Goldi (MPEG) 72373 male (PA; Municipality Santarém [left bank rio Tapajós], RESEX Tapajós-Arapiuns). Among them, there is slight variation in the amount of olive wash in the hindcrown. Unlike the rest of the type series, the holotype shows almost no indication of darker centers to crown feathers, these instead being almost uniformly "dark bluish gray".

Ecology and behavior.— Prior to the discovery of *Tolmomyias sucunduri* at Boím in 1995, the *assimilis* species-group was known on the west bank of the Tapajós from a single female collected in 1917 by Sneath at Vila Braga (Oren and Parker 1997). The undescribed species had escaped collection and had been overlooked in more recent surveys, no doubt, because it inhabits the canopy of tall forest and its voice is so markedly different from other members of the complex as to be "unrecognizable." *Tolmomyias sucunduri* is an inveterate member of canopy mixed-species foraging flocks comprising mostly other insectivores and usually some frugivores and nectarivores. It almost always accompanies flocks in pairs, the members of which are often several meters apart and mostly just inside the periphery of treecrowns, rarely descending below the subcanopy. The broad, flat bill is used as a scoop to take mostly small arthropod prey in short-range (less than about 1 m) sally-strikes or upward-directed hopping motions to the undersides of live leaves, and birds frequently sit still and peer around for a minute or more. In all these respects, *T. sucunduri* behaves like the other members of the *T. assimilis* complex (BMW *pers. obs.*). Stomach contents of 9 individuals were entirely insects, with Coleoptera, Hymenoptera, and Hemiptera in almost all of them (see SI for a more detailed listing by Order and Family).

Vocalizations.— The primary song of Amazonian members of the *Tolmomyias assimilis* complex, delivered irregularly throughout the day, may be characterized as a simple series of, usually, three or four notes or syllables (sometimes up to six are delivered; there is much intra-individual variation; Fig. 4). The song increases in amplitude through the first two notes, which are typically shorter than subsequent notes and with greater inter-note interval than subsequent ones, which are both uniformly louder and longer, often the only notes of the song clearly audible from the ground. Both sexes sing, with female songs slightly "thinner" and higher-pitched than males'. An evenly paced call-series of (usually) 3-7 loud, sharp "chip" notes is also frequently given by all taxa, either preceding the song or by itself (Fig. 4D, F), but this call-series appears to be given less often by *T. sucunduri*.

The louder, longer notes of songs of all Amazonian *Tolmomyias* in the *assimilis* complex possess a harsh or "snarling" quality that sets them apart from other members of the genus. Our sample of 13 individual *Tolmomyias sucunduri* consistently shows the widely modulated or "washboard" quality of these notes that is diagnostic of the species and is never even approached by other taxa (Fig. 4A, B; interested readers should listen to the selection of recordings available on the Internet Bird Collection (IBC) website for a clear understanding of distinctions through inter-taxon comparison). South of approximately 05°40'S, however, this distinctive vocalization loses its identity, apparently due to hybridization with *T. assimilis/calamae* (Figs. 4C, E, F) because songs of birds in that area not only sound intermediate to us, but also show variation far outside the norm for any taxon in the complex such that no two individuals sound quite the same.

Range delimitation and Relationships.— Although we have no phylogenetic analysis of even a limited part of the *Tolmomyias assimilis* complex for this publication, we are completely confident that *T. sucunduri* is an integral member of this species-group. In the distribution of the complex, the Madeira-Tapajós interfluvium is a particularly complicated region. Nominate *T. a. assimilis*, from Borba on the right bank of the lower Rio Madeira, together with *T. a. calamae* from farther upriver also on the right bank, occupy the region west of the Rio Canumã/Sucunduri, and



are replaced east of these rivers by *T. sucunduri*; this pattern is paralleled by taxa in the *Willisornis poecilinotus* (Scale-backed Antbird) complex (Isler and Whitney 2011). Judging from the geographic spread of vocal types, the Madeiran population(s) passes the Sucunduri in the narrow headwaters of the river, some 400 km to the east, and we further postulate that it has pushed northward through the restricted, cone-shaped region between the upper Sucunduri and the Rio Tapajós to reach approximately 05°45'S, where these birds have achieved contact, we think probably secondary contact, with the Tapajós representative of the radiation, which is *T. sucunduri*. At roughly this latitude, there appears to be a gradient of hybridization at least 30 km wide, as judged by the prevalence of hybrid-type vocalizations there (collected specimens represented by black triangles in Fig. 1), and we expect that genetic introgression will prove to be considerably more pervasive east of the Sucunduri. Our hypotheses regarding the origin and dynamics of this contact zone, which is just as clearly marked for some other species-pairs of birds and also mirrored by numerous north-south drop-outs of named and unnamed taxa (BMW, unpublished data), are under development and research is ongoing. Collections of voice-recorded individuals in the *Tolmomyias assimilis* complex are steadily mounting (black dots in Fig. 1 provide a partial view of samples currently accumulated from the Madeira-Tapajós interfluvium) and will eventually permit a distribution-wide, concerted-data-set assessment of relationships and taxonomic limits in the remarkably widespread *Tolmomyias assimilis* radiation.

Conservation.— *Tolmomyias sucunduri* appears to be common throughout its range and is not currently threatened.

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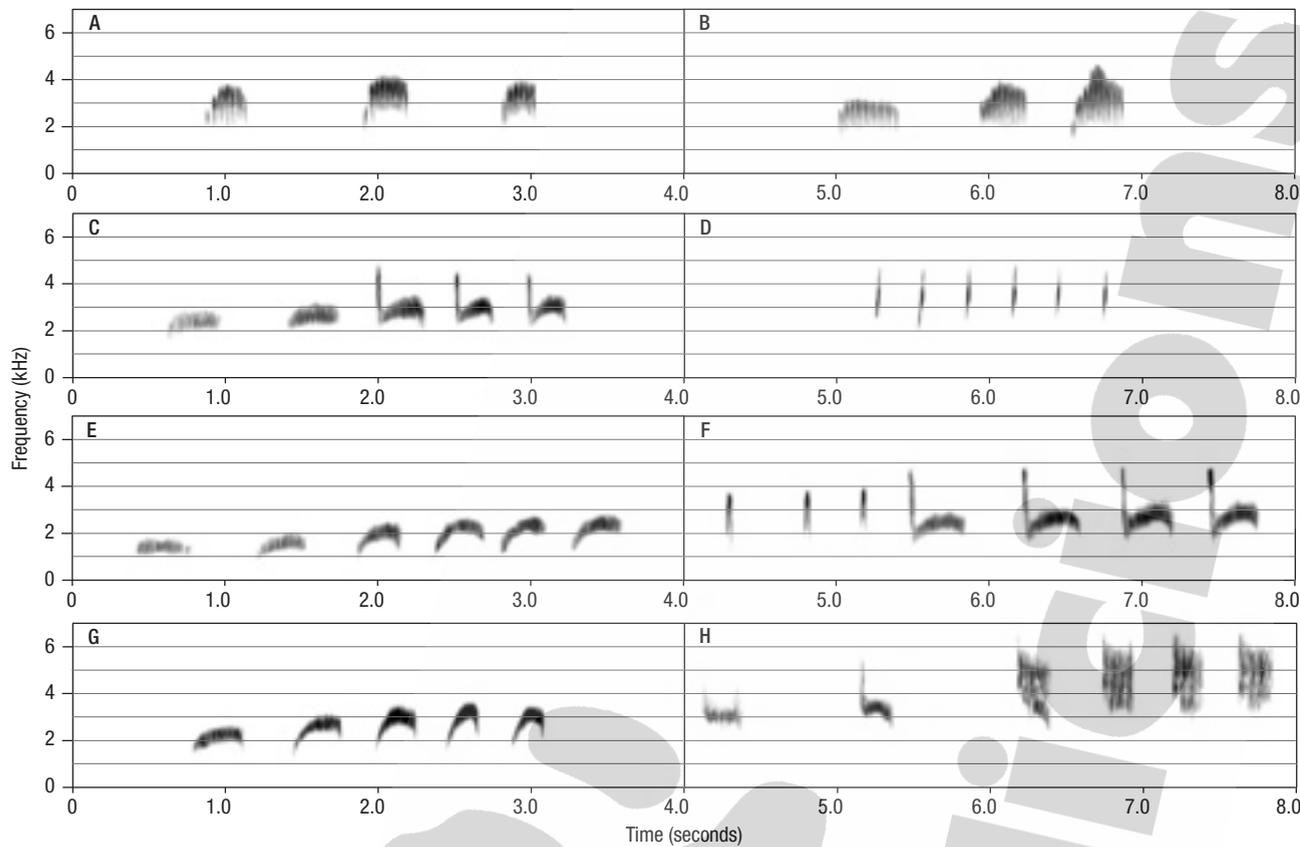


Figure 3. Spectrograms of typical vocalizations of *Tolmomyias sucunduri* in comparison to homologous vocalizations of some other members of the *Tolmomyias assimilis* complex in central Amazonian Brazil. (A) One song of *T. sucunduri* (paratype MZUSP 86974; recording BMW-7387); (B) Another individual of *T. sucunduri* (AM; right bank Rio Sucunduri at Igarapé Biribá, 16 July 2010; recording BMW-10050); (C) One song of *T. assimilis assimilis* from the type locality (AM; right bank Rio Madeira near Borba, 19 October 1993; MPEG 53182, Whitney recording); (D) Typical call series of *T. assimilis assimilis*, which is shared by other members of the *assimilis* complex (AM; right bank Rio Madeira near Borba, 19 October 1993; MPEG 53183, Whitney recording); (E) One song of *T. assimilis calamae* from the type locality (RO; right bank Rio Machado/Ji-Paraná above Palmeiras, 25 June 2002; Whitney recording); (F) Another song of *T. assimilis calamae* (MT; left bank Rio Claro at "Pousada Jardim d'Amazônia", 17 June 2010; recording BMW-9365); (G) song of *T. assimilis* (currently considered subspecies *assimilis*) from west of the Rio Madeira (AM; left bank Rio Madeira about 50 km south Humaitá; 12 August 2009; MZUSP 86239, recording BMW-7760); (H) song of *T. assimilis* (currently considered subspecies *paraensis*) from east of the Rio Tapajós (PA; right bank Rio Teles Pires, left bank lower Rio São Benedito, 19 June 1999; MPEG 54725, Whitney recording).

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